BIOCLIMATIC FACTORS LIMITING THE DISTRIBUTION OF *IRIS SIBIRICA* ACROSS EURASIA

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With a wide range in Eurasia, *Iris sibirica* has an irregular distribution pattern and is listed in regional and national Red Data Books and on Red Lists of many countries in Europe and Asia. The abiotic causes of the species rarity (bioclimatic limiting factors) and adaptations in different parts of its range are still poorly understood. The formalisation of *I. sibirica*'s ecological niches in the n-dimensional space of environmental factors will clarify these issues. We hypothesised that the ecological niches of *I. sibirica* were differentiated in the European and Asian parts of its range, allowing the species to adapt under diverse environmental conditions of plain and mountain habitats. This study aimed to (1) identify abiotic boundaries for various parts of the *I. sibirica* range in Eurasia (i.e. population groups), (2) test whether the ecological niches of Eurasian population groups were differentiated in environmental space, (3) provide information on environmental reasons of the species rarity in various parts of the range. To test whether the ecological niches of *I. sibirica* overlapped in various parts of its range, we applied the kernel density estimation method for niche visualisation in PCA (Principal Component Analysis) axis space. We have also used quantitative niche overlap metrics such as Schoener's D, Hellinger's I and COUE (Centroid shift, Overlap (Stability), Unfilling, Expansion). WorldClim bioclimatic variables were used to formalise the temperature and precipitation components of ecological niches. By a non-hierarchical iterative k-means clustering of abiotic variables in presence points, West European (463 points), East European-Siberian (186 points) and Mountain (112 points) population groups of *I. sibirica* were distinguished. In terms of temperature and precipitation parameters, the Mountain population habitats were similar to those of the West European populations (Stability of 0.90–0.99), but clearly differed from habitats of the East European-Siberian populations (Expansion of 0.85–1.00). In both cases, the ecological niche of the Mountain population group was clearly wider in the precipitation component. This is probably due to the relatively humid climate and orographic heterogeneity of mountainous areas, which enables *I. sibirica* to occupy sites with a wide range of precipitation but suitable moisture availability (e.g. couloirs, microrelief depressions). The ecological niches of the West European and East European-Siberian populations clearly differed by temperature component, but overlapped by precipitation component in the environmental space of PCA axes. Schener's D and Hellinger's I values were ranged from 0.02 to 0.21 for temperature variables and from 0.24 to 0.71 for precipitation variables. For the East European-Siberian population group, Unfilling in the temperature component of niche was 0.84–0.88. Thus, *I. sibirica* is adaptable to a wide range of temperature conditions in Eurasia, but has a narrow specialisation in moisture availability and is limited in suitable habitats (e.g. wet, swampy and marshy meadows), especially in the more continental and less humid East European-Siberian part of its range.

Key words: ecological niche models, kernel density estimation, niche overlap metrics, population groups, species distribution

Introduction

Iris sibirica L. (Iridaceae) is a widespread species with a fragmented distribution in Eurasia. The species was first described by Linnaeus (1753) from Austria, Switzerland, Siberia («Austriae, Helvetiae, Sibiriae pratis»). In Europe, it is most widely distributed in the central part (Hrivnák et al., 2024). The Asian range covers an area from Western Siberia to Mongolia (Webb, 1980; Meusel & Jäger, 1992; Alexeyeva, 2008). Some researchers have also included Japan, China, and Korea in the Asian range of the species (Tzvelev, 1979; Scrypec et al., 2020). The exact distribution of *I. sibirica*, e.g. Eurasian (Alexeyeva, 2008), Euro-Siberian (Kostrakiewicz-Gierałt & Podgórska, 2020; Hrivnák et al., 2024), Euro-West Siberian (Scrypec et al., 2020), Central European-West Siberian (Gatina, 2015), remains controversial.

Iris sibirica has a strong affiliation to wet meadows (Salamon-Albert et al., 2010; Hrivnák et al., 2024). It occupies wet meadows, forests, and mountain habitats (Gao et al., 2014; Mu-Za-Chin & Shukal, 2016; Kostrakiewicz-Gierałt &

Podgórska, 2020; Kryukova et al., 2023). *Iris sibirica* is listed in Red Data Books and on Red Lists of many Eurasian countries (e.g. Kostrakiewicz, 2007; Grulich, 2012; Gatina, 2015; Hrivnák et al., 2024), as well as on the Global IUCN Red List of Threatened Species (Khela, 2013). It has disappeared from natural localities in Europe due to wetland disturbance caused by agricultural use, recreational activities and climate change altering water regime of floodplains, marshes, and wet meadows (Gatina, 2015; Kostrakiewicz-Gierałt & Podgórska, 2020; Straubinger et al., 2023; Hrivnák et al., 2024). As stated in the Red Data Book of the Stavropolsky Krai (2013) and the Red Data Book of the Republic of Crimea (2015), in the Russian Federation the species main threats are also related to harvesting of *I. sibirica* as an ornamental and medicinal plant. While the main anthropogenic causes of its local rarity are known, the abiotic factors that limit the species abundance and drive its regional rarity have not been systematically investigated.

Many recent studies in this area has focused on the building of correlative Ecological Niche Models (ENMs), which represent statistical methods that link distribution data as dependent variables to environmental estimates as independent predictors (Peterson et al., 2011; Elith & Franklin, 2013; Guisan et al., 2017). Correlative ENMs are mathematical approximations to the species ecological niches that can be visualised in the environmental space (an n-dimensional hypervolume of environmental predictors) (Guisan et al., 2017; Sillero & Barbosa, 2021; Sillero et al., 2021, 2023). The spatial representation of ecological niches through ENMs has become a popular tool for assessing niche overlap between species or for comparing ecological niches in the different parts of species range (Warren et al., 2010; Broennimann et al., 2012; Blonder et al., 2014; Sillero et al., 2021). The method identifies species adaptation and limiting factors in various parts of the range and is increasingly used in conservation planning for rare plant species (Yilmaz et al., 2017; Cotado & Munné-Bosch, 2020; Qazi et al., 2022).

Iris sibirica is a suitable biological model for such studies given its wide but fragmented distribution, strong association with wet meadows (an indicator of wetland health) and regional rarity. ENMs with a spatial representation can clarify the species adaptations in plain and mountain habitats in European and Asian regions, as well as the bioclimatic factors limiting its distribution across Eurasia (environmental constraints). We believe that additional studies of the distribution patterns and ecological niches of *I. sibirica* will help to identify conservation priorities for the species in various parts of its range.

Therefore, this study was conducted with the following specific objectives: (1) to delineate *I. sibirica* population groups in Eurasia using bioclimatic variables, (2) to test whether their ecological niches differ in environmental space, and (3) to explain the regional rarity of the species based on abiotic factors. We hypothesised that the ecological niches of *Iris sibirica* in European and Asian regions differ, reflecting adaptations to plain versus mountain habitats. Therefore, we expected to find that (1) the West European populations had a broader temperature niche component, (2) the Mountain population niche showed greater variability in precipitation, and (3) the East European-Siberian population group had a narrower precipitation niche, reflecting more continental climate of its habitats. The main assumption of the study was that we focused exclusively on the abiotic (Climate Envelope) component of the species fundamental niche without accounting for biotic interactions.

Material and Methods

Target species and study area

Iris sibirica is a clonal herbaceous perennial with creeping or ascending rhizomes and numerous hydrochorous seeds that provide its reproduction, dispersal and rooting (Gao et al., 2014; Hrivnák et al., 2024; POWO, 2025). In Eurasia, the species primarily occupies wet meadows and riparian habitats (Salamon-Albert et al., 2010; Gao et al., 2014). It has a scattered distribution throughout its extensive range (Alexeyeva, 2008; Hrivnák et al., 2024) and is listed as a rare, threatened, Near Threatened or Endangered species on regional and national Red Lists and in Red Data Books (Kostrakiewicz, 2007; Grulich, 2012; Gatina, 2015; Mu-Za-Chin & Shukal, 2016; Scrypec et al., 2020; Kryukova et al., 2023; Hrivnák et al., 2024). *Iris sibirica* is also listed on the Global IUCN Red List of Threatened Species in the category Near Threatened (Khela, 2013).

The study area covered the native range of *I. sibirica* in the temperate biome of Eurasia including Western, Central and Eastern Europe, Western and Eastern Siberia, the Caucasus, northwestern

Kazakhstan and northern Turkey (Alexeyeva, 2008; Boltenkov et al., 2020; Hrivnák et al., 2024) between -7.458–81.875° N and -10.625–180.000° E (Fig. 1). Geographical records outside the native range were excluded. These were occurrences in North America related to the invasion of cultivated plants into natural ecosystems (Pirogov, 2022). Geographic records in Japan, China and Korea were excluded as belonging to other similar species such as *Iris sanguinea* Donn ex Hornem., typical for this part of Asia (Yutang et al., 2000; Scrypec et al., 2020).

Manipulation and evaluation of input data

Occurrence data prepare

The primary set of species geographic records included 21 899 occurrence data from the Global Biodiversity Information Facility (GBIF.org, 2024) and 83 expedition survey points. The use of geographic records from biodiversity databases such as GBIF often faces the problem of over-spatialisation of presence points due to the highest «search effort» in the most accessible areas, which can lead to an increase in their importance in model (Syfert et al., 2013; Aiello-Lammens et al., 2015). The problem of sampling bias in occurrence data relative to the object actual distribution can skew results and complicate model interpretation (Hijmans, 2012; Aiello-Lammens et al., 2015). Considering the number of GBIF points in the study, a correction for sampling bias was required. In addition, the GBIF points outside the natural habitats of the species (e.g. *I. sibirica* in settlement landscaping) had to be excluded from the analysis.

Therefore, we prepared GBIF occurrence data in four steps: (1) checking and removing duplicates – 4798 records remained, (2) sifting cultivation points in settlements using the Global Human Settlement Layer – 2871 records, (3) filtering out points outside natural plant communities with the Human Footprint Index Map – 1287 records, and (4) spatial thinning after testing points for spatial clustering by the Average Nearest Neighbour Index – 678 final records left. The steps for GBIF occurrence data manipulation, including the methods and the R packages (R Core Team, 2025), were specified in Electronic Supplement 1 (Occurrence data prepare).

GBIF-model development, evaluation and verification

To assess the accuracy and sufficiency of GBIF final records in characterising the ecological niche of *I. sibirica*, we built, evaluated and verified a species distribution model (SDM) in Eurasia. We used the Maxent ver. 3.4.3 (Phillips et al., 2017) and associated performance criteria to build a SDM and evaluate its quality. Additionally, the Maxent model was validated by field points.

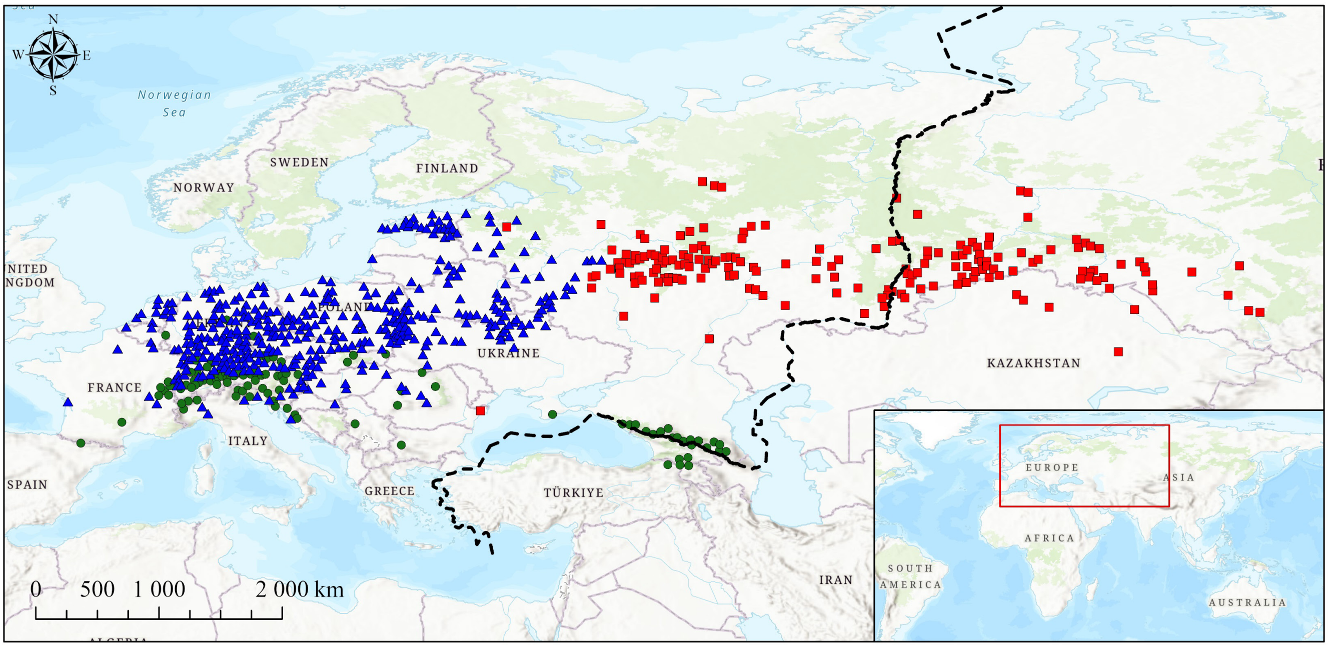

Fig. 1. The geographic location of the study area with the occurrence points of *Iris sibirica* clustered by three Eurasian population groups. The West European population group is marked in blue, the East European-Siberian population group in red, and the Mountain population group in green. Triangles, squares and dots represent 678 sparse GBIF records and 83 field points (761 occurrences in total). Occurrence records were projected in WGS84. The black dashed line marks the continental boundaries of Europe vs. Asia. The map was created with QGIS ver. 3.42.2.

GBIF-model development: the final set of 678 GBIF sparse records were used as presence points for the SDM. The number of background points was 10 000. To address the problem of sampling bias in background points, we used a bias file for selecting background points in the same geographic space as the occurrence records (Kramer-Schadt et al., 2013; Syfert et al., 2013; Aiello-Lammens et al., 2015; Lissovsky & Dudov, 2020). With the bias file, the model is less affected by sampling bias and the analysis focuses on differences in the features of presence points and equally biased background points (Sillero et al., 2021). The methods and the R packages for background points and bias file creation were specified in Electronic Supplement 1 (GBIF-model development, evaluation and verification; The background points and bias file creation).

A set of WorldClim2 bioclimatic parameters (Fick & Hijmans, 2017; WorldClim2, 2025) was employed as environmental variables for SDM. It is a widely used raster image set with gridded climate data, characterised by global coverage and high accuracy (Fick & Hijmans, 2017). WorldClim2 includes 19 bioclimatic parameters that may have correlated at presence points of *I. sibirica*. The correlation of predictors can result in a misestimation of variable significance and incorrect description of variable influence. Therefore, including variables in the models without analysing them for strong correlations is often considered a mistake (Sillero & Barbosa, 2021; Sillero et al., 2021). With the VIF (Variance Inflation Factor) test, we selected uncorrelated environmental layers (Electronic Supplement 1 (GBIF-model development, evaluation and verification; Addressing collinearity of environmental predictors)). As a result, six WorldClim2 predictors were involved in the analysis, such as mean monthly temperature amplitude (bio2, °C), temperature seasonality (bio4, %), mean temperature of wettest quarter (bio8, °C), precipitation seasonality (bio15, %), precipitation of warmest quarter (bio18, mm), precipitation of coldest quarter (bio19, mm) (Electronic Supplement 1: Table S2, Table S3). The resolution of the layers was 5 km per pixel.

Maxent, a robust and efficient modelling method (Elith et al., 2011; Vignali et al., 2021), generates probabilities of object occurrence in each grid cell using predictor values similar to those in actual object locations. With various Maxent settings (e.g. features, regularisation multiplier), models with varying rigor in assessing habitat suitability can be built. Evaluation and validation of such candidate models allows to select the optimal model according to the performance criteria. The methods and R packages for calculating the optimal Maxent settings, as well as the performance criteria of the candidate models, were specified in Electronic Supplement 1 (GBIF-model development, evaluation and verification; SDM algorithm). The LQPH (Linear-Quadratic-Product-Hinge) feature type and the regularisation multiplier of 0.5 were identified as the optimal Maxent settings. Using these settings and five-fold cross-validation (Phillips & Dudík, 2008), the resulting Maxent model was built in the dismo package (ver. 1.3-14) in R (Hijmans et al., 2017).

GBIF-model evaluation: performance criteria for the resulting model were AUCtest (area under receiver operating curve from validation data) and TSStest (True Skill Statistics from validation data) averaged over five replications. AUC assesses the specificity and sensitivity of models in distinguishing presence data from background points (Fielding & Bell, 1997). It is highly dependent on input data and model settings (Lissovsky & Dudov, 2020) and is therefore often replaced by AUCtest and AUCtrain (AUC from validation and training data). The closer AUCtest and AUCtrain are to 1, the higher the model performance (AUC of 0.7–0.8 for good models and AUC above 0.8 for excellent models) (Phillips et al., 2006). TSS evaluates the model quality by the number of correctly classified presences (Sensitivity) and absences (Specificity): Sensitivity + Specificity – 1 (Allouche et al., 2006). It ranges from -1 to 1, with 0 for random classification. The resulting Maxent model had a quite good performance (prediction accuracy) according to values of AUCtest (0.95 ± 0.008) and TSStest (0.81 ± 0.005).

GBIF-model verification: as predicted by the resulting Maxent model, built from 678 GBIF occurrence data, all 83 field points had an occurrence probability above 0.5 (50% habitat suitability threshold) (Fig. 2). Among them, 12 and 44 points had predicted probabilities of occurrence above 0.8 and 0.9, respectively, accounting for 65.1% of the highly accurate predictions (80% and 90% habitat suitability thresholds).

The resulting Maxent model predicted low (up to 0.5) occurrence probabilities for 108 points from the final set of GBIF data (Fig. 2). These 15% GBIF points can probably be attributed to habitats outside the predicted ecological tolerance of *I. sibirica* in terms of the analysed bioclimatic parameters. Most of these points were located at the borders of the species range.

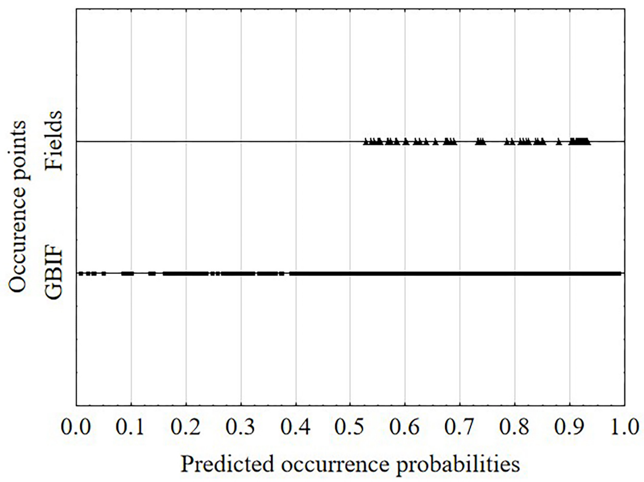

Fig. 2. Results of field verification of *Iris sibirica* Maxent model built from GBIF occurrence data.

Thus, the results of performance evaluation and field verification of the species distribution model demonstrated the accuracy and sufficiency of 678 sparse GBIF records for describing the ecological niches of *I. sibirica* in Eurasia. Therefore, we used the bioclimatic attributes of these occurrence data, as well as 83 field points (761 occurrences in total), to build the ecological niche models. The cartographic Maxent model (distribution map based on 761 records), and the methods and R packages for its construction were specified in Electronic Supplement 1 (GBIF-model development, evaluation and verification; The predictive map of the species distribution).

Ecological niche modelling

Separation of species populations

To test whether the ecological niches of *I. sibirica* from various parts of the range were differentiated in environmental space, it was necessary to separate population groups. In this study, we understand population groups of *I. sibirica* as groups of populations adapting to various ecological conditions. Such conditional population groups were identified by a non-hierarchical iterative k-means algorithm (Davidson, 2002). This easy to implement and execute method (Jain, 2010), based on Euclidean distance in the data space, allowed species occurrence points (their abiotic attributes) to be assigned to different population groups. The full set of 19 WorldClim2 bioclimatic variables was used as the abiotic attributes of the presence points, along with altitude (m a.s.l.) sourced from the Shuttle radar topographic mission (SRTM) digital altitude model (SRTM, 2025). The expanded abiotic dataset allows a more complete formalisation of the species fundamental niche. The non-hierarchical iterative k-means algorithm assigned 761 presence points of *I. sibirica* to three population groups, i.e. West European populations (WEP, 463 points), East European-Siberian populations (EESP, 186 points), and Mountain populations (MP, 112 points) (Fig. 1; Electronic Supplement 2: Fig. S4, Table S5). A similar location of the *I. sibirica* range centres (isolated extensive areas with a high, about 1, probability of species occurrence) was also predicted by the Maxent distribution map (Electronic Supplement 1: Fig. S3).

Ecological niche models and niche overlap

We applied the Kernel Density Estimation (KDE) (Blonder et al., 2014) to formalise the ecological niches of population groups. The KDE method was suggested to visualise ecological niches as Hutchinson hypervolumes in the n-dimensional space of ecological variables (Blonder et al., 2014). The method allowed a comparison of the width, shape and overlap of the ecological niches. In this paper, ecological niches were agglomerations of points in the orthogonal space of PCA (Principal Component Analysis) axes that represented biologically important complex factors combining the original bioclimatic variables and altitude. The Hutchinson hypervolume points were suitable values of these variables for species populations. PCA was performed in the FactoMineR package (ver. 2.7) in R (Le et al., 2008). Axis extraction and visualisation were carried out in the factoextra package (ver. 1.0.7) in R (Kassambara & Mundt, 2019) and in the ggplot2 package (ver. 3.4.0) in R (Wickham, 2009).

Schoener's D (Schoener, 1968) and Hellinger's I (Warren et al., 2008) metrics provide efficient and convenient quantitative assessments of ecological niche overlap, ecological similarity or specialisation of species (populations). These similarity metrics are calculated by comparing the habitat suitability scores predicted by Maxent model for various species (populations) in each grid cell. They range from 0 (ecological niches do not overlap) to 1 (ecological niches are identical, i.e. all grid cells are equally suitable for both species or populations). Schoener's D differs from Hellinger's I by the assumption that habitat suitability scores are proportional to species abundance (Warren et al., 2010). The metrics were calculated using the ENMTools package (ver. 1.1.2) in R (Warren et al., 2010).

The COUE (Centroid shift, Overlap, Unfilling, Expansion) scheme is effective for qualitative and quantitative comparing species niches in various geographical areas (Guisan et al., 2014). The method was developed to compare the niches of invasive species in native and exotic ranges by assessing four metrics of niche change, i.e. centroid shift, overlap, unfilling, and expansion (Guisan et al., 2014). Centroid shift (C) measures changes in mean niche position across ranges, but cannot assess patterns of niche change. Overlap (O) is similar to niche overlap assessed by Schoener's D and Hellinger's metrics. It characterises niche stability (S) and measures the proportion of niche (0 to 1) present in both ranges. Unfilling (U) measures the proportion of niche within the first range that does not overlap with the niche within the second range. Expansion (E) corresponds to the proportion of niche in the second range that does not overlap with the niche within the first range (Guisan et al., 2014). To calculate the Stability, Unfilling and Expansion of niches between *I. sibirica* population groups, we analysed species occurrence density in the ecospat package (ver. 4.1.1.) in R (Warren et al., 2010).

Results

Overlap of ecological niches in the PCA axes space

The principal component analysis identified four complex factors with a cumulative variation of about 91% in the abiotic attributes of *I. sibirica* occurrence points (Electronic Supplement 3: Table S6). The main complex Factor 1 included seven temperature bioclimatic variables with factor loadings > 0.7, i.e. annual mean temperature, mean monthly temperature amplitude, temperature seasonality, min temperature of coldest month, temperature annual range, mean temperature of driest quarter, and mean temperature of coldest quarter. Four precipitation variables (annual precipitation, precipitation of wettest month, precipitation wettest and warmest quarters) formed the second component of PCA. The first two factors accounted for 61% of variance in abiotic parameters of the species habitats. The third and fourth PCA axes were formed by pairs of temperature (max temperature of warmest month and mean temperature of warmest quarter) and precipitation (precipitation seasonality and precipitation of coldest quarter) variables, respectively (Electronic Supplement 3: Table S6).

By the main temperature Factor 1 (33% of total variance), the ecological niches of *I. sibirica* were obviously differentiated between EESP and WEP (Fig. 3). The largest niche overlaps were observed in WEP – MP pair. The ecological niches between EESP and MP overlapped to a lesser extent, as a significant fraction of hypervolumes did not intersect in the two-dimensional environmental space.

By the precipitation Factor 2 (28% of total variance), the ecological niches of *I. sibirica* overlapped in EESP – WEP pair and to a lesser extent in WEP – MP pair. The niche relationship in the EESP – MP pair could rather be called differentiation, although the hypervolumes partially overlapped in ecological space. Overlaps of ecological niches were observed by the less significant temperature Factor 3 and precipitation Factor 4 (14% and 16% of total variance). For three complex environmental factors, the ecological niche of MP was obviously wider than that of the lowland EESP and WEP. The exception was the main temperature Factor 1, for which the niche sizes of the three population groups were similar (Fig. 3).

Overlap of ecological niches by environmental variables

Schoener's D and Hellinger's I quantitative metrics of niche overlap

We studied the overlap/differentiation of ecological niches between *I. sibirica* population groups by initial environmental variables with factor loadings > 0.7 on the two main complex PCA factors. There were 11 such temperature and precipitation parameters (Table 1).

Most of bio1–bio11 variables combined into main Factor 1 had low quantitative niche overlap metrics in EESP – WEP pair. Schoener's D values for these variables ranged mainly from 0.02 to 0.11(0.20), and Hellinger's I values ranged from 0.05 to 0.21(0.32) (Table 1). Since Schoner's D and Hellinger's I values < 0.2 indicate pronounced niche differentiation (less than 20% overlap) (Warren et al., 2008), the results indicated the divergence between EESP and WEP groups in the temperature component of environmental niches. The exception was bio2 (mean monthly temperature amplitude), which indicated overlap of ecological niches for all pairs of population groups. In particular, the average annual mean temperature (bio1) in EESP habitats was 4.3°C lower than in WEP habitats (Electronic Supplement 2: Table S5, Fig. S4). The EESP habitats had lower, by 8.3–10.2°C, average values of min temperature of the coldest month (bio6), mean temperature of the driest quarter (bio9), and mean temperature of the coldest quarter (bio11). In EESP habitats, the temperature seasonality (bio4) and temperature annual range (bio7) were higher, by 219% and 10.5°C, respectively. The higher temperature variability characterised the climate of EESP habitats as more continental relative to WEP habitats.

In WEP – MP pair, with the largest niche overlap by Factor 1, Schoener's D and Hellinger's I metrics were closest to 1 for all temperature variables (Table 1), i.e. the temperature components of the ecological niches were nearly identical (Schoener, 1968; Warren et al., 2008). The min temperature of the coldest month (bio6), mean temperature of the driest and coldest quarters (bio9 and bio11) differed by only 0.5–1.7°C (Electronic Supplement 2: Table S5). The differences in temperature seasonality (bio4) and temperature annual range (bio7) were only 40% and 1.9°C, respectively, which was much smaller than in EESP – WEP pair.

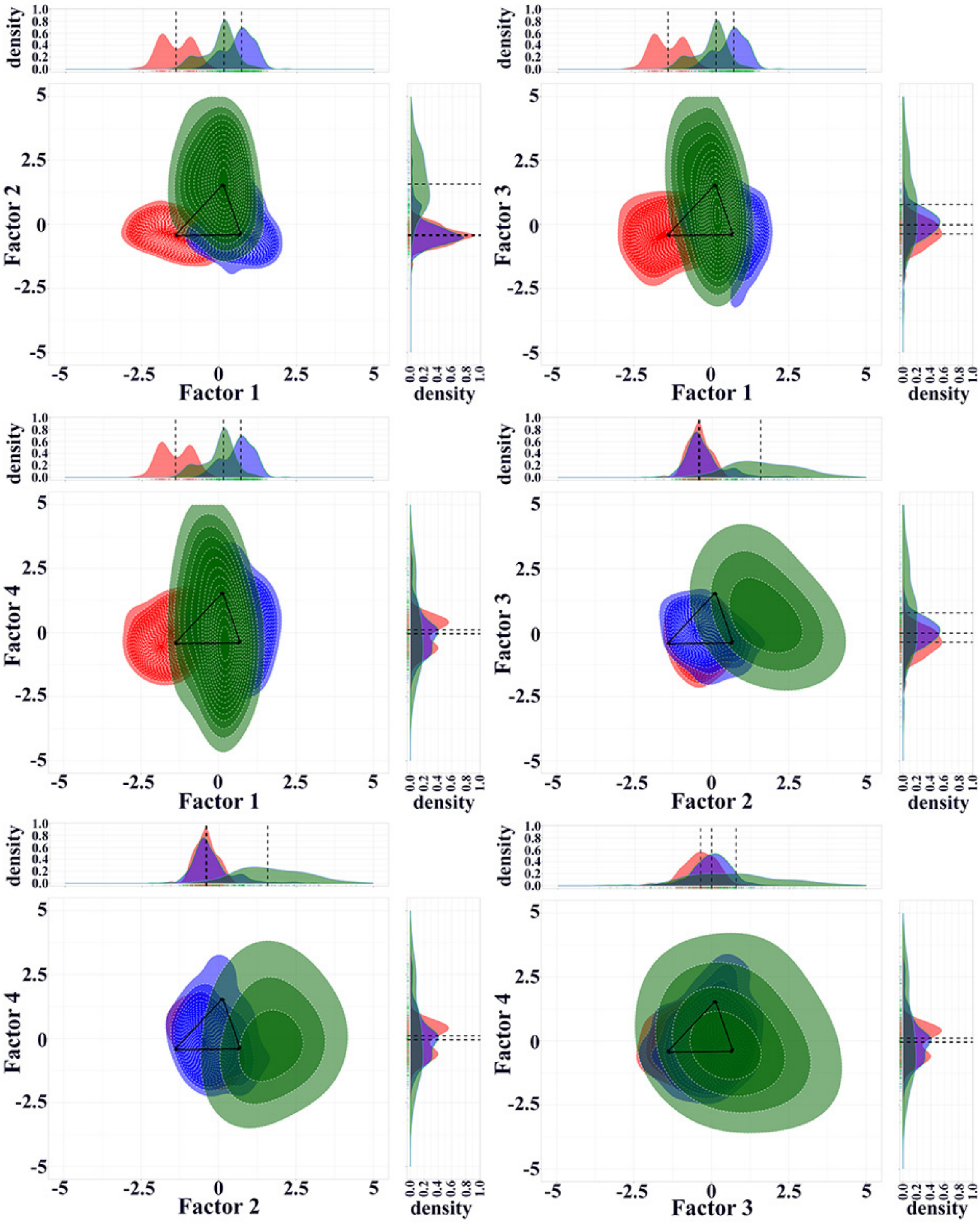

Fig. 3. Visualisation of ecological niches of *Iris sibirica* population groups in the orthogonal space of PCA axes. The West European population group is marked in blue, the East European-Siberian population group in red, and the Mountain population group in green. Black arrows connect the centroids of the ecological niches. Black dashed lines in the margin plots show the centroids of the ecological niches.

Table 1. Metrics of change, overlap and differentiation of ecological niches between *Iris sibirica* population groups assessed by environmental variables

Variables	Pairs of population groups	COUE metrics of niche change			Schoener's D	Hellinger's I
		Expansion	Stability	Unfilling		
bio1	EESP – WEP	0.66	0.34	0.71	0.11	0.21
	EESP – MP	0.36	0.64	0.00	0.34	0.61
	WEP – MP	0.15	0.85	0.02	0.65	0.86
bio2	EESP – WEP	0.10	0.90	0.03	0.55	0.80
	EESP – MP	0.03	0.97	0.09	0.72	0.88
	WEP – MP	0.01	0.99	0.01	0.72	0.93
bio4	EESP – WEP	0.96	0.04	0.86	0.02	0.05
	EESP – MP	1.00	0.01	1.00	0.00	0.00
	WEP – MP	0.00	1.00	0.14	0.65	0.87
bio6	EESP – WEP	0.82	0.18	0.87	0.05	0.10
	EESP – MP	0.80	0.20	0.65	0.10	0.20
	WEP – MP	0.02	0.99	0.05	0.81	0.95
bio7	EESP – WEP	0.95	0.05	0.84	0.03	0.05
	EESP – MP	0.97	0.03	0.96	0.01	0.02
	WEP – MP	0.00	1.00	0.07	0.77	0.93
bio9	EESP – WEP	0.54	0.46	0.35	0.20	0.32
	EESP – MP	0.25	0.75	0.33	0.37	0.56
	WEP – MP	0.04	0.96	0.00	0.75	0.92
bio11	EESP – WEP	0.83	0.17	0.88	0.05	0.09
	EESP – MP	0.85	0.15	0.63	0.09	0.17
	WEP – MP	0.01	0.99	0.02	0.83	0.97
bio12	EESP – WEP	0.24	0.76	0.43	0.24	0.40
	EESP – MP	0.92	0.08	0.28	0.01	0.09
	WEP – MP	0.29	0.71	0.00	0.35	0.58
bio13	EESP – WEP	0.04	0.96	0.14	0.49	0.71
	EESP – MP	0.90	0.10	0.51	0.03	0.10
	WEP – MP	0.24	0.76	0.12	0.29	0.53
bio16	EESP – WEP	0.09	0.91	0.21	0.33	0.57
	EESP – MP	0.92	0.08	0.47	0.02	0.07
	WEP – MP	0.25	0.75	0.06	0.27	0.51
bio18	EESP – WEP	0.07	0.93	0.16	0.39	0.64
	EESP – MP	0.84	0.17	0.11	0.04	0.15
	WEP – MP	0.25	0.75	0.00	0.30	0.55

Note: WEP – West European populations; EESP – East European-Siberian populations; MP – Mountain populations; bio1 – mean annual temperature, °C; bio2 – mean monthly temperature amplitude, °C; bio4 – temperature seasonality, %; bio6 – min temperature of coldest month, °C; bio7 – temperature annual range (bio5-bio6), °C; bio9 – mean temperature of the driest quarter, °C; bio11 – mean temperature of the coldest quarter, °C; bio12 – annual precipitation, mm; bio13 – precipitation of wettest month, mm; bio16 – precipitation of wettest quarter, mm; bio18 – precipitation of warmest quarter, mm.

In EESP – MP pair, the largest niche differentiations by Factor 1 were observed for bio4, bio6, bio7, and bio11. Schoener's D values for these temperature variables ranged from 0.00 (niches do not overlap) to 0.10 (niche overlap of only 10%), and Hellinger's I values ranged from 0.00 to 0.20 (Table 1). The differences in these parameters were comparable to those in EESP – WEP pair. Temperature seasonality (bio4) and temperature annual range (bio7) were differentiated by 259% and 12.4°C, respectively, with higher values for EESP habitats (Electronic Supplement 2: Table S5). By the average values of min temperature of the coldest month (bio6) and mean temperature of the coldest quarter (bio11), the EESP habitats were colder by 7.2°C and 9.9°C, respectively. Some niche overlap in EESP – MP pair was provided by bio1 (annual mean temperature), bio2 (mean monthly temperature amplitude) and bio9 (mean temperature of the driest quarter) with Schoener's D and Hellinger's I of 0.34–0.72 and 0.56–0.88, respectively.

By precipitation Factor 2, niche overlaps were observed in EESP – WEP pair and to a lesser extent in WEP – MP pair (Fig. 3). Schoener's D and Hellinger's I metrics for bio12–bio18 variables combined into this complex factor ranged here from 0.24 to 0.49 and 0.40 to 0.71, respectively (Table 1). WEP occurred in slightly wetter habitats than EESP, with higher values of annual precipitation (by 152 mm), precipitation of the wettest month (by 8.6 mm), precipitation of the wettest (by 32 mm) and warmest (by 27 mm) quarters (Electronic Supplement 2: Table S5). In WEP – MP pair, more humid climate conditions were observed in the mountain population habitats: by 360 mm for annual precipitation, by 48 mm for precipitation of the wettest month, and by 140 mm and 116 mm for precipitation of the wettest and warmest quarters. The weakest niche overlap by Factor 2 was in EESP – MP pair (Schoener's D of 0.01–0.04 and Hellinger's I of 0.09–0.15), although the differences in precipitation conditions between these population groups were quite similar to those in WEP – MP pair: 512 mm for annual precipitation, 56 mm for precipitation of the wettest month, 172 mm and 143 mm for precipitation of the wettest and warmest quarters (Electronic Supplement 2: Table S5).

All three population groups of *I. sibirica* in Eurasia differed significantly in altitude, which averaged about 1950 m a.s.l. for MP habitats, 600 m a.s.l. for WEP habitats, and only 150 m a.s.l. for EESP habitats (Electronic Supplement 2: Table S5). However, the factor loadings of this environmental parameter did not exceed 0.62 (Electronic Supplement 3: Table S6), so we did not analyse altitude variability in the population habitats.

COUE metrics of niche overlap

The Stability metric was positively correlated with the Schoener's D and Hellinger's I metrics (Pearson correlation coefficient: r = 0.91 and r = 0.96, respectively). In EESP – WEP pair, the precipitation component of ecological niches (bio13, bio16, bio18) had the highest Stability values of 0.91–0.96 (Table 1, Fig. 4).

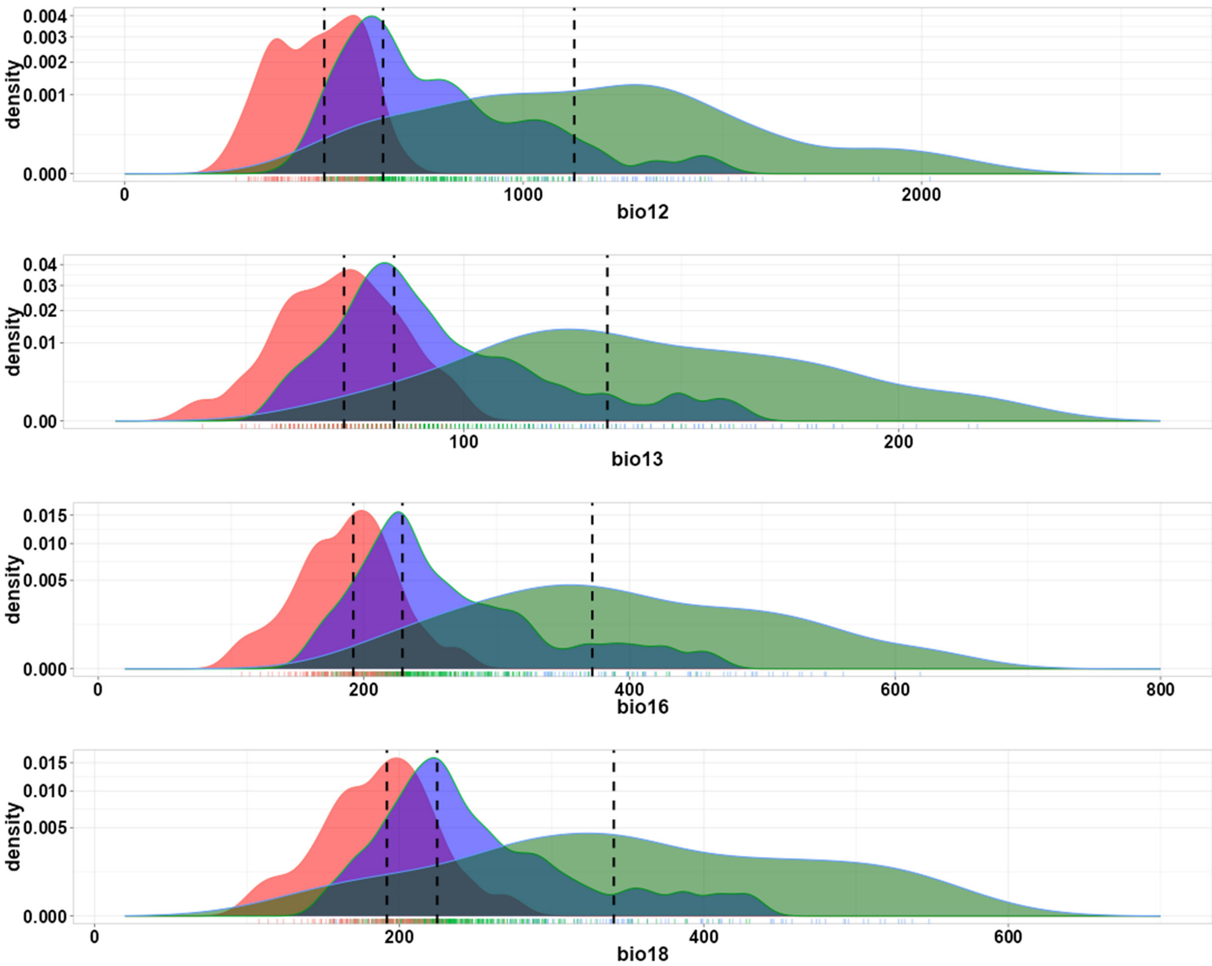

Fig. 4. Visualisation of changes in the precipitation component of *Iris sibirica* ecological niches between Eurasian populations. The West European population group is marked in blue, the East European-Siberian population group in red, and the Mountain population group in green. Black dashed lines show the medians of precipitation variables. Overlapping niche fractions indicate the Stability metric of niche change. Non-overlapping niche fractions indicate Unfilling and Expansion metrics of niche change.

In WEP – MP pair, the temperature component of the niches was the most stable with Stability of 0.96–1.00 for bio6, bio7, bio9 (Table 1, Fig. 5). Between all three population groups, the monthly mean temperature amplitude (bio2) was also stable (Stability of 0.90–0.99) (Table 1, Fig. 5). This was the only stable parameter of *I. sibirica* ecological niches in EESP – MP pair.

In the temperature component (bio4, bio6, bio7, and bio11), the EESP ecological niche was obviously unfilled compared to the WEP niche (Unfilling of 0.84–0.88) (Table 1, Fig. 5). In turn, a significant portion of the WEP ecological niche did not overlap with the EESP niche in the temperature component comprised by the same variables bio4, bio6, bio7, and bio11 (Expansion of 0.82–0.96).

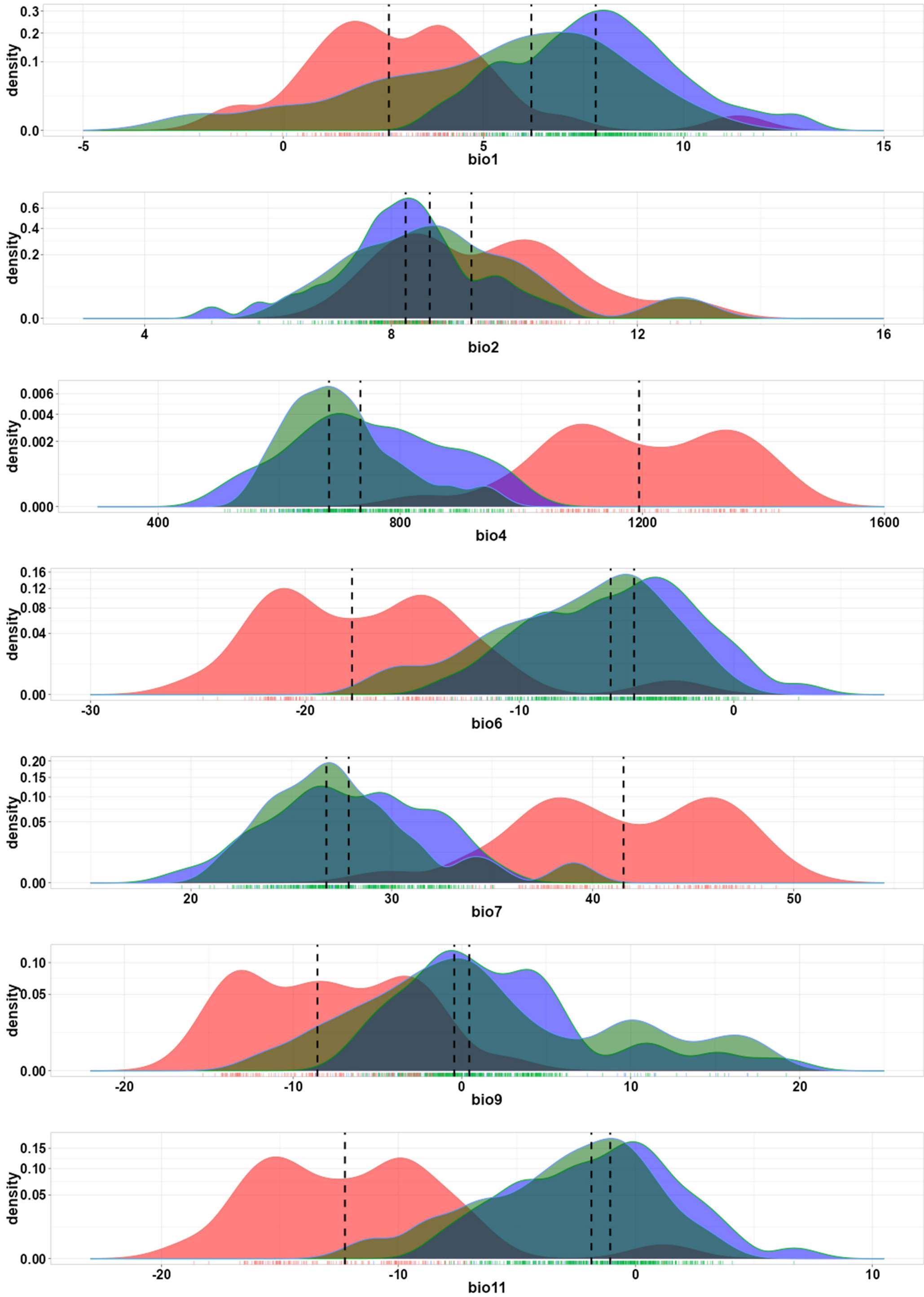

Fig. 5. Visualisation of changes in the temperature component of *Iris sibirica* ecological niches between Eurasian populations. The West European population group is marked in blue, the East European-Siberian population in red, and the Mountain population in green. Black dashed lines show the medians of temperature variables. Overlapping niche fractions indicate the Stability metric of niche change. Non-overlapping niche fractions indicate Unfilling and Expansion metrics of niche change.

The EESP ecological niche also had little overlap with the MP niche in the temperature variability parameters bio4 and bio7 (Unfilling of 1.00 and 0.96, respectively). In turn, Expansion of the MP niche relative to the EESP niche was in both the temperature (0.85–1.00 for bio4, bio6, bio7, and bio11) and precipitation (0.90 and 0.92 for bio12, and bio16) components. In WEP – MP pair, significant overlap was observed in both temperature and precipitation components of the niches (Fig. 4, Fig. 5). The Unfilling and Expansion values here did not exceed 0.14 and 0.29, respectively (Table 1).

Discussion

Using correlative ecological niche modelling, we formalised the ecological niches of *I. sibirica* population groups in different parts of the Eurasian range and assessed niche overlap/ differentiation between the West European, East European-Siberian and Mountain populations. Our results partially supported field-based reports on the ecological preferences of *I. sibirica* in Eurasia (e.g. Gao et al., 2014; Mu-Za-Chin & Shukal, 2016; Kostrakiewicz-Gierałt & Podgórska, 2020; Scrypec et al., 2020; Kryukova et al., 2023; Hrivnák et al., 2024).

Distribution type of Iris sibirica

The separation of West European and East European-Siberian population groups of *I. sibirica* by abiotic attributes of occurrence points was probably due to the obvious difference in environmental conditions between Western Europe and Asia. Hence the apparent narrowing of the actual (Fig. 1) and predicted (Electronic Supplement 1: Fig. S3) species ranges at 37°36′ E.

The Mountain population group was probably abiotically separated due to the environmental specificity of mountainous areas because of vertical zonation. While the Caucasian populations were geographically isolated, the mountain populations of Western Europe were assigned to a separate cluster despite their close proximity to other West European populations of *I. sibirica* (Fig. 1, Fig. S3). The ecogeographic differentiation of Caucasian populations was probably related to the survival of *I. sibirica* during the Last Glacial Maximum in scattered ice-free mountain refugia isolated from the adjacent Russian Plain according to paleogeographic data (Petrova et al., 2017).

Analysis of variance of environmental variables in species occurrence points indicated a high quality of such clustering (Electronic Supplement 2: Table S5). Thus, the abiotic boundaries for various parts of *I. sibirica* range in Eurasia allowed us to define the species distribution type as West European-East European-Siberian.

Niche differentiation by temperature component

A review of articles demonstrated that *I. sibirica* prefers moderately warm to warm climates with mild winters (average temperature of the coldest month from 0°C to -16°C) and avoids extremely continental areas (Ellenberg et al., 1991; Mu-Za-Chin & Shukal, 2016; Ovchinnikova & Shabalkina, 2019; Tichý et al., 2023). According to Levchenko (2022), the annual mean temperature (bio1) has a large contribution (67%) in the Maxent model of the species distribution in Eurasia and mainly determines the concentration of the optimal habitats in Western Europe. Our Maxent model also predicted extensive areas of Western and Central Europe with the most suitable abiotic conditions for *Iris sibirica* (occurrence probability about 1). These regions, as well as relatively small areas in Western Siberia and the Caucasus, should be prioritised for monitoring the climatogenic dynamics of the species and conservation efforts.

At the same time, *I. sibirica* is more tolerant to low temperatures than other *Iris* species (Wang et al., 2012). It can inhabit regions with rather severe winters (Ovchinnikova & Shabalkina, 2019) and in northern areas of Western Europe it is suitable as a four-season evergreen plant for wastewater treatment in winter (Gao et al., 2014).

Thus, previous findings demonstrated that *I. sibirica* prefers the warm climate of Western Europe, but can also adapt to relatively cold climates such as those in Eastern Europe and Siberia. This is in line with our results on the differentiation of the species ecological niches between West European and East European-Siberian population groups by temperature component. Unfortunately, there are no reliable data on the dynamics of *I. sibirica* dispersal across Eurasia. Assuming the Asian origin of the species, differentiation of its ecological niche during westward dispersal was accompanied by an expansion of the temperature component due to adaptation, which often occurs when species inhabit new geographical areas (Wang et al., 2008; Atwater et al., 2018; Banerjee et al., 2019). Therefore, the EESP ecological niche was unfilled in the temperature component compared to the WEP niche (Table 1, Fig. 5), confirming hypothesis (1).

In the reverse scenario of species dispersal from west to east Eurasia, the temperature component of the niche may have narrowed. The increase in annual mean temperature against the background of global climatic changes will probably contribute to the filling of the temperature niche and the species dispersal in the Asian part of its range, which is consistent with the assumption of Levchenko (2022). Thus, the studies revealed a lack of spatial and temporal niche conservatism (temperature component) for *I. sibirica*, whereby the species can only occupy areas ecologically similar to habitats in its original range (Peterson, 2004).

Niche differentiation by precipitation component

Iris sibirica is a moisture-demanding species (Tichý et al., 2023; Hrivnák et al., 2024). Under soil moisture deficiency, plant size and population viability decreased (Kostrakiewicz, 2008; Kryukova et al., 2023), and *I. sibirica* tended to occupy microrelief depressions (Kozyr et al., 2008). These observations were supported by physiological studies that revealed low water deficit (5.5%), high relative turgescence (94.5%) and narrow variability in water retention capacity for *I. sibirica* leaves (Beksheneva & Reut, 2020). The plants successfully vegetate under sufficient humidification, such as in the humid subtropics of Sochi, Russia (Slepchenko et al., 2018), but wilt under insufficient moisture (Beksheneva & Reut, 2020).

According to European soil moisture scales, *I. sibirica* preferred wet to damp habitats (8 out of 12 points according to the Ellenberg scale (Ellenberg et al., 1991)) and soils from moderately dry to damp (3 out of 5 points according to the Landolt scale (Landolt, 1977)). In European Russia, soil moisture in *I. sibirica* habitats varied from wet-steppe and meadow-steppe to wet-meadow and swamp-meadow according to the Ramensky scale (Ramensky et al., 1956). However, in general, the types of *I. sibirica* habitats were similar throughout its Eurasian range. In Western Europe, there was a variety of wetlands, specifically wet, marshy and swampy meadows, floodplain meadows and forests, wet in-forest meadows, forest glades, wet macro-forb communities and shrubs, and fens (Botta-Dukát et al., 2005; Gao et al., 2014; Kostrakiewicz-Gierałt & Podgórska, 2020; Evstigneev & Gornov, 2021; Hrivnák et al., 2024). In the East European-Siberian part of the species range, *I. sibirica* habitats included wet meadows, lowland marshy meadows, floodplain meadows and forests, forest edges and glades, sparse forests, lakeshores, overgrown dry lakes, raw lowland, and low mineral islands (Kozyr et al., 2008; Ovesnov & Efimik, 2014; Gatina, 2015; Mojsejchik & Sozinov, 2017; Ovchinnikova & Shabalkina, 2019; Kryukova et al., 2023). According to the Maxent model of species distribution in Eurasia, annual precipitation bio12 was quite important environmental predictor with contributions to the model of 15% (Levchenko, 2022).

These observations and findings agreed with our results on the important role of precipitation in the distribution of *I. sibirica* in Eurasia and the overlap of the species ecological niches by precipitation component between West European and East European-Siberian population groups. The results allowed us to declare the spatial and temporal conservatism in the precipitation niche component of *I. sibirica*, which refuted hypothesis (3) on the relatively narrow precipitation niche of East European-Siberian populations. High stability of the precipitation niche makes the species vulnerable to global climatic changes associated with redistribution of precipitation.

Ecological niche of the Mountain group of populations

Mountainous areas have a pronounced diversity of hydrological habitat conditions due to altitudinal zonality and orographic heterogeneity. For *I. sibirica*, this provides a large number of moisture-acceptable habitats and the ability to inhabit areas with a wide range of precipitation. Thus, in the mountains of Europe and the Caucasus, *I. sibirica* inhabits wet meadows, damp forest meadows, forest edges (Litvinskaya & Murtazaliev, 2013; Hrivnák et al., 2024), as well as microrelief depressions in meadow-steppe habitats (Tsepkova & Chadaeva, 2019). This corresponds to the ecological profile of *I. sibirica* based on the Ramensky scale (Ramensky et al., 1956). Accordingly, our studies revealed a relatively wide precipitation niche of Mountain populations, confirming the hypothesis (2).

The mountainous areas are generally characterised by a more humid climate than the latitudinally neighbouring plains due to the increase in precipitation with altitude. This converges the ecological niches of the Mountain and West European population groups in the precipitation component. To some extent, these results can be explained by the predominance of mountain points from Western Europe (Alps, Pyrenees, British Isles, Apennine Mountains) in the total sample.

Conclusions

In this study, we aimed to assess whether the ecological niches of European and Asian populations of *I. sibirica* differ in temperature and precipitation parameters. By clustering abiotic variables in species presence points, we defined three distinct distribution regions or population groups, namely West European, East European-Siberian, and Mountain. The ecological niches of East European-Siberian and West European population groups clearly differed in the temperature component (Unfilling > 0.80; Expansion of 0.82–0.96 in bio4, bio6, bio7, and bio11) with lower temperature parameters and higher temperature seasonality (by 219%) in the East European-Siberian part of the range. However, in the precipitation component, the ecological niches in this pair of population groups overlapped strongly (Stability > 0.90 in bio13, bio16, bio18). The widest precipitation niche of Mountain populations can be explained by orographic heterogeneity and increased precipitation at higher altitudes. The generally more humid and less continental climate of mountainous areas makes the temperature and precipitation niches of Mountain and West European populations similar (Unfilling < 0.15; Expansion < 0.30).

These results confirmed the hypotheses that (1) West European populations occupy a wider temperature niche then East European-Siberian populations, and (2) the precipitation parameters in the habitats of Mountain population had greater variability, but refuted the assumption that (3) the East European-Siberian populations had a narrower precipitation niche. The temperature niche expansion in Western Europe contributed to a wider distribution of *I. sibirica* in this part of the range. Here, extensive areas of optimal species habitats are prioritised for monitoring the climatogenic dynamics and conservation efforts. On the other hand, due to temperature niche plasticity (species tolerance to temperature parameters), *I. sibirica* can adapt to colder habitats in Eastern Europe and Asia. Thus, habitat temperature parameters are not the main limiting factor for the species distribution throughout Eurasia. In contrast, the precipitation niche conservatism (species moisture specialisation) limits the potential habitats in more continental regions, determining the reduction of suitable areas and relative rarity of *I. sibirica* in the Eastern European-Siberian part of the range. An increase in habitat temperature parameters against the backdrop of global climatic changes may drive the species dispersal in Eastern Europe and Asia depending on the redistribution of precipitation.

Future research should focus on the climatogenic dynamics of PCA parameters as well as Schoener's D, Hellinger's I and COUE metrics of *I. sibirica* ecological niches. Future studies should also include biotic data (e.g. competition, pollinators) to better understand the realised niche and true limits of *I. sibirica* distribution. From a conservation perspective, monitoring of the location and size of predicted optimal areas in the West European and East European-Siberian parts of the species range is also required. We recommend prioritising monitoring, wetland protection and microhabitat restoration for Eastern European-Siberian populations, which are especially vulnerable to changes in water availability.

Overall, the integrated approach (SDM + PCA + COUE) provides a robust tool for formalising ecological niches and guiding conservation strategies for *Iris sibirica* and other wetland species under climate change. It enabled the estimation of parameters, plasticity and stability of ecological niches, evaluate and verify models, and visualises the species potential distribution.

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Supporting Information

Additional data for the paper by Pshegusov et al. (2025) may be found in the **Supporting Information**.

References

Aiello-Lammens M.E., Boria R.A., Radosavljevic A., Vilela B., Anderson R.P. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38(5): 541–545. DOI: 10.1111/ecog.01132

Alexeyeva N.B. 2008. Genus *Iris* L. (Iridaceae) in the Russia. *Turczaninowia* 11(2): 5–68. [In Russian]

Allouche O., Tsoar A., Kadmon R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (tss). *Journal of Applied Ecology* 43(6): 1223–1232. DOI: 10.1111/j.1365-2664.2006.01214.x

Atwater D.Z., Ervine C., Barney J.N. 2018. Climatic niche shifts are common in introduced plants. *Nature Ecology and Evolution* 2(1): 34–43. DOI: 10.1038/s41559-017-0396-z

Banerjee A.K., Mukherjee A., Guo W., Ng W.L., Huang Y. 2019. Combining ecological niche modeling with genetic lineage information to predict potential distribution of *Mikania micrantha* Kunth in South and Southeast Asia under predicted climate change. *Global Ecology and Conservation* 20: e00800. DOI: 10.1016/j.gecco.2019.e00800

Beksheneva L.F., Reut A.A. 2020. Water regime of some representatives of the genus Iris L. during introduction in the Southern Urals. *Ekosistemy* 22: 82–89. DOI: 10.37279/2414-4738-2020-22-82-89 [In Russian]

Blonder B., Lamanna C., Violle C., Enquist B.J. 2014. The n-dimensional hypervolume. *Global Ecology and Biogeography* 23(5): 595–609. DOI: 10.1111/geb.12146

Boltenkov E., Artyukova E., Kozyrenko M., Erst A., Trias-Blasi A. 2020. *Iris sanguinea* is conspecific with *I. sibirica* (Iridaceae) according to morphology and plastid DNA sequence data. *PeerJ* 8: e10088. DOI: 10.7717/peerj.10088

Botta-Dukát Z., Chytrý M., Hájková P., Havlová M. 2005. Vegetation of lowland wet meadows along a climatic continentality gradient in Central Europe. *Preslia* 77(1): 89–111.

Broennimann O., Fitzpatrick M.C., Pearman P.B., Petitpierre B., Pellissier L., Yoccoz N.G., Thuiller W., Fortin M.J., Randin C., Zimmermann N.E., Graham C.H., Guisan A. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* 21(4): 481–497. DOI: 10.1111/j.1466-8238.2011.00698.x

Cotado A., Munné-Bosch S. 2020. Distribution, trade-offs and drought vulnerability of a high-mountain Pyrenean endemic plant species, *Saxifraga longifolia*. *Global Ecology and Conservation* 22: e00916. DOI: 10.1016/j.gecco.2020.e00916

Davidson I. 2002. Understanding k-means non-hierarchical clustering. *SUNY Albany – Technical Report* 2: 2–14.

Elith J., Franklin J. 2013. Species distribution modeling. In: S.A. Levin (Ed.): *Encyclopedia of Biodiversity (Second Edition)*. Vol. 6. Oxford: Academic Press. P. 692–705.

Elith J., Phillips S.J., Hastie T., Dudík M., Chee Y.E., Yates C.J. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17(1): 43–57. DOI: 10.1111/j.1472-4642.2010.00725.x

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W., Paulißen D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18: 1–248.

Evstigneev O.I., Gornov A.V. 2021. Reserve meadow: results of 30 years of monitoring. *Russian Journal of Ecosystem Ecology* 6(2). DOI: 10.21685/2500-0578-2021-2-2

Fick S.E., Hijmans R.J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12): 4302–4315. DOI: 10.1002/joc.5086

Fielding A.H., Bell J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24(1): 38–49. DOI: 10.1017/S0376892997000088

Gao J., Wang W., Guo X., Zhu S., Chen Sh., Zhang R. 2014. Nutrient removal capability and growth characteristics of *Iris sibirica* in subsurface vertical flow constructed wetlands in winter. *Ecological Engineering* 70: 351–361. DOI: 10.1016/j.ecoleng.2014.06.006

Gatina E.L. 2015. To distribution of *Iris sibirica* L. in the territory of Perm region. *Bulletin of Perm University. Biology* 3: 203–206. [In Russian]

GBIF.org. 2024. *GBIF Occurrence Download*. Available from https://doi.org/10.15468/dl.4rxt2u

Grulich V. 2012. Red List of vascular plants of the Czech Republic: 3rd edition. *Preslia* 84(3): 631–645.

Guisan A., Petitpierre B., Broennimann O., Daehler C., Kueffer Ch. 2014. Unifying niche shift studies: Insights from biological invasions. *Trends in Ecology and Evolution* 29(5): 260–269. DOI: 10.1016/j.tree.2014.02.009

Guisan A., Thuiller W., Zimmermann N. 2017. *Habitat Suitability and Distribution Models: With Applications in R.* Cambridge: University Printing House. 462 p. DOI: 10.1017/9781139028271

Hijmans R.J. 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology* 93(3): 679–688. DOI: 10.1890/11-0826.1

Hijmans R.J., Phillips S.J., Leathwick J., Elith J. 2017. *dismo: Species Distribution Modeling. R package version 1.3-3*. Available from https://CRAN.R-project.org/package=dismo

Hrivnák R., Slezák M., Dudáš M., Galvánek D., Labovská T., Miháliková T. 2024. Distribution of plant species *Iris sibirica* and its vegetation affinity in Slovakia. *Biologia* 79(9): 2649–2664. DOI: 10.1007/s11756-024-01719-0

Jain A.K. 2010. Data Clustering: 50 Years Beyond K-Means. *Pattern Recognition Letters* 31(8): 651–666. DOI: 10.1016/j.patrec.2009.09.011

Kassambara A., Mundt F. 2019. *Factoextra: Extract and Visualize the Results of Multivariate Data Analyses*. Available from https://rdrr.io/cran/factoextra/

Khela S. 2013. *Iris sibirica* (Europe assessment). In: *The IUCN Red List of Threatened Species 2013: e.T203236A2762502*. Available from https://www.iucnredlist.org/species/203236/2762502

Kostrakiewicz K. 2008. Population structure of a clonal endangered plant species *Iris sibirica* L. in different habitat conditions. *Polish Journal of Ecology* 56(4): 581–592.

Kostrakiewicz K. 2007. The effect of dominant species on numbers and age structure of *Iris sibirica* L. population on blue moor-grass meadow in Southern Poland. *Acta Societatis Botanicorum Poloniae* 76(2): 165–173. DOI: 10.5586/asbp.2007.020

Kostrakiewicz-Gierałt K., Podgórska M. 2020. Regeneration of the rare meadow species *Iris sibirica* in a post-cultural land. *Botany Letters* 167(3): 331–339. DOI: 10.1080/23818107.2020.1784272

Kozyr M.S., Yakushenko D.M., Podorozhniy D.S. 2008. The ecological and coenotic characteristic of *Iris sibirica* L. in the flood-lands of Seim river. *Introduktsiya Roslyn* 4: 51–58. [In Ukrainian]

Kramer-Schadt S., Niedballa J., Pilgrim J.D., Schröder B., Lindenborn J., Reinfelder V., Stillfried M., Heckmann I., Scharf A.K., Augeri D.M., Cheyne S.M., Hearn A.J., Ross J., Macdonald D.W., Mathai J., Eaton J., Marshall A.J., Semiadi G., Rustam R., Bernard H., Alfred R., Samejima H., Duckworth J.W., Breitenmoser-Wuersten C., Belant J.L., Hofer H., Wilting A. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions* 19(11): 1366–1379. DOI: 10.1111/ddi.12096

Kryukova A.V., Mustafina A.N., Abramova L.M., Golovanov Y.M., Muldashev A.A. 2023. Morphology Features and Seed Productivity of *Iris sibirica* L. (Iridaceae Juss.) in the Trans-Urals of the Bashkortostan Republic. *Vestnik Tomskogo Gosudarstvennogo Universiteta, Biologiya* 64: 30–51. [In Russian]

Landolt E. 1977. *Ökologische Zeigerwerte zur Schweizer Flora*. Zürich: Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel. 208 p.

Le S., Josse J., Husson F. 2008. FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software* 25(1): 1–18. DOI: 10.18637/jss.v025.i01

Levchenko L.S. 2022. Potential range change of the protected species *Iris sibirica* L. under the influence of projected climate change. In: A.M. Adam, N.I. Laptev, N.L. Yablochkina, N.N. Ilyinskikh, M.V. Olonova (Eds): *Ecology and Environmental Management*. Tomsk: Literaturnoe byuro. P. 48–50. [In Russian]

Lissovsky A.A., Dudov S.V. 2020. Advantages and limitations of application of the species distribution modeling methods. 2. Maxent. *Zhurnal Obshchei Biologii* 81(2): 135–146. DOI: 10.31857/S0044459620020049 [In Russian]

Litvinskaya S.A., Murtazaliev R.A. 2013. *Flora of the North Caucasus*. Moscow: Phyton XXI. 687 p. [In Russian]

Meusel H., Jäger E.J. 1992. *Vergleichende Chorologie der Zentraleuropaischen Flora. Band III.* Jena, Stuttgart, New York: Gustav Fischer Verlag. 333 p.

Mojsejchik E.V., Sozinov O.V. 2017. Species diversity of mineral island of the Zvanets Reserve. In: *Biological Autumn of 2017 (To the science year in Belarus)*. Minsk: Belarusian State University. P. 197–199. [In Russian]

Mu-Za-Chin V.V., Shukal V.V. 2016. The characteristic of *Iris sibirica* L. (Iridaceae) coenopopulations in river floodplains in the Bryansk region. *Bulletin of Bryansk dpt. of RBS* 2(8): 36–43. [In Russian]

Ovchinnikova Yu.A., Shabalkina S.V. 2019. On ecological preferences of *Iris sibirica* L. In: T.Y. Ashihmina (Ed.): *Ecology of the native land: problems and solutions*. Kirov: Vyatka State University. P. 277–282. [In Russian]

Ovesnov S.A., Efimik E.G. 2014. Flora of the historico-natural complex «Spasskaya gora» (Perm region). *Bulletin of Udmurt University. Series Biology. Earth Sciences* 4: 18–26. [In Russian]

Peterson A.T. 2004. Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology* 78(4): 419–33. DOI: 10.1086/378926

Peterson A.T., Soberón J., Pearson R.G., Anderson R.P., Martínez-Meyer E., Nakamura M., Araújo M.B. 2011. *Ecological Niches and Geographic Distributions (MPB-49)*. Princeton: Princeton University Press. 328 p. DOI: 10.1515/9781400840670

Petrova I.V., Sannikov S.N., Tembotova F.I., Sannikova N.S., Farzaliev V.S., Mollaeva M.Z., Egorov E.V. 2017. Genogeography of *Pinus sylvestris* L. Populations in the Greater Caucasus and Crimea. *Russian Journal of Ecology* 48(6): 524–531. DOI: 10.1134/S106741361706008X

Phillips S.J., Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31(2): 161–175. DOI: 10.1111/j.0906-7590.2008.5203.x

Phillips S.J., Anderson R.P., Schapire R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190(3–4): 231–259. DOI: 10.1016/j.ecolmodel.2005.03.026

Phillips S.J., Anderson R.P., Dudík M., Schapire R.E., Blair M.E. 2017. Opening the black box: an open-source release of Maxent. *Ecography* 40(7): 887–893. DOI: 10.1111/ecog.03049

Pirogov Yu.K. Inaturalist platform as a tool for studying species of the genus Iris L. modern ranges of *Iris sibirica* and *Iris sanguinea* based on iNaturalist data. In: V.V. Chub (Ed.): *Iris-2022*. Moscow: Moscow University Press. P. 96–100. [In Russian]

POWO. 2025. *Plants of the World Online*. Kew: Royal Botanic Gardens. Available from http://www.plantsoftheworldonline.org/

Qazi A.W., Saqib Z., Zaman-ul-Haq M. 2022. Trends in species distribution modelling in context of rare and endemic plants: a systematic review. *Ecological Processes* 11(1): 40. DOI: 10.1186/s13717-022-00384-y

R Core Team. 2025. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from https://www.R-project.org

Ramensky L.G., Tsatsenkin I.A., Chizhikov O.N., Antipin N.A. 1956. *Ecological assessment of fodder lands by vegetation cover*. Moscow: State Publishing House of Agricultural Literature. 471 p. [In Russian]

Red Data Book of the Republic of Crimea. Simferopol: IT ARIAL, 2015. 480 p. [In Russian]

Red Data Book of the Stavropolsky Krai. Stavropol: IP Andreev Igor Vladimirovich, 2013. 383 p. [In Russian]

Salamon-Albert É., Lőrincz P., Attila B. 2010. *Iridetum sibiricae* Philippi 1960 in Hungary. *Acta Botanica Hungarica* 52(1–2): 177–196. DOI: 10.1556/ABot.52.2010.1-2.e3

Schoener T.W. 1968. The *Anolis* Lizards of Bimini: Resource Partitioning in a Complex Fauna. *Ecology* 49(4): 704–726. DOI: 10.2307/1935534

Scrypec K.I., Tasenkevich L.O., Seniv M.M. 2020. *Iris sibirica* (Iridaceae) on the territory of Western Ukraine. *Biosystems Diversity* 28(3): 211–215. DOI: 10.15421/012027

Sillero N., Barbosa A.M. 2021. Common mistakes in ecological niche models. *International Journal of Geographical Information Science* 35(2): 213–226. DOI: 10.1080/13658816.2020.1798968

Sillero N., Arenas-Castro S., Enriquez-Urzelai U., Vale C.G., Sousa-Guedes D., Martínez-Freiría F., Real R., Barbosa A.M. 2021. Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. *Ecological Modelling* 456: 109671. DOI: 10.1016/j.ecolmodel.2021.109671

Sillero N., Campos J., Arenas-Castro S., Barbosa A.M. 2023. A curated list of R packages for ecological niche modelling. *Ecological Modelling* 476: 110242. DOI: 10.1016/j.ecolmodel.2022.110242

Slepchenko N.A., Kozina V.V., Shoshina Ye.I. 2018. *Iris sibirica* in Russian humid subtropics. In: *Problems of Botany of Southern Siberia and Mongolia*. Barnaul: Barnaul State University. P. 513–515. [In Russian]

SRTM. 2025. *Shuttle Radar Topography Mission*. Available from https://srtm.csi.cgiar.org/

Straubinger C., Reisch C., Poschlod P. 2023. Effects of historical management on the vegetation and habitat properties of wet meadows in Germany. *Restoration Ecology* 31(5): e13839. DOI: 10.1111/rec.13839

Syfert M.M., Smith M.J., Coomes D.A. 2013. The effects of sampling bias and model complexity on the predictive performance of maxent species distribution models. *PLoS ONE* 8(2): e55158. DOI: 10.1371/journal.pone.0055158

Tichý L., Axmanová I., Dengler J., Guarino R., Jansen F., Midolo G., Nobis M.P., Van Meerbeek K., Aćić S., Attorre F., Bergmeier E., Biurrun I., Bonari G., Bruelheide H., Campos J.A., Čarni A., Chiarucci A., Ćuk M., Ćušterevska R., Didukh Ya., Dítě D., Dítě Z., Dziuba T., Fanelli G., Fernández-Pascual E., Garbolino E., Gavilán R.G., Gégout J.C., Graf U., Güler B. et al. 2023. Ellenberg-type indicator values for European vascular plant species. *Journal of Vegetation Science* 34(1): e13168. DOI: 10.1111/jvs.13168

Tsepkova N.L., Chadaeva V.A. 2019. Demographic indicators of *Iris sibirica* L. cenopopopulations under conditions of post-grazing demutation of mountain meadows in the territory of Protected Areas of the Western and Central Caucasus. In: *Current issues of biodiversity conservation and ecologically balanced nature management in the Western Caucasus*. Nalchik: Tembotov Institute of Ecology of Mountain Territories of RAS. P. 121–122. [In Russian]

Tzvelev N.N. 1979. Genus. 2. *Iris* L. In: *Flora of European part of USSR*. Vol. 4. Leningrad: Nauka. P. 299–307. [In Russian]

Vignali S., Lörcher F., Hegglin D., Arlettaz R., Braunisch V. 2021. Modelling the habitat selection of the bearded vulture to predict areas of potential conflict with wind energy development in the Swiss Alps. *Global Ecology and Conservation* 25: e01405. DOI: 10.1016/j.gecco.2020.e01405

Wang W.L., Gao J.Q., Guo X., Li W.C., Tian X.Y., Zhang R.Q. 2012. Long-term effects and performance of two-stage baffled surface flow constructed wetland treating polluted river. *Ecological Engineering* 49: 93–103. DOI: 10.1016/j.ecoleng.2012.08.016

Wang Y.S., Xie B.Y., Wan F.H., Xiao Q.M., Dai L.Y. 2008. Application of ecologic niche models in explanation of niche shift of invasive alien species. *Acta Ecologica Sinica* 28: 4974–4981.

Warren D.L., Glor R.E., Turelli M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62(11): 2868–2883. DOI: 10.1111/j.1558-5646.2008.00482.x

Warren D.L., Glor R.E., Turelli M. 2010. ENMTools: A Toolbox for Comparative Studies of Environmental Niche Models. *Ecography* 33(3): 607–611. DOI: 10.1111/j.1600-0587.2009.06142.x

Webb D.A. 1980. *Iris* L. In: T.G. Tutin, V.H. Heywood (Eds.): *Flora Europaea. Alismataceae to Orchidaceae*. Vol. 5. Cambridge: Cambridge Univversity Press. P. 87–92.

Wickham H. 2009. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag. 213 p.

WorldClim2. 2025. *WorldClim climate data base*. Available from https://worldclim.com/version2

Yilmaz H., Yilmaz O.Y., Akyüz Y.F. 2017. Determining the factors affecting the distribution of *Muscari latifolium*, an endemic plant of Turkey, and a mapping species distribution model. *Ecology and Evolution* 7(4): 1112–1124. DOI: 10.1002/ece3.2766

Yutang Z., Noltie H.J., Mathew B. 2000. Iridaceae A. L. Jussieu. In: Z.Y. Wu, P.H. Raven (Eds.): *Flora of China*. Vol. 24. Beijing, St. Louis: Science Press, Missouri Botanical Garden Press. P. 297–313.

БИОКЛИМАТИЧЕСКИЕ ФАКТОРЫ, ОГРАНИЧИВАЮЩИЕ РАСПРОСТРАНЕНИЕ *IRIS SIBIRICA* В ЕВРАЗИИ

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Обладая широким ареалом в Евразии, *Iris sibirica* имеет неравномерное распространение и занесен в региональные и национальные Красные книги многих стран Европы и Азии. Абиотические причины редкости вида (биоклиматические лимитирующие факторы) и особенности его адаптации в разных частях ареала до сих пор остаются малоизученными. Формализация экологических ниш *Iris sibirica* в n-мерном пространстве экологических факторов позволит прояснить эти вопросы. Мы предположили, что экологические ниши вида дифференцированы в европейской и азиатской частях его ареала, что позволяет ему адаптироваться в различных экологических условиях равнинных и горных местообитаний. Целью данного исследования было (1) определить абиотические границы различных частей ареала *Iris sibirica* в Евразии (т.е. популяционные группы), (2) проверить, насколько экологические ниши популяционных групп дифференцированы в экологическом пространстве, (3) получить информацию об экологических причинах редкости *Iris sibirica* в различных частях ареала. Чтобы проверить, перекрываются ли экологические ниши *Iris sibirica* в разных частях его ареала, мы применили метод оценки плотности ядра для визуализации ниш в пространстве осей PCA (Principal Component Analysis). Мы также использовали количественные метрики перекрытия ниш, такие как Schoener's D, Hellinger's I и COUE (Centroid shift, Overlap (Stability), Unfilling, Expansion). Биоклиматические переменные WorldClim использованы для формализации температурного и влажностного (параметры осадков) компонентов экологических ниш. С помощью неиерархической итеративной кластеризации k-средних абиотических переменных в точках присутствия были выделены Западноевропейская (463 точки), Восточноевропейско-Сибирская (186 точек) и Горная (112 точек) группы популяций *Iris sibirica*. По параметрам температуры и осадков местообитания Горной группы популяций были сходны с таковыми Западноевропейской группы (Stability 0.90–0.99), но заметно отличались от местообитаний Восточноевропейско-Сибирских популяций (Expansion 0.85–1.00). В обоих случаях экологическая ниша Горной группы популяций была явно шире по компоненте осадков. Вероятно, это связано с относительно влажным климатом и орографической неоднородностью горных районов, что позволяет *Iris sibirica* занимать участки с широким диапазоном количества осадков, но подходящей влагообеспеченностью (например, кулуары, понижения микрорельефа). Экологические ниши Западноевропейской и Восточноевропейско-Сибирской групп популяций четко различались по температурному компоненту, но перекрывались по компоненту осадков в экологическом пространстве осей PCA. Значения метрик Schoener's D и Hellinger's I варьировали от 0.02 до 0.21 для температурных переменных и от 0.24 до 0.71 для параметров осадков. Для Восточноевропейско-Сибирской группы популяций незаполнение (Unfilling) температурного компонента ниши составило 0.84–0.88. Таким образом, *Iris sibirica* адаптирован к широкому диапазону температурных условий Евразии, но имеет узкую специализацию по влагообеспеченности территорий и ограничен в подходящих местообитаниях (например, влажные, болотистые и заболоченные луга), особенно в более континентальной и менее влажной Восточноевропейско-Сибирской части своего ареала.

Ключевые слова: группы популяций, метрики перекрытия ниш, модели экологических ниш, оценка плотности ядра, распределение видов