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RESEARCH ARTICLE

Ecological and geographical studies of *Poa versicolor* (Poaceae) aggregate in Asian Russia and adjacent territories

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Abstract

Aggregate *Poa versicolor* (Poaceae) contains closely related xeromorphic species distributed mainly in temperate regions of Asia. The most common species are *P. transbaicalica*, *P. relaxa*, *P. ochotensis*, *P. botryoides* and *P. argunensis*. They play an important role in the structure of steppe communities, but this aggregate is known to be difficult for the systematics. The previous research of morphological diversity and distribution confirmed morphological and geographical diversification within the aggregate, however, their ecological-climatic niches were not studied. The goal of this study was to reveal whether the species of the *P. versicolor* aggregate occupied the equivalent or similar niches, or the morphological diversification was accompanied by niche change. Equivalence and similarity tests were used. A comparative study of the ecological-climatic niches showed that the niches only of the most similar pairs *P. transbaicalica* – *P. botryoides*, and *P. argunensis* – *P. botryoides* were identical or equivalent. All other pairs of species were not identical and confirmed the expected diversification, revealed by previous morphological and geographic analysis. Nevertheless, the studies using the background test, which takes into account environmental features, has revealed niche conservatism at the aggregate level. The ecological- climatic niches of five species within the *P. versicolor* aggregate proved to be similar, but not equivalent in all species. Thus, our data show that partial or complete geographic divergence and morphological diversification of species is not accompanied by diversification of their ecological niches.

Keywords

Ecological niche modeling, niches comparison, niche conservatism, grasses distribution

Introduction

The ecological niche is known to have been resulted from adaptations of a species to different environmental conditions. It is as indispensable feature of the species like its morphological and genetic characteristics (Stuessy 2009). The identification of ecological niche and its divergence is no less important for the study of microevolutionary processes and speciation than the study of changes in morphological features (Grant 1984, 1991). An ecological niche, as opposed to an actually existing range, is a hypothetical and abstract idea that allows us to better visualize the evolutionary and ecological factors affecting a species (Solbrig and Solbrig 1982) and is identified on the basis of actually existing environmental data. The degree of specialization and ecological niche width play a crucial role in the ability of species to adapt to environmental changes, and niche divergence can signalize the evolutionary processes. The reflection of the niche in reality is the range. As noted by A.A. Lisovsky and colleagues (2020), range is a function of species distribution from ecological niche parameters. The theoretical aspect of the relationship between ecological niches and geographic distribution is discussed and explained in detail in the paper "Ecological niches and geographic distributions" (Peterson et al. 2011). Revealing the patterns of plant range formation is a fundamental problem that is closely related to species history in the context of global and local evolution of the natural environment and biodiversity research. The knowledge of these regularities provides opportunities to assess the prospects for the further existence of species and the alteration of their ranges under the influence of various factors. It is most closely related to the solutions of many theoretical and practical problems of floro- and faunogenesis, biogeography, conservation and rational use of natural resources (Soberon and Peterson 2005; Thompson et al. 2011; Guisan et al. 2017; Smith et al. 2019, etc.).

In recent years, extensive and accessible information on the Earth-wide environment, as well as evolving GIS technologies that make it possible to model, assess and compare ecological requirements of species and to define their niches, have significantly expanded the capabilities of ecologists. New approaches make it possible to model both the ecological niche and the dynamics of species ranges based on association with various environmental factors. All this aroused a keen interest in the ecological niche not only among ecologists, but also among systematists and biogeographers (Rice et al. 2003; Soberon 2007; Peterson et al. 2011; Franklin 2013; Guisan et al. 2017; Brown and Carnaval 2019). A large number of works have been devoted to the identification, evaluation and comparison of ecological niches (Warren et al. 2008, 2011; Broennimann et al. 2012; Zhu et al. 2013; Aguirre-Gutierrez et al. 2014) and niche-based modeling of suitable areas (Guisan and Zimmermann 2000). Much work has been devoted to investigating the conservatism and dynamics of the ecological niche (Soberon, Peterson 2005; Holt 2009; Smith et al. 2019; Shitikov et al. 2022), its diversification both at the species level (Kozak and Weins

2006; Raxworthy et al. 2007; Giraldo-Kalil et al. 2023) and at the intraspecific level (Pyron and Burbrink, 2009; Smith et al. 2019; Bried and Siepielski 2019).

The aggregate *Poa versicolor* belongs to the section *Stenopoa* Dumort. which is one of the largest and most systematically difficult intrageneric groups of the bluegrass genus (*Poa* L.).

Species of the aggregate *P. versicolor* are distributed in semi-arid habitats from Central Europe to Kamchatka, covering Central and Eastern Europe (Edmondson 1990; Tzvelev 1976; Tzvelev and Probatova 2019; Prokudin 1977), the Caucasus and Turkey (Menitsky and Popova 2006; Davis 1985), Middle and Central Asia and the Himalayas (Ovchinnikov and Chukavina 1957; Keng 1959; Bor 1960; Tsvelev 1976; Rajbhandari 1991; Liu 2003; Zhu 2006; Kellogg et al. 2020). Depending on the species concept, in Asian Russia, Middle Asia and Kazakhstan aggr. *P. versicolor* includes from 1 (polytypic *P. versicolor* Bess, Tsvelev 1976) to 9 variously specialized moderately xeromorphic species. According to various estimates, the aggregate as a whole has up to 25 species.

Many species of *P. versicolor* aggregate, as well as bluegrasses in general, are economically valuable and play a significant role in the formation of steppe communities. Therefore, clarification of their distribution and study of their ecological-climatic niches is not only theoretical, but also of great practical importance.

The most common species of aggr. *P. versicolor* in Asian Russia and adjacent territories are *P. transbaicalica* Roshev., *P. ochotensis* Trin., *P. botryoides* (Trin. ex Griseb.) Kom. and *P. argunensis* Roshev. The ranges of *P. reverdattoi* Roshev., *P. pseudodahurica* Olonova, *P. gnutikovii* Probat., *P. udensis* Trautv. et C.A. Mey. are much narrower. *Poa relaxa* Ovcz. replaces *P. transbaicalica* in the mountains of Middle Asia. Three species – *P. hylobates* Bor, *P. araratica* Trautv. and *P. sterilis* M. Bieb. are not included in this aggregate until the taxonomic situation is clarified.

The bulk of the species are presumably xeromorphic derivatives of the mesomorphic boreal species *P. palustris*, whose origin was caused by Pleistocene climate cooling and drying over a vast area of Eurasia. These climate changes caused to range shifts and hybridization, whereas geological processes promoted differentiation and isolation of some populations. The *P. versicolor* aggregate can be separated to some extent conditionally, because it is related to other relative aggregates: thus, *P. ochotensis* Trin. probably resulted from introgressive hybridization between Siberian *P. transbaicalica* and Sino-Japanese *P. sphondylodes* Trin. Since morphologically it is more similar to aggregate *P. versicolor*, according to N.N. Tsvelev (1976, 2009), it is considered within this complex as a subspecies of *P. versicolor* Bess or species within aggr. *P. versicolor*.

Our ecological and geographical studies covered *P. transbaicalica*, *P. relaxa*, *P. ochotensis*, *P. botryoides* and *P. argunensis*. The remaining species have not yet been included in the analysis due to the lack of accurate distribution data.

Evolution in the section followed the path of xerophilization (Serebryakova 1965; Tsvelev 1976). According to the degree of xeromorphism (the position of the upper node, the ratio between the lengths of the sheath and blade of the flag leaf, the shape of the panicle and the ratio between its length and the length of the longest branch), the species of the aggregate represent the following evolutionary series: *P. relaxa*, *P. transbaicalica*, *P. ochotensis*, *P. argunensis*, and *P. botryoides*. As literature data (Tsatsenkin 1967; Korolyuk et al. 2005, 2006) show, these species (except for *P. ochotensis*, data for which have not been found yet) correspond to the following values on the soil moisture scale: 54, 51.1, 50.6, 49.5. At the same time, *P. argunensis* demonstrates high morphological variability, apparently due to high ecological plasticity and tolerance: a number of specimens from Eastern Siberia in their morphotype are similar to the most xeromorphic specimens of *P. botryoides* and even dwarf alpine *P. attenuata* Trin. Thus, comparison of morphological adaptations of these species and their optimums on the soil moisture scale confirms morphological and ecological diversification within the aggregate. However, the comparison of ecological niches of species within *P. versicolor* aggregate was not carried out.

The goal of this study was to investigate whether the species of *P. versicolor* aggregate was accompanied by niche divergence in their evolution. For this purpose, we compared the ecological-climatic niches of five morphologically and ecologically different species included in the aggregate.

Material and methods

The identification of the ecological-climatic niche is based on a combination of occurrence data (their geographic coordinates) and climatic characteristics of these points. Therefore, clarification of the distribution of *P. versicolor* aggregate was special and important part of the work.

As the correct identification of material is crucial, special attention was paid to the selection of occurrence data for mapping and further analyzing. Collections from AA, ALTB, K, KUZ, IRKU, LE, MAG, MHA, MW, NS, NSK, PE, SASY, TAD, TASH, TK, UUH, VLA, US (Holmgren et al. 1990), as well as personal collections kindly provided by N.S. Probatova† (FSC Biodiversity, Vladivostok), E.I. Pospelova (Moscow State University, Moscow), R.J. Soreng (Smithsonian Institution, Washington), A.Yu. Korolyuk (CSBG, Novosibirsk) were used. Since approaches and principles of species identification, as well as views on their extent and boundaries, have changed repeatedly over the many years of collection storage, only those materials that were personally investigated and identified were taken into account. Some of records were obtained from maps placed in reliable sources: Arctic Flora of the USSR (Tsvelev 1964), Flora of Central Siberia (Peshkova 1979), Flora of Siberia (Olonova 1990) and Vascular Plants of the Soviet Far East (Probatova 1985). In cases where the species identification was not in doubt, materials including photographs and location coordinates from the GBIF and Moscow State University Digital Herbarium databases (Seregin 2023) were also used. Since the *P. versicolor* aggregate is considered to be one of the most systematically difficult groups of the section, many specimens were not included in the database because of their obscure status.

The study of the origin and spatial distribution of biodiversity is currently one of the most important problems of biology, since it is closely related to solutions to many theoretical and practical problems of flora- and faunogenesis, biogeography, conservation and rational use of natural resources (Ivanova Shashkov 2017; Vaganov et al. 2019). Therefore the specification of species distribution, digitalization of this material and visualization in the form of electronic maps are of the special significance.

Species distribution maps in digital format were generated using DIVA-GIS (Hijmans et al. 2005) and ArcGIS (ESRI 2012). The DIVA-GIS program extracted the values of 19 biologically relevant climatic data with a spatial resolution of 2.5 arc-min. from the WORDCLIM database (Hijmans et al. 2004) for each occurrence (Bio 1 – annual mean temperature, Bio 2 – mean diurnal temperature range (mean of monthly max t° – min t°), Bio 3 – isotermality (Bio 1/ Bio 7) × 100, Bio 4 – temperature seasonality (standard deviation of monthly t°), Bio 5 – maxim. t° of the warmest period, Bio 6 – minimum temperature of the coldest period, Bio 7 – temperature annual range (Bio 5 – Bio 6), Bio 8 – mean temperature of the wettest quarter, Bio 9 – mean temperature of the driest quarter, Bio 10 – temperature of the warmest quarter, Bio 11 – mean temperature of the coldest quarter, Bio 12 – mean annual precipitation, Bio 13 – precipitation of the wettest period, Bio 14 – precipitation of the driest period, Bio 15 – precipitation seasonality (standard deviation of monthly precipitation), Bio 16 – precipitation of the wettest quarter, Bio 17 – precipitation of the driest quarter, Bio 18 – precipitation of the warmest quarter, Bio 19 – precipitation of the coldest quarter). The BIOCLIM option (Nix 1986) was used to identify the ecological-climatic niche and visualize species bioclimatic parameters (species climatic profile). The resulting histograms, based on occurrences, reflect the limits of variability and show the frequencies of different climatic parameters observed within species.

Of course the revealing the species-specific amplitude of these variables does not reflect the entire ecological niche, but gives a good notion of the ecological and climatic requirements of a species. To visualize virtual ecological-climatic niches and reveal their relative position, climatic parameters of species occurrence were included in Principal Component analysis (PCA) and plot of the object projections in PC axes I – II was constructed.

To investigate niche conservatism and/or diversification, the following steps were taken: identification and investigation of ecological-climatic profiles of species, representing individual amplitude of species existence within certain biologically relevant climatic parameters; comparison of the niches of five species using the principal component analysis (PCA); modeling the ecological-climatic niches and constructing the habitat suitability models; comparison the obtained niches using niche identity and similarity tests.

Virtual ecological-climatic niche models were constructed using MaxEnt program (Phillips et al. 2006; Phillips and Dudik 2008). This method is considered to be one of the most efficient among other methods that do not require data on species absence (Anderson et al. 2003; Elith et al. 2006). Obtained models were projected onto maps constructed using ArcGIS 10 software (ESRI, 2012). The predictive capabilities of the model created using the MaxEnt method are evaluated using the receiver operating characteristic (ROC) curve. ROC is a graph that allows us to evaluate the quality of binary classification. It reflects the ratio between the proportion of objects from the total number of feature carriers correctly classified as feature carriers (ordinate axis) and the proportion of objects not carrying features, incorrectly classified as feature carriers (abscissa axis). Quantitative interpretation of the ROC is given by the AUC (area under curve) – the area bounded by the ROC and the axis of the fraction of false positive classifications (the fraction of objects not carrying features misclassified as carrying features). AUC estimates a model's ability to indicate the presence of a species at a point of raster, where it is highly likely to be located. AUC measures the ability of a model to discriminate between raster cells where a species is present and where it is absent, providing a measure of overall accuracy that is independent of threshold. AUC is a measure of the area under the ROC, ranging from 0.5 (random accuracy) to 1 (perfect discrimination). If the AUC is equal to or below 0.5, the model has no predictive value. A value of 0.8 for the AUC indicates an 80% probability that where a species is predicted to be found, it will actually be found (in this case, the model predicts the suitability of areas to its climatic requirements rather than the species' presence, which depends on many other conditions besides climate) (Phillips and Dudik 2008).

After removing nearby locations, 241 locations of *P. transbaicalica*, 158 of *P. botryoides*, 101 of *P. relaxa*, 77 of *P. argunensis*, and 48 locations of *P. ochotensis* were selected for analysis. These occurrences are assumed to generally cover the ranges and describe climatic niches of these species. Then we used 75% of the occurrences for the model training, and 25% for testing. A threshold of 10 percentiles was adopted to exclude untypical occurrences and extreme values of variables.

The MaxEnt program also provides for the possibility of estimating the contribution of climatic variables to model construction by several methods. In our study, we used the permutation (Scheldeman and van Zonneveld 2010). The permutation approach detects it by randomly permuting the values of that variable among the training points (both presence and background) and measuring the resulting decrease in training AUC. A large decrease indicates that the model depends heavily on that variable (Scheldeman and van Zonneveld 2010; Brown 2014a).

In order to avoid "overfitting" of the model and high colinearity of climatic variables, which prevent the proper assessment of their contribution in the model building, Brown (2014, a, b) recommends to reduce autocorrelation of input environmental data by removing highly correlated variables. After testing autocorrelations of environmental data (Brown 2014a), variables with a correlation coefficient more than 0.7 were deleted, and the models were constructed based on Bio 1, Bio 7, Bio 8, Bio 12, Bio 14, Bio 19.

Modern methods allow not only to reveal the ecological-climatic component of the general ecological niche of species, but also to compare them. Revealing statistically significant differences between niches of different species is an important tool for the study of divergence and evolution. Currently, such comparison methods as the I-test (identity test) and B-test (background test), implemented in programs (Warren et al. 2008, 2011), are widely recognized, and provide an opportunity to compare ecological niches. The niche identity or equivalence test assesses if the niches of two species are significantly different from each other, or they are identical. It uses the environmental data of their occurrences and does not take into account the data of surrounding space (Warren et al. 2021). Thus, as R.M. Zink (2015:80) wrote, ”it is possible to obtain a significant niche identity test if populations live in differing environments, but this does not mean, necessarily, that the species have diverged ecologically, only that they are able to survive in different climates because of ecological plasticity”. Indeed, when the conditions, used by one species are not available for another one, the conclusion of ecological niche differentiation will not be correct (Kambhampati and Peterson 2007). In addition, A.T. Peterson (2011) warns that this test is very sensitive to sampling peculiarities and tends to overestimate differences between niches. Therefore, until a better tool becomes available, he recommends focusing on the biological significance of the findings when interpreting the results obtained.

B-test allows to reveal, “whether two species are more or less similar than expected based on the differences in the environmental background in which they occur” (Warren et al. 2011:19). This rest “involves multiple iterations in which the niche overlap is calculated between 1 taxon’s ENM and an ENM constructed from random points within the range of the second taxon, where the number of random points is the same as the number of actual points for that taxon (subspecies in the present study). Tests are conducted in both directions. … If niches overlap more than expected, it is interpreted as evidence for niche conservatism; if niches overlap less than expected, one can assume niche divergence” (Zink 2015: 80).

To calculate the niche overlap between pair of species we used I-metric and Schoener’s D-metric (Warren et al. 2008), which ranges from 0 (no overlap) to 1 (complete overlap). We considered that ecological niches of two species were less equivalent or less similar if the value of niche overlap was significantly lower than the overlap values form the null distribution ($p \leq 0.05$). Both tests involved 100 iterations of randomized locality points for every pair of species. The niche comparisons were performed in the R 4.1.1. (R Core Team, 2021) using CRAN packages, and the basic algorithm of Warren et al. (2021).

Numerical data were processed using PCA in Statistica Version 10 program (StatSoft 2011), calculations for the comparison of ecological niches were performed on the SKIF-Cyberia supercomputer of the National Research Tomsk State University (Blaginin et al. 2022).

Result

The work on geographical reference of herbaria collections was continued and new occurrences of aggregate's species were obtained. As a result, the database of distribution of bluegrasses of Stenopoa section was significantly improved, and this work is still in progress.

The delimitation of the ranges of Middle Asian *P. relaxa* and East European-Siberian *P. transbaicalica* proved to be difficult. This is caused mainly by the significant polymorphism of both species. Thus, according to Ovchinnikov and Chukavina (1957) and N.N. Tsvelev (1976), the range of *P. relaxa* is limited to the mountains of Middle Asia. Nevertheless *P. relaxa* has been reported in the Ulutau (Ulytau) region in Central Kazakhstan (Gamayunova 1956; Kupriyanov 2020) and the Altai alpines (Nosov et al. 2017). Both of these occurrences are significantly distant from the main range of the species.

A.N. Kupriyanov reported *P. relaxa* in Central Kazakhstan based on a single specimen (Ulutau Mountains, Aydarly ur., meadows, 20 V 2010, A. Kupriyanov, V. Mikhailov. KUZ. Determ. M. Olonova.), and noted this species as very rare. A revision of herbarium collections did not reveal *P. relaxa* in Central Kazakhstan. A special, more detailed study of the specimen stored in KUZ made us doubt the correctness of the primary identification and, taking into account the new experience and data, we attributed this specimen to *P. transbaicalica*. Indeed, Ulytau region is characterized by flat relief with altitudes within 200–300 m asl (Gvozdetsky and Nikolaev 1971), and the occurrence of a Middle Asian mountain species there is unlikely. S.A. Abdulina (1999), as well as I.O. Baitulin and Y.A. Kotukhov (2011) do not include this species in the list of the plants of Kazakhstan.

In the Altai Mountains, N.N. Nosov and his colleagues registered *P. relaxa* in two places: "Altai Republic, Kosh-Agach district. Approaches to the Maliy Aktru. Rocks, moraine. 2331 m above sea level. 50°04′117″N 87°46′267″E. 20 VIII 2010. Collected by A. V. Rodionov, E. O. Punina, A. A. Gnutikov. Opr: N. N. Nosov, N. N. Tsvelev" (LE) and "Altai Republic, Ulagan district. Near Aktash village. Path to the TV tower. Stony slope. 2576 m a.s.l. 50°19′544″N 87°44′327″E. 30 VIII 2010. Collected by A.V. Rodionov, E.O. Punina, A.A. Gnutikov. Opr: N.N. Nosov, N.N. Tsvelev" (LE). The authors point out the affinity and morphological similarity of this species with *P. altaica* Trin. (Nosov et al. 2017), belonging to aggregate *P. glauca*. Long-term and detailed studies of bluegrasses in the area of Aktru glaciological station, as well the population of Stenopoa on rocky slopes in the area of the TV tower of Aktash settlement did not confirm the occurrence of *P. relaxa* in the Altai mountains. Both morphologically and ecologically these plants, inhabiting wet rocks near melting glaciers, are much closer to Siberian *P. altaica* (aggregate *P. glauca*) than to xerophilic Middle Asian *P. relaxa* (aggregate *P. versicolor*) as a whole.

A refined digital map of locations of the five common species of *P. versicolor* aggregate in Asian Russia and adjacent territories has been obtained (Fig. 1), and some conclusions about their distribution can already be made.

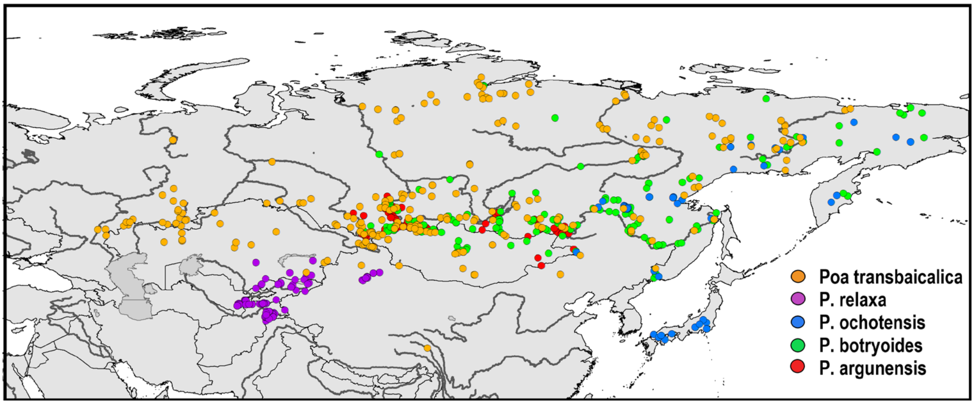

Figure 1. Distribution of *Poa botryoides*, *P. transbaicalica*, *P. argunensis*, *P. ochotensis* and *P. relaxa*.

Analysis of the distribution of the five most common species of the aggregate showed that the widest range is occupied by *P. transbaicalica*: it occures from the Russian Far East and, according to literature, reaches Eastern Europe (Tsvelev 1976; Prokudin 1977; Edmondson 1990). It is distributed mainly in the steppe zone; in the forest zone it occupies southern steppe and rocky slopes. In the mountains of Southern Siberia its range overlaps with the more xeromorphic and xerophilous *P. botryoides*, which occupies more arid areas in the same territory, and in Western Siberia is grows only within the Altai-Sayan Mountain country. In the mountains of South Siberia it also neighbors with *P. argunensis*, which range is narrower, and in the East it overlaps with the predominantly Far Eastern *P. ochotensis*. In the mountains of Middle Asia, *P. transbaicalica* is replaced by *P. relaxa*, which probably resulted from long-standing hybridization of *P. transbaicalica* and *P. litvinoviana* (Ovchinnikov and Chukavina 1957), belonging to the aggregate of *P. glauca* Vahl, or other species of this aggregate. Presumably hybridogenic (involving *P. sphondylodes* Trin.) *P. ochotensis* has a disjunctive range with enclaves on Sakhalin and the Japanese Islands. Thus, *P. relaxa* has a completely isolated range, and the ranges of *P. argunensis*, *P. botryoides* and *P. ochotensis* are not in contact with this species. The ranges of the other species under consideration are overlapping to a greater or lesser extent.

For a preliminary study of the ecological and climatic niches of *P. botryoides*, *P. transbaicalica*, *P. argunensis*, *P. ochotensis* and *P. relaxa* and to reveal possible diversification of their niches, ecological-climatic profiles were constructed. They are represented by histograms of frequencies of values of bioclimatic variables characterizing the points where the species were registered (Fig. 2).

The obtained histograms were asymmetric or sometimes even bimodal. Bimodal graphs are especially characteristic for variables characterizing the temperature regime. This was especially pronounced in the plots of *P. argunensis* and *P. ochotensis*, which are known to have disjunctive ranges. The most of variables, which describe the precipitation levels are sharply asymmetric, with the maximum shifted to the left, drier part. Visual comparison of climatic profiles demonstrates the interspecific differences in many predictors. The most significant differences were observed for Bio 9, Bio 7, Bio 11. All of them characterize temperature characters.

Comparison of optimal values of variables in different species (Fig. 2) showed that, despite some similarity of graphs in configuration, both limiting and optimal values in different species, may be similar in some cases and show differences in other cases. Thus, in terms of Bio 1 (mean annual temperature), *P. transbaicalica* differs significantly from all analyzed species: one of the peaks lies within -11.4 – -5.7° C, while the limits within the other species are from -5 to 0.7° C; in terms of Bio 7 (temperature annual range), *P. botryoides* and *P. argunensis* showed almost identical values. These two species also demonstrated the similarity in Bio 3, Bio 10, Bio 13, and other predictors. Bio 16 and Bio 18 plots (precipitation of the wettest and driest quarter) were similar to each other both in configuration and in the value of limiting and optimal values as well. It was demonstrated within *P. transbaicalica*, *P. botryoides*, and *P. argunensis* the most clearly.

Significant similarities in configuration and limiting values are also observed for the Bio 14, Bio 17 and Bio 19 histograms, reflecting the precipitation of the driest month, the driest quarter, and the coldest quarter, respectively. The similarities between the histograms of Bio 14 and Bio 17 are easily explainable as they describe the values of the same indicators for different time periods, while the similarities of Bio 17 and Bio 19 can be explained by the high correlation between season and precipitation.

Thus, in general, the analysis did not reveal the undoubted ecological diversification among species: the species similar in some ecological and climatic characteristics may differ significantly in others. Nevertheless the histograms showed that all species responded differently to climatic factors, which confirms the data of Tsatsenkin, (1967) and Korolyuk with colleagues (Korolyuk et al. 2005, 2006). This suggests the diversification of ecological-climatic niches of the studied species.

For a more detailed study of the relative position of the virtual ecological-climatic niches a PCA was carried out (Fig. 3). The first two components reflect almost 70% of the variability.

PCA and factor analysis allow to evaluate the role of each variable in the formation of factors (principal component). The values of factors (>0.7) determining the loadings on the principal components are given in Table 1. At the same time, PC I is determined mainly by variables of temperature regime: the minimum temperature of the coldest month (Bio 6), seasonality of temperature (Bio 4) and average annual amplitude of temperature fluctuation (Bio 7), while II PC characterizes precipitation (Table 1).

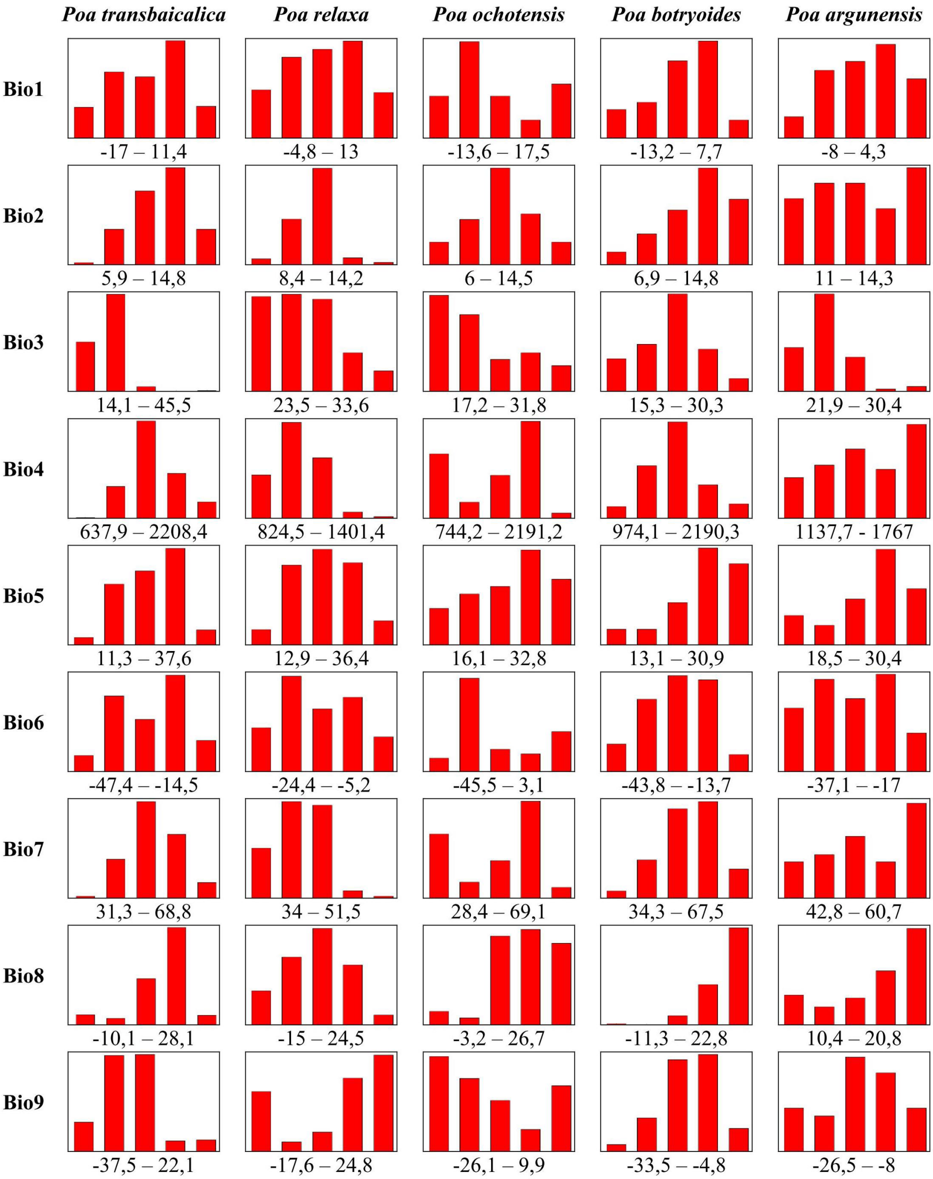

Figure 2. Variability of Bio1-19 climatic characteristics observed in the area of distribution of *Poa versicolor* aggregate in Asia (*P. relaxa*, *P. transbaicalica*, *P. ochotensis*, *P. botryoides*, *P. argunensis*). Abscissa axis – factor intensity, ordinate axis – observed frequencies of occurrence. Continuing on the next page.

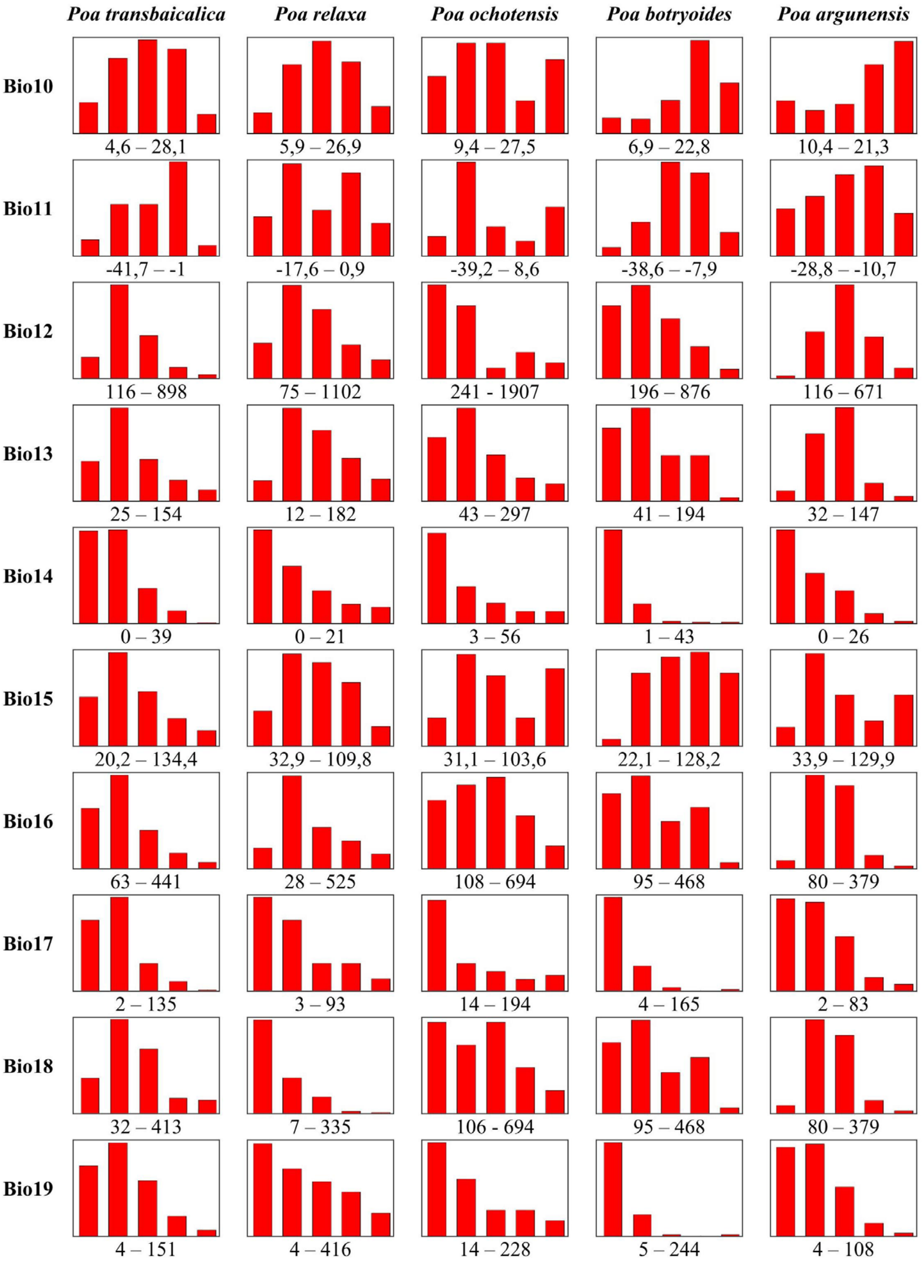

Figure 2. Continuing from the previous page.

According to PCA (Fig. 3) the clusters of *P. botryoides* and *P. argunensis* are almost completely included in the area of *P. transbaicalica*, although the higher xeromorphic level of *P. botryoides* is known and morphologically confirmed. Field observations also confirm greater xerophilicity of this species. Expected heterogeneity of *P. argunensis*, which has a disjunctive range, was confirmed as well. The analysis also revealed the heterogeneity of the ecological-climatic niche of *P. ochotensis*. Its habitats from Sakhalin Island and the Japanese Islands formed a small, separate group in the lower right corner of the graph, differing from the main core both along PCI, which is determined mainly by temperature regime and along PCII, which characterizes precipitation (Table 1). The remaining points of *P. ochotensis* are widely scattered throughout the graph and overlap with *P. transbaicalica*. The obtained plot confirms the isolation of *P. relaxa*, the divergence to be mainly along the PCI, which caused by temperature regime as a whole (Table 1).

Table 1. Values of factors (>0.7) determining loads on main components (Quartimax raw function)

Factor I		**Factor II**	
Bio 1	0.8014	Bio 8	0.7217
Bio 4	-0.9376	Bio 13	0.7705
Bio 6	0.9530	Bio 16	0.7326
Bio 7	-0.9394	Bio 18	0.8809
Bio 9	0.9109		
Bio 11	0.9315		
Bio 19	0.8017		

To display the possible implementation of the virtual ecological-climatic niches of *P. versicolor* aggregate in space the models of territories with suitable climate were constructed using MaxEnt algorithm (Fig. 4). The resulting models in general indicate areas suitable for the growth of species, derived from climatic factors involved in analysis. These maps detect the suitable areas only, recognize the possible distribution of species in accordance with climate. The competitive capabilities and biological features of species which provide their successful expansion and anthropogenic impact are not taken into consideration.

A comparison of the suitable territories, obtained from MaxEnt, once again confirmed the difference in the climatic requirements of species, established by comparing ecological niches.

The AUC scores of almost all models exceed 0.9, which corresponds to the excellent predictive capabilities of the models (Araujo et al. 2005; Scheldeman van Zonneveld 2010). The exceptions were the models for *P. transbaicalica*. Its AUC values were in the range of 0.8–0.9, which corresponds to a good assessment, as well as the AUC value of the testing model for *P. ochotensis*, the value of which was 0.768 (an acceptable value).

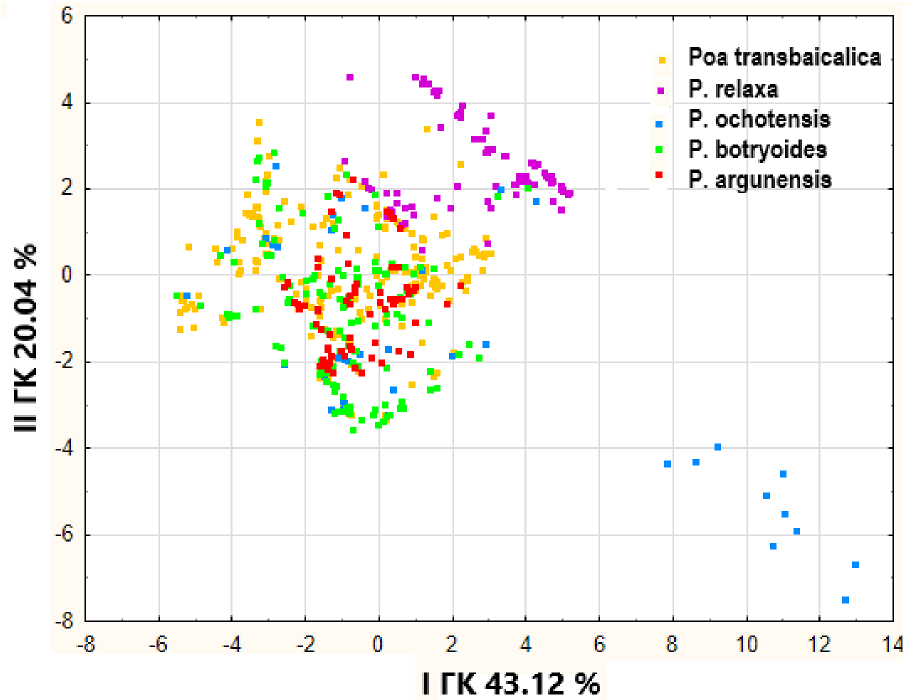

Figure 3. Projections of the ecological – climatic niches of *Poa transbaicalica*, *P. relaxa*, *P. ochotensis*, *P. botryoides* and *P. argunensis* in axes I and II of PC based on 19 climatic factors (factor values in the text).

Permutation analysis revealed the predominant role of Bio1 (mean temperature) almost within all models, but in Pacific species *P. ochotensis*. Bio7 (temperature annual range) is significant for *P. relaxa*, *P. transbaicalica* and *P. ochotensis*, but in the models of the most xeromorphic *P. botrioides* and *P. argunensis* this variable gives way to Bio14, which concerns the precipitation of the driest quarter. The Table 2 shows, that the species under consideration has different sets of climatic variables, which do the most significant contribution in the model of niche and explaining the geographical distribution.

The preliminary analysis allowed to expect that the ecological-climatic niches of *P. botryoides* and *P. argunensis* lie entirely within the niche of *P. transbaicalica*, and overlap with each other. In other words, the niches of these species might have not diverged despite morphological diversification. Nevertheless, the models of suitable territories, obtained for other species of aggregate *P. versicolor*, differ from each other quite significantly, and it may be the evidence of niches diversification as well.

In order to confirm or reject the hypothesis of niche conservation within aggregate *P. versicolor*, and to find out whether the niches of *P. botryoides* and *P. argunensis* differ from each other, the niches of all species under consideration were compared.

Identity (I-test) and niche similarity (background, or B-test) tests were carried out to verify preliminary results obtained in the PC analysis. In order to assess whether the niches of species pairs differed, an ecological-climatic model identity test (I test) was first performed in the ENMTools software package (Warren et al. 2021), comparing *P. relaxa*, *P. transbaicalica*, *P. ochotensis*, *P. botryoides* and *P. argunensis* in pairs. Niche overlap values derived from actual occurrence data were compared with values derived from empirical data (Table 3).

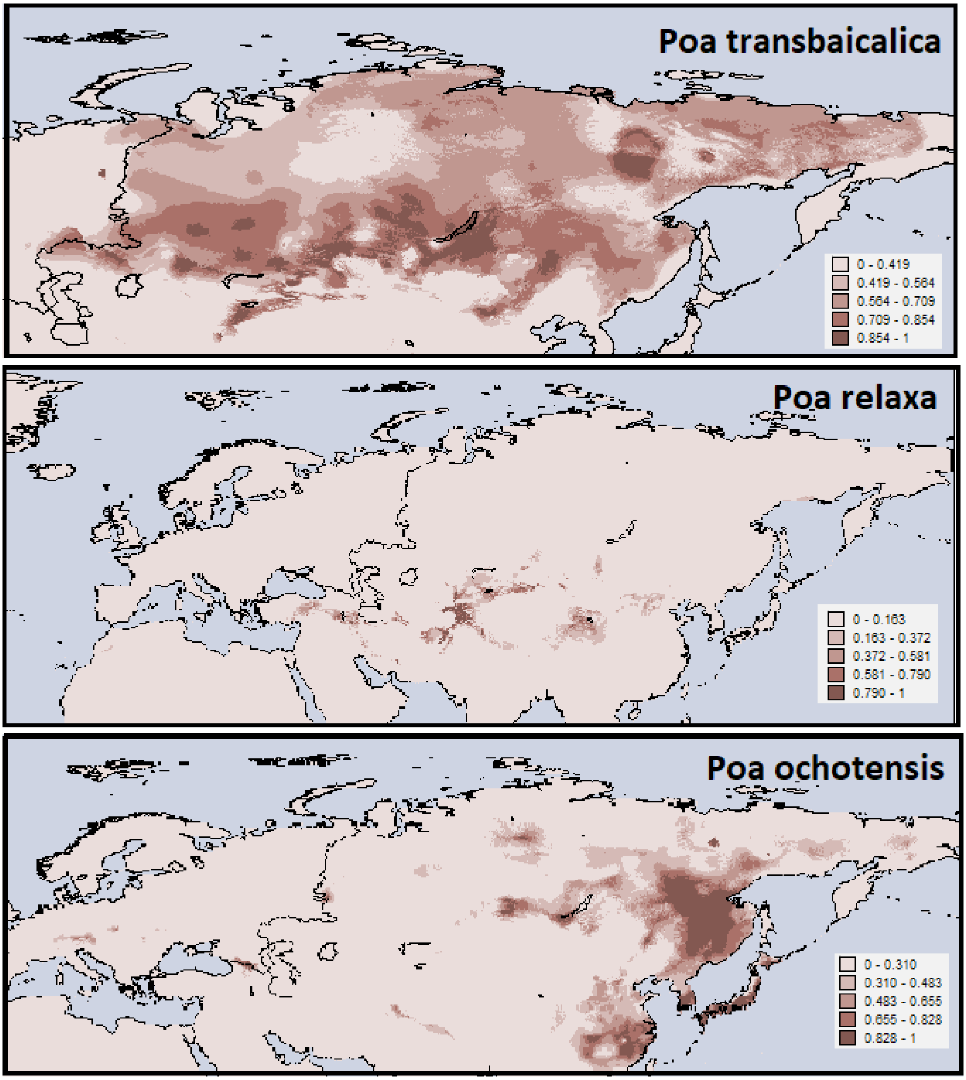

Figure 4. Geographical projections of the habitat suitable models, constructed with the use of the MaxEnt algorithm on the basis of the BIO1, BIO7, BIO8, BIO12, BIO14 and BIO19 climatic variables of the modern climate. Continuing on the next page.

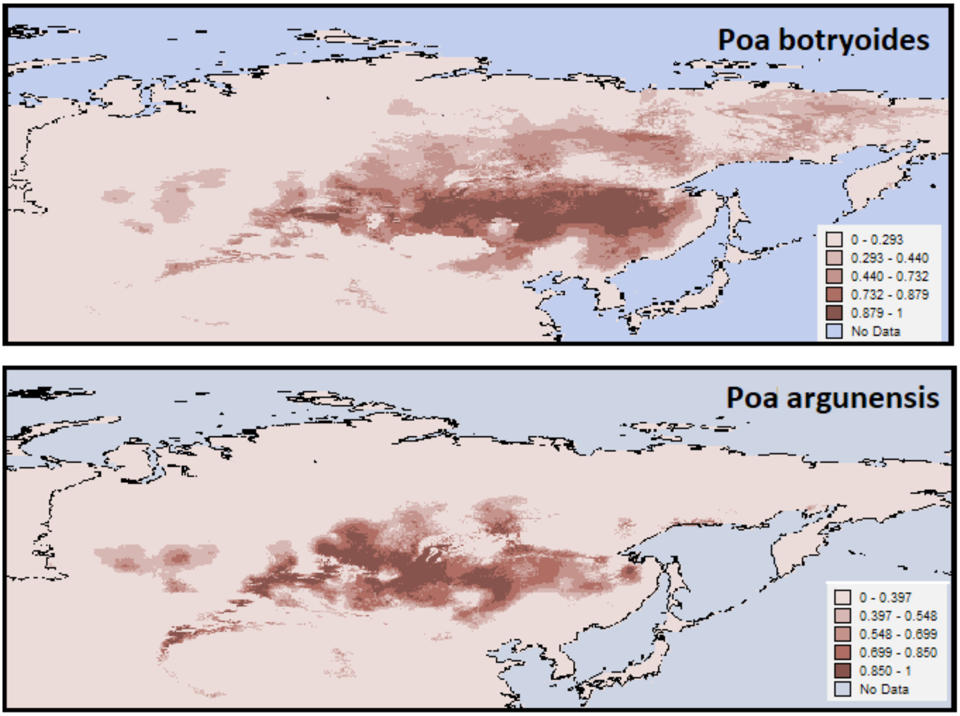

Figure 4. Continuing from the previous page.

Table 2. Main parameters of ecological-climatic niches models of *Poa versicolor* aggregate constructed with the use of the MaxEnt algorithm

	P. relaxa **n = 101**	***P. transbaicalica*** **n = 241**	***P. ochotensis*** **n = 48**	***P. botryoides*** **n = 158**	***P. argunensis*** **n = 77**
n tr/n tst	76/25	181/60	36/12	118/40	58/19
AUCtr/ AUCtst	0.987/0.956	0.866/0.869	0.922/0.768	0.932/0.918	0.958/0.950
Standart deviation	0.018	0.016	0.070	0.015	0.015
Logistic trethshold	0.284	0.419	0.252	0.293	0.397
Assessment (Permutation)	Bio1 = 55.5 Bio7 = 17.2 Bio14 = 15.3 Bio12 = 5.7 Bio8 = 64.6 Bio19 = 1.7	Bio7 = 42.2 Bio1 = 34.2 Bio12 = 8.2 Bio14 = 7.5 Bio19 = 5.1 Bio8 = 2.8	Bio7 = 41.8 Bio12 = 37.9 Bio14 = 10.9 Bio1 = 4.5 Bio8 = 3.2 Bio19 = 1.7	Bio1 = 43 Bio14 = 26.8 Bio7 = 12.6 Bio19 = 2.7 Bio12 = 6 Bio8 = 8.8	Bio1 = 60.3 Bio14 = 15.9 Bio19 = 8.5 Bio7 = 7.6 Bio12 = 7 Bio8 = 0.7

Notes: n tr – size of training sampling, n tst – size of testning sampling; AUCtr is the AUC of training sampling, AUCtst is the AUC testing sampling.

I-tests showed, that only the niches of *P. transbaicalica – P. botryoides*, and *P. argunensis – P. botryoides* were identical or equivalent. Indeed, only between these species the empirical values exceeded the critical values (Table 3) with p values = 0.2376 and 0.0594, respectively. Moreover, the difference between the critical and empirical values of *P. argunensis – P. botryoides* is extremely small. In the other pairs of species, the critical values were higher than the empirical values, indicating niche divergence (p = 0.0099).

Table 3. Identity test. Matrix of empirical and critical values of niche overlap between species of aggregate *Poa versicolor* (I metric values are above diagonal, D metric values are below diagonal)

Species	*P. transbaicalica*	*P. relaxa*	*P. ochotensis*	*P. botryoides*	*P. argunensis*
P. transbaicalica	empirical critical	0.5428 0.8960	0.8050 0.8994	**0.8662** **0.8055**	0.6880 0.8607
P. relaxa	0.3065 0.7275	empirical critical	0.5418 0.8049	0.4770 0.8494	0.4261 0.7715
P. ochotensis	0.5515 0.6820	0.2928 0.5467	empirical critical	0.8674 0.8971	0.6267 0.8918
P. botryoides	**0.6249** **0.5328**	0.2524 0.6173	0.6067 0.6605	empirical critical	0.7665 0.7846
P. argunensis	0.3927 0.5946	0.2322 0.4984	0.3537 0.6690	**0.5393** **0.5386**	empirical critical

To ensure that these niche diversification is not caused by different availability of habitat conditions for the compared species, the similarity tests, which take into account the environmental conditions of both species, were carried out for all pairs of studied species.

The background similarity tests showed greater niche conservation between the aggregate species than the identity test did (Table 4). According to this test, the null hypothesis of niche similarity could be rejected only in the pair *P. ochotensis – P. relaxa*, only in one direction and only when using I-metrics, however, the difference cannot be recognized as statistically reliable, because p=0.4654 (Table 5), which is much higher than the threshold value of 0.05 accepted in biology. Thus, at this stage of evolution, niche conservatism is kept within all studied species of the aggregate.

Table 4. Background similarity test. Matrix of empirical values of niche overlap between species of *Poa versicolor* aggregate – forward and reverse analyses (empirical value on top of cells, critical value on bottom)

Forward analyses			**Reverse analyses**		
Pairs of species	D	I	Pairs of species	D	I
P. transbaicalica	**0.2866**	**0.5243**	*P. relaxa*	**0.2866**	**0.5243**
P. relaxa	**0.1865**	**0.4207**	*P. transbaicalica*	**0.2262**	**0.4313**

Forward analyses			**Reverse analyses**		
Pairs of species	D	I	Pairs of species	D	I
P. transbaicalica	**0.5073**	**0.7717**	*P. ochotensis*	**0.5073**	**0.7717**
R. ochotensis	**0.4627**	**0.7460**	*P. transbaicalica*	**0.4501**	**0.7196**
P. transbaicalica	**0.5731**	**0.8154**	*P. botryoides*	**0.5790**	**0.8258**
P. botryoides	**0.5512**	**0.7982**	*P. transbaicalica*	**0.5029**	**0.7660**
P. transbaicalica	**0.3737**	**0.6458**	*P. argunensis*	**0.3737**	**0.6458**
P. argunensis	**0.3400**	**0.6229**	*P. transbaicalica*	**0.2919**	**0.5594**
P. relaxa	**0.2810**	**0.5201**	*P. ochotensis*	**0.2815**	0.5223
P. ochotensis	**0.2504**	**0.4876**	*P. relaxa*	**0.2773**	0.5698
P. relaxa	**0.2550**	**0.4662**	*P. botryoides*	**0.2550**	**0.4662**
P. botryoides	**0.1960**	**0.3985**	*P. relaxa*	**0.1621**	**0.3658**
P. relaxa	**0.1813**	**0.3609**	*P. argunensis*	**0.1856**	**0.3709**
P. argunensis	**0.1378**	**0.3101**	*P. relaxa*	**0.1222**	**0.2831**
P. ochotensis	**0.5697**	**0.8385**	*P. botryoides*	**0.5652**	**0.8356**
P. botryoides	**0.4857**	**0.7487**	*P. ochotensis*	**0.4844**	**0.7744**
P. ochotensis	**0.3523**	**0.6187**	*P. argunensis*	**0.3540**	**0.6219**
P. argunensis	**0.3261**	**0.5851**	*P. ochotensis*	**0.2898**	**0.5436**
P. botryoides	**0.5537**	**0.7868**	*P. argunensis*	**0.5537**	**0.7868**
P. argunensis	**0.3989**	**0.6593**	*P. botryoides*	**0.4264**	**0.6881**

Table 5. Matrix of p-values of niche overlap analysis between species of *Poa versicolor* aggregate (above the diagonal – forward analysis, below – reverse analysis)

Species	*P. transbaicalica*	*P. relaxa*	*P. ochotensis*	*P. botryoides*	*P. argunensis*
P. transbaicalica	1	0.1188	0.2871	0.1386	0.1782
P. relaxa	**0.0396**	1	0.4654	0.2277	0.3762
P. ochotensis	0.4555	0.0990	1	0.2574	0.2376
P. botryoides	0.0891	0.0990	0.3960	1	**0.0297**
P. argunensis	0.1782	0.1782	0.4555	0.1683	1

Discussion

Since the evolution is an adaptive process (Yablokov and Yusufov 1989), ecological aspects of evolution received considerable attention (Simpson, 1961; Takhtajian, 1970; Eldredge and Gould, 1972; Rasnitsyn 1983, 1987; Severtsov 1988, 2008; Grant, 1991; Rautian and Zherikhin 1997). Quantitative ecology and biogeography began to develop especially intensively with the advent of GIS-technologies, and will continue to do so in the coming decades (Peterson 2011).

A.S. Severtsov (2008), studying evolutionary processes at the ecological niche level, made hypothesis that the cause of evolutionary stasis (a state in which species can remain phenotypically unchanged for hundreds of thousands of years) was the counterbalance of opposing vectors of directional selection and intraspecific diversity, including balanced genetic polymorphism, ecological races and subspecies. When the counterbalance of existing vectors of selection is disturbed or when a new, unbalanced vector of directional selection emerge, the state of stasis is replaced by progressive evolution. Fundamental niche represents the limits of adaptiveness in all characters, and the realized niche is limited not so much by competition as by the insufficiency of resources for the use of excessive morpho-functional capabilities. On this basis, A.S. Severtsov suggested that the ecological niche is more conservative than the range. The range can expand due to the reserves of the fundamental niche, while the niche changes itself very slowly. At the phenotypic level, the stasis is the absence of the generation of new adaptations, but at the genetic level it is the improvement of the genetic support of already existing adaptations. Any adaptation, as long as it retains its adaptive value, prevents progressive evolution. Thus, the broader the fundamental niche is, the more likely the long-term state. Progressive evolution, which results in intraspecific differentiation and speciation, begins when there is an imbalance of selection vectors affecting the population (Severtsov 2008).

With the development of niche modeling and comparison technologies, ecologists have been able to test existing hypotheses with alternative methods and to propose new ones. Ecological niche models, which are created by combining species distribution data with layers from environmental databases, are increasingly being used to answer fundamental questions about niche evolution, speciation, and the accumulation of ecological diversity in clades. Many papers have been devoted to conceptual issues of niche modeling and the study of niche evolution (Guisan and Zimmerman 2000; Soberon 2007; Brown and Carnaval 2019; Silva et al. 2020; Warren et al. 2021, etc.).

The problem of ecological niche conservatism, is prominent in evolutionary ecology, it is of great importance to systematics as well. Now the ecological niche dynamics over time no longer in doubt (Soberon and Peterson 2005; Holt 2009; Peterson et al. 2011; Sexton et al. 2017; Saupe et al. 2018, etc.), however, the problem is how long it can persist unchanged in species. Ecological niche diversification at temporal scales is significant for research of microevolutionary processes and speciation.

Peterson (2011), basing on a large number of publications devoted to niche conservatism concludes that, as a rule, relatively recent geologic-scale and short-term events such as invasive species expansion and range changes during Pleistocene climate change did not lead to changes or diversification of ecological niches, but that niche conservatism was disrupted over geologically long time scales. Analyzing the literature on studies of niche conservatism, Peterson et al. (1999, 2011) suggested the dominant pattern of minimal changes in the parameters of the ecological niche during short or medium time intervals.

Eventually, it was found that speciation is rarely accompanied by significant changes in ecological niche (Peterson et al. 1999, 2011; Zhu et al. 2013; Namyatova, 2020; Vaissi and Rezaei 2022, etc.). Meanwhile, examining pairs of bird, mammal, and butterfly species in southern Mexico, Peterson et al. (1999) found that speciation takes place in geographic rather than ecological parameters, and ecological divergence happen later than geographic divergence. Thus, the studies by many experts using geographic information technologies and statistical calculations have confirmed Severtsov's hypothesis of niche dynamics (Peterson et al. 1999, 2011; Peterson 2011; Thompson et al. 2011; Hiller et al. 2019).

A comparative study of the ecological-climatic niches of five morphologically different species of the *P. versicolor* aggregate showed that the niches only of the most similar *P. transbaicalica – P. botryoides*, and *P. argunensis – P. botryoides* were identical or equivalent. All other pair of species were not identical and confirmed the expected diversification, revealed by previous research. Thus, taking into account geographical and ecological isolation of *P. relaxa* from other species of the aggregate, the differences of its ecological-climatic niche from the niches of all other species are also explainable. The range of the Far Eastern *P. ochotensis* partially overlaps with *P. botryoides*, however, the I-test demonstrated the isolation of its niche. It is interesting, that the ranges of *P. botryoides – P. argunensis – P. transbaicalica* overlap with each other, but the ecological-climatic niche of *P. argunensis* is not identical to that of *P. transbaicalica*. Nevertheless, the studies of possible diversification using the background test, which is more suitable for testing evolutionary and biogeographic hypotheses (Peterson 2011) and takes into account environmental features, revealed niche conservatism at the aggregate level. The ecological-climatic niches of the studied species within the *P. versicolor* aggregate proved to be similar, but not equivalent in all species. Thus, our data show that partial or complete geographic divergence and morphological diversification of species is not yet accompanied by diversification of the ecological-climatic niche.

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