

Structure of Ecologo-Climatic Niches of *Poa palustris* L. and *P. nemoralis* L. (Poaceae) in Asian Russia

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Abstract—In addition to a specific morphotype, each species has a unique ecologo-climatic niche and a geographical area. The study of ecologo-climatic and geographical divergence may significantly contribute to the comprehension of species genesis and amount. The aim of this work is to compare ecologo-climatic niches of *Poa palustris* L., *P. nemoralis* L., and populations combining the features of both species (assigned in this work to the hybridogenic complex of *P. intricata* Wien), as well as reveal their identity. As a result of these researches, the areas of the both species were verified. The ecologo-climatic niches were determined with the use of GIS technologies and on the basis of their coordinates. Then potential areas of species—the regions where climatic conditions are favorable for their growth—were determined on the basis of six independent bioclimatic variables. A comparison of the ecologo-climatic niches calculated by MaxEnt software has shown that their distinctions are statistically significant.

Keywords: ecologo-climatic modeling, MaxEnt, *Poa*, distribution

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INTRODUCTION

The climatic profile of a species determined on the basis of climate parameters of biological importance is often called an ecological niche, but this is not really correct. This concept was first introduced by J. Grinnell (1917), who determined the ecological niche as a place occupied by a species in biocenosis, including the combination of its biocenotic relations and demands for environmental factors. The concept of ecological niche was then elaborated in a number of works (Elton, 1927; Hutchinson, 1957; MacArthur, 1968; Dzhiller, 1988). At the present time, there is more than one interpretation of this term (Ozerskii, 2011). The ecological niche may be determined as a sum of factors at which the species exists, with the predominating role of its place in the food chain. It may be also described as a combination of all factors of the environment at which the species may exist in nature. Preference is now given to the model by J.E. Hutchinson, according to which the ecological niche is an n-dimensional volume on the axes of which ecologic factors are given. The conditions under which the species can exist are characterized by a particular range of each factor. If the limit points of the ranges of each factor are projected, we will obtain an n-dimensional figure, where n is the number of ecological factors significant for the species. According to Hutchinson, the ecological niche may be fundamental (determined by the combination of conditions and resources, which enables the species to main-

tain the viable population) and realized (its properties are determined by competing species). It is pointed out that the factors are independent, and the reaction to one of them does not depend on the effect of another factor (Grant, 1980).

According to conventional notions, an ecological niche should be determined with the consideration of factors such as humidity, illumination, and temperature regime at sites of plant growth, and it is calculated by ecological scales (Ramenskii et al, 1956; Tsatsenkin, 1967; Seledets and Probatova, 2007). In addition, an indirect effect of micro- and mesofeatures of topography, shadowing, groundwater level, and granulometric composition of soil is considered. This approach requires very detailed instrumental research or the use of laborious bioindication methods. At the same time, GIS technologies enable one not only to determine the range of each biologically important climatic variable typical for the taxon, but also to reveal the areas with climatic parameters favorable for its growth. These data are obtained with the use of precise geographical coordinates of known sampling sites of plants and of 19 biologically important ecologo-climatic parameters received for the entire land surface by the extrapolation of data of meteorological stations from 1950 to 2000, which are freely available in the Internet (Hijmans et al., 2004, online). The determined niches only reflect the general tendencies in the change of the main ecological factors and do not take

the features of particular habitats into account. This is especially pronounced in mountain regions, where humidification and temperature conditions may strongly differ at a distance of several meters. Thus, the niche determined by the described GIS technologies should be called ecologo-climatic (and not ecologic).

The model of distribution pattern of a species constructed on the basis of the revealed ecologo-climatic niche reflects only the probability distribution of climatic conditions which are favorable for the growth of particular species. Nevertheless, the successful introduction of a species into plant communities and its development there considerably depends on other factors: competitive ability and biological features of the species and interrelations between the components of the community. This model corresponds to a potential area of a species according to T.A. Rabotnov (1983) and determines the area where climatic conditions are favorable for species growth. This notion is similar to the concept of ecological area elaborated by V.P. Seledets and N.S. Probatova (Seledets and Probatova, 2007). However, contrary to the ecological area, which provides a more detailed characteristic of the environmental conditions, the identification of a potential area does not require a detailed research and data on species location on ecological scales and may be determined by GIS technologies.

Biologically significant climatic factors strongly determine the modern shapes of areas and their change over the geological periods. Therefore, determining ecologo-climatic niches of taxa is an important component of ecological and biogeographical researches.

Poa palustris L. and *P. nemoralis* L. are the best known and most widespread mesomorphic species of meadow grass (*Poa* L.) (the *Stenopoa* Dum section). These species pronouncedly differ by two qualitative features: the former has a naked rachilla and long (over 2 mm) ligule; the latter is characterized by tomentose rachilla and short (no longer than 1 mm) ligule. It is known that, in addition to morphological distinctions, *P. palustris* and *P. nemoralis* differ in ecological conditions: the former prefers open habitats, while the latter usually occupies more or less shadowed areas. The shift of area boundaries of *P. palustris* and *P. nemoralis* in the Pleistocene Period provided great opportunities for their hybridization (Tsvelev, 1974). As a result, a number of forms which bear features of the both species in different combinations appeared in northeastern Europe and Siberia. These presumably hybridogenic populations are now widespread in Siberia (Olonova, 2001; Olonova et al., 2016). At the present time, it is proposed to assign them to a hybridogenic unit: aggr. *P. intricata* (Olonova, 2010).

Modern areas of *P. palustris* and *P. nemoralis* are close, but do not coincide: the former is a boreal species and the latter is a nemoral one. Both of them play a significant role in the structure of plant communi-

ties; therefore, the study of their ecologo-climatic optimums is not only of scientific, but also of practical interest. The overlap of areas does not indicate a similarity of ecological niches. In connection with this, it should be learned whether the ecological niches of the studied species differ and, if so, the range of the difference.

It is known that the ecological niche of hybrids is usually wider than that of parent species (Clausen and Hiesey, 1958; Tsvelev, 1972), which was experimentally confirmed by the example of meadow grass (Hiesey and Nobs, 1970, 1982). In connection with this, it is interesting to analyze the ecologo-climatic niche of hybridogenic aggr. *P. intricata*.

The aim of this work was to study ecologo-climatic niches of *P. palustris*, *P. nemoralis*, and hybridogenic aggr. *P. intricata* in Asian Russia.

MATERIALS AND METHODS

Herbarium collections (ALTB, KUZ, IRKU, LE, MAG, MHA, MW, NS, NSK, SASY, TK, UUH, and VLA) were used for determining the location and mapping of areas of *P. palustris*, *P. nemoralis*, and *P. intricata* in Asian Russia. Some sites were taken from the Arctic Flora of the USSR (Tsvelev, 1964), Flora of Central Siberia (Peshkova, 1979), Flora of Siberia (Olonova, 1990), and the many-volume summary *Sosudistye rasteniya Sovetskogo Dal'nego Vostoka* (Probatova, 1985). For modeling of their potential distribution in Asian Russia, we took into consideration 290 sites of *P. palustris*, 229 sites of *P. nemoralis*, and 97 sites of *P. intricata*, which obviously completely characterize the climatic niches of these species. Climate data¹ with a spatial resolution of 2.5 arc minutes obtained by the extrapolation of data of meteorological stations (over the 1950–2000 period) were taken from the WORDCLIM database (Hijmans et al., 2004, online). For the identification of ecologo-climatic niche and visualization of bioclimatic parameters of the species, the BIOCLIM algorithm of the Diva-GIS software (Hijmans et al., 2005) was used (Nix, 1986). The models of distribution patterns of the species were constructed with the use of MaxEnt software (Phillips et al., 2006; Phillips and Dudik, 2008). This method is now one of the most efficient in mod-

¹ BIO1, Annual mean temperature; BIO2, Mean diurnal range (monthly average); BIO3, Isothermality (BIO1/BIO7) × 100; BIO4, Temperature Seasonality (Coefficient of Variation); BIO5, Max Temperature of Warmest Period; BIO6, Min Temperature of Coldest Period; BIO7, Temperature Annual Range (BIO5–BIO6); BIO8, Mean Temperature of Wettest Quarter; BIO9, Mean Temperature of Driest Quarter; BIO10, Mean Temperature of Warmest Quarter; BIO11, Mean Temperature of Coldest Quarter; BIO12, Annual Precipitation; BIO13, Precipitation of Wettest Period; BIO14, Precipitation of Driest Period; BIO15, Precipitation Seasonality (Coefficient of Variation); BIO16, Precipitation of Wettest Quarter; BIO17, Precipitation of Driest Quarter; BIO18, Precipitation of Warmest Quarter; and BIO19, Precipitation of Coldest Quarter.

eling the distribution pattern of species on the basis of data on its presence (Anderson et al., 2003; Elith et al., 2006; Franklin, 2009). The models constructed as a result of the analysis were projected on the maps compiled with the use of the ArcGIS 10 software (ESRI, 2012). The prognostic possibility of each model was evaluated by the Area Under Curve parameter (Phillips et al., 2011, online).

The role of each variable upon modeling may be assessed if the models are constructed on the basis of slightly interdependent variables to avoid a negative impact on the result (Brown, 2014a, 2014b). The test for the independence of variables made it possible to select eight biologically significant climatic variables (BIO1, BIO2, BIO5, BIO7, BIO8, BIO12, and BIO15); the correlation coefficient between them does not exceed 0.7 and models have been constructed on their basis. The effect of each variable on the resulting model has been assessed by three independent methods: the percentage contribution, permutation, and Jackknife tests (Scheldeman and van Zonneveld, 2010).

To check the hypothesis of the identity of niches, the models were constructed on the basis of all 19 variables.

The test for identity of niches (*I*-test) conducted in ENMTools software (Warren et al., 2008, 2011) makes it possible to compare ecological niches of taxa with overlapped areas and reveal a statistically significant difference between models of ecologo-climatic niches. This test requires their comparative analysis with the use of the measures of standardized Hellinger distance (*I*) and the Schoener index (*D*) (Warren et al., 2008). The test for identity was performed between all studied taxa in ten replications (ten replicas).

RESULTS AND DISCUSSION

Each species is adapted to a particular range of ecologo-climatic conditions. It may be assessed with respect to each parameter and compared for different species with the use of the BIOCLIM software, which visualizes the ecologo-climatic niche occupied by the species as histograms. They reflect frequencies of various climatic parameters revealed for the species in the given area (Fig. 1). The intensity of the factors is given on the abscissa axis and frequencies of occurrence are shown on the axis of ordinates.

The analysis of the histograms of climatic variables and the comparison of data obtained for *P. palustris*, *P. nemoralis*, and *P. intricata* has shown that the maximums of all three species approximately coincide, though their distribution sometimes differs from the normal. The distribution of *P. nemoralis* is characterized by two-peak curves for nine variables, reflecting both temperature characteristics (BIO2, BIO4, BIO5, BIO7, BIO8, and BIO10) and precipitations (BIO13, BIO16, and BIO18). The two peaks are pronounced to different rates, from obvious (BIO2, BIO13, BIO16, and BIO18) to poor (BIO4, BIO6, BIO7, and BIO10).

It is seen that these two peaks are higher for the variables of precipitations and are more slightly pronounced for temperature parameters. This is obviously explained by the very nonuniform distribution of climatic conditions in the studied area: humidification sharply increases on the Pacific coast, and diagrams of the most parameters, describing humidification, are sharply asymmetric. Two peaks of diagrams of *P. nemoralis* are obviously explained by the fact that specific features of the modern climate and historical reasons have resulted in the division of the area of this species in Asian Russia into two slightly isolated parts: Siberian and Far Eastern. Each of them is characterized by particular distribution curve.

The two-dimensional diagrams of distribution of species with respect to the longitude are pronouncedly specified into two groups along the longitudinal gradient independently of the type of climatic variables (Fig. 2). The line of discontinuity passes near 110°–120° east longitude at the conventional boundary between Siberia and the Far East. In the southern part of it, the monsoon climate determines the distribution of precipitations. The specific land line in the east also changes the cloud shape; however it can be seen on all the diagrams that *P. palustris* and *P. intricata* tend to the continental part (though *P. palustris* successfully competes with *P. nemoralis* in the east), while the cloud of *P. nemoralis* is pronouncedly displaced to the east for particular reasons. It is apparent that this discontinuity, which is more pronounced for *P. nemoralis*, is reflected on the plots as a two-peak curve. More comprehensive researches of this species with the use of molecular-genetic methods will probably answer the question of its possible divergence into continental and pacific races. It is seen that representatives of hybridogenic *P. intricata* are mainly allocated to continental Siberia. In addition, the diagrams show that ecologo-climatic amplitudes of hybridogenic *P. intricata* are larger than those of the supposed parental species.

The diagrams reflect the differences in climatic demands of the studied species. These regularities are supplemented by models of potential distribution of the species based on bioclimatic characteristics. Predictive maps of the distribution pattern of *P. palustris*, *P. nemoralis*, and *P. intricata* were compiled for a comparison of their climatic niches in Asian Russia (Fig. 3). These maps reflect the potential dispersal of species determined by climate. The competitive capabilities and biological features of species which provide their successful expansion and anthropogenic impact are not taken into consideration.

The predictive maps compiled by the MaxEnt algorithm in general correspond to the distribution of the studied species in Asian Russia. With consideration for the threshold of 10 percentiles and upon the transformation of all subthreshold values to zero (Table 1), the resulting model predicts low probabilities of distribution of all species over most of Eastern Siberia, which

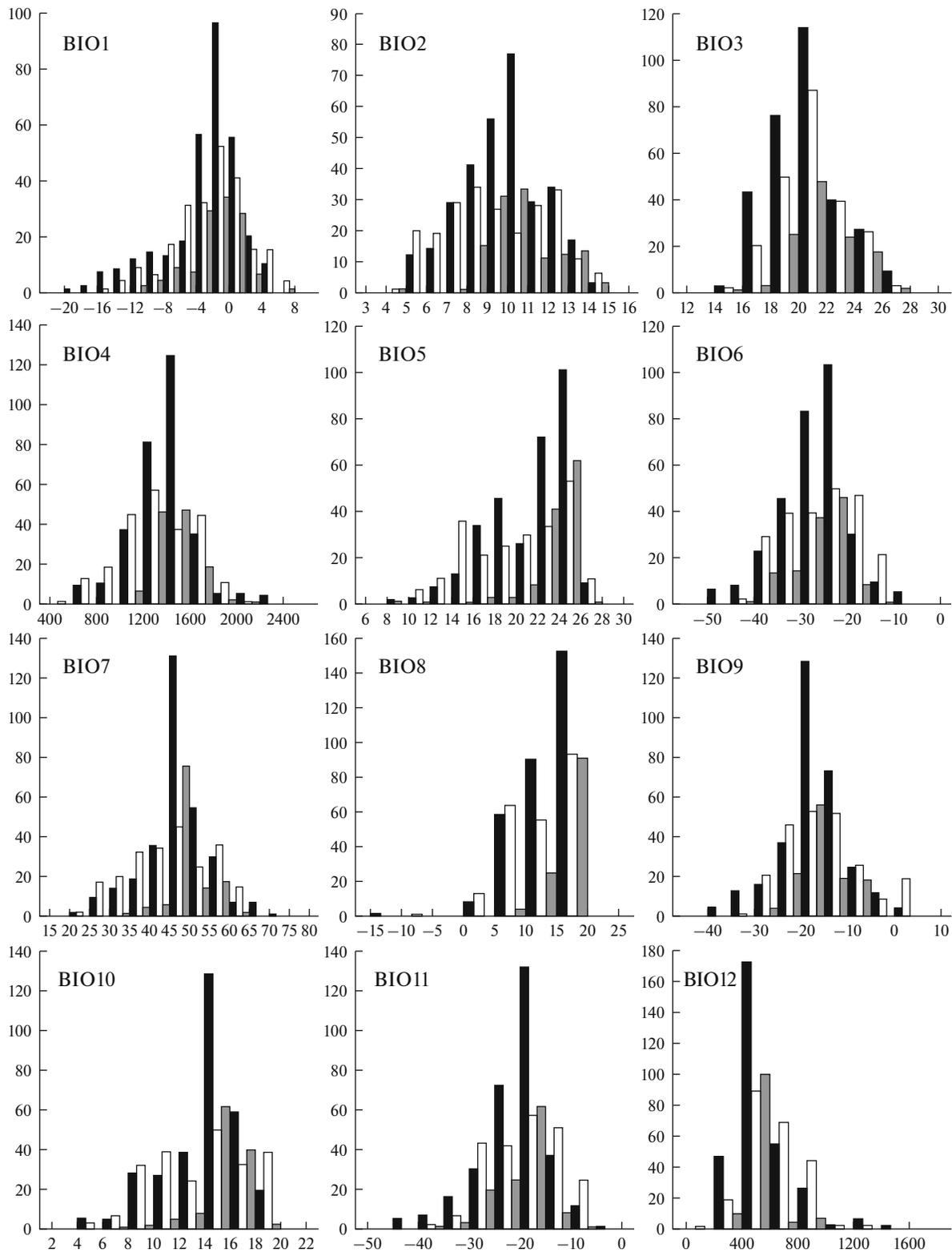


Fig. 1. Histograms of different climatic parameters BIO1–BIO19 of *P. palustris* ($n = 290$), *P. nemoralis* ($n = 229$), and *P. intricata* ($n = 97$) in Asian Russia (the abscissa axis reflects the factor rate and the ordinate axis shows is frequencies).

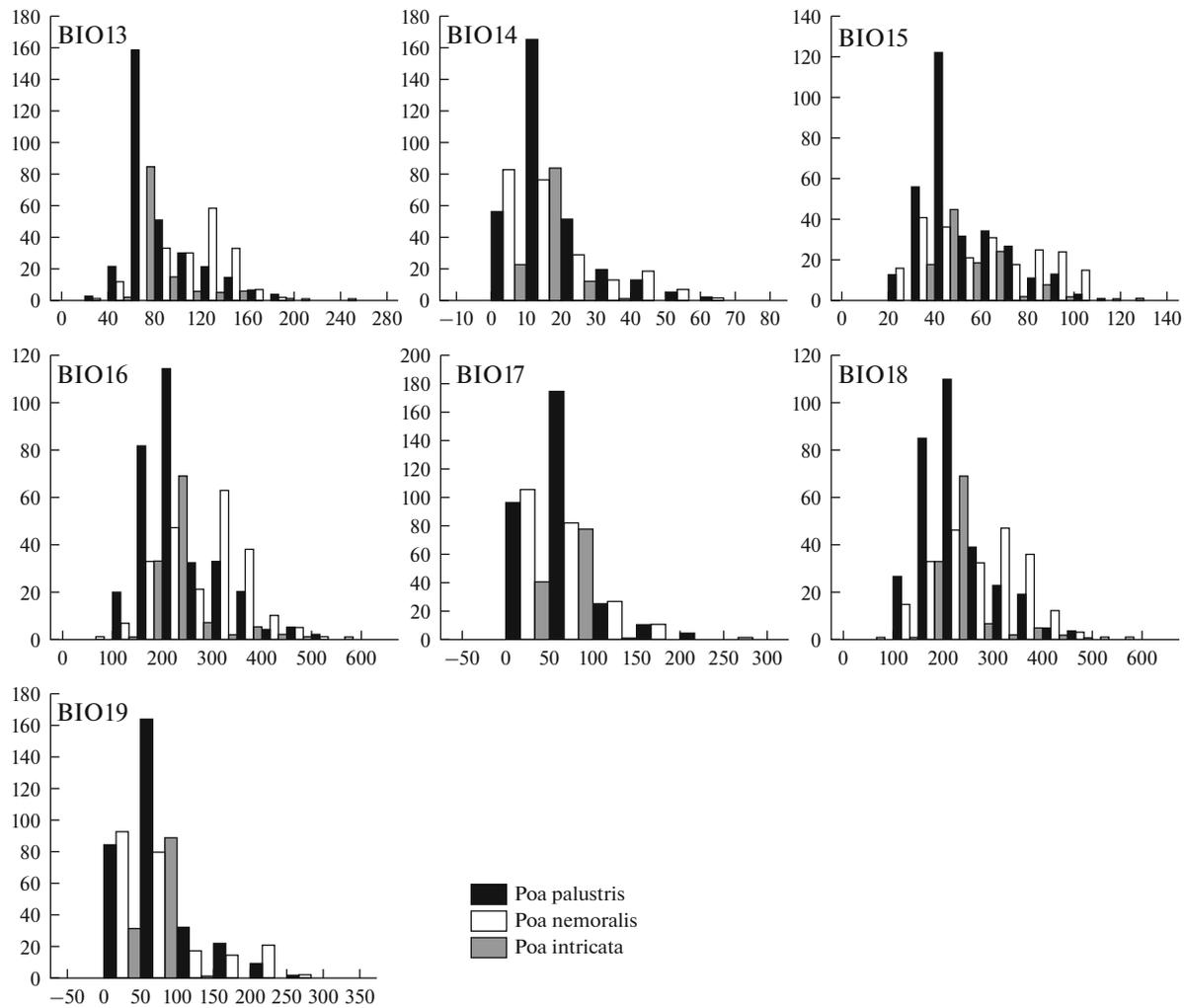


Fig. 1. (Contd.)

is characterized by an arid climate and low temperatures, and in the Arctic. According to the samples and published data, *P. palustris* is widespread in Western Siberia and in the Far East, reaching the Arctic tundra in some places. Parallel to this, its presence in Central Asia and Sichuan has been predicted. The assessment of the constructed model has shown high values of Area Under Curve (AUC): the AUC training and AUC testing are equal to 0.887 and 0.871, respectively (Table 1). Both characteristics exceed 0.8, which corresponds to a good prognostic possibility of the model (Scheldeman and van Zonneveld, 2010). The standard deviation is 0.016.

The area of *P. nemoralis* is slightly shifted to the east, to the nemoral zone of the Pacific coast, where it is also widespread in areas with a colder climate. This species is quite common in Magadan oblast and Kamchatka (Probatova, 1985). Similar to the previous species, the conditions of most of Eastern Siberia, except for humid areas of the Baikal Region, are unfavorable

for the growth of *P. nemoralis*. Nevertheless, according to its climatic niche, it can survive on the Arctic coast in the lower reaches of the Ob River, in the mountains of Central Asia, and in the rather humid areas of Sichuan. The AUC training and AUC testing of this model were equal to 0.920 and 0.902, respectively, which corresponds to the excellent prognostic possibility of the model.

The potential area of the third species—hybridogenic *P. intricata*—differs from that of presumably parent species. The probability of its distribution is high in Southern Siberia, but it is low in the Far East, especially in the northern regions, unlike *P. palustris* and *P. nemoralis* (Fig. 3c). The prognostic possibilities of this model are also assessed as excellent and good (AUC training and AUC testing are equal to 0.922 and 0.884, respectively) (Table 1).

In addition to the prediction of the areas favorable for growth of the species with respect to their climatic indexes, the MaxEnt algorithm also makes it possible

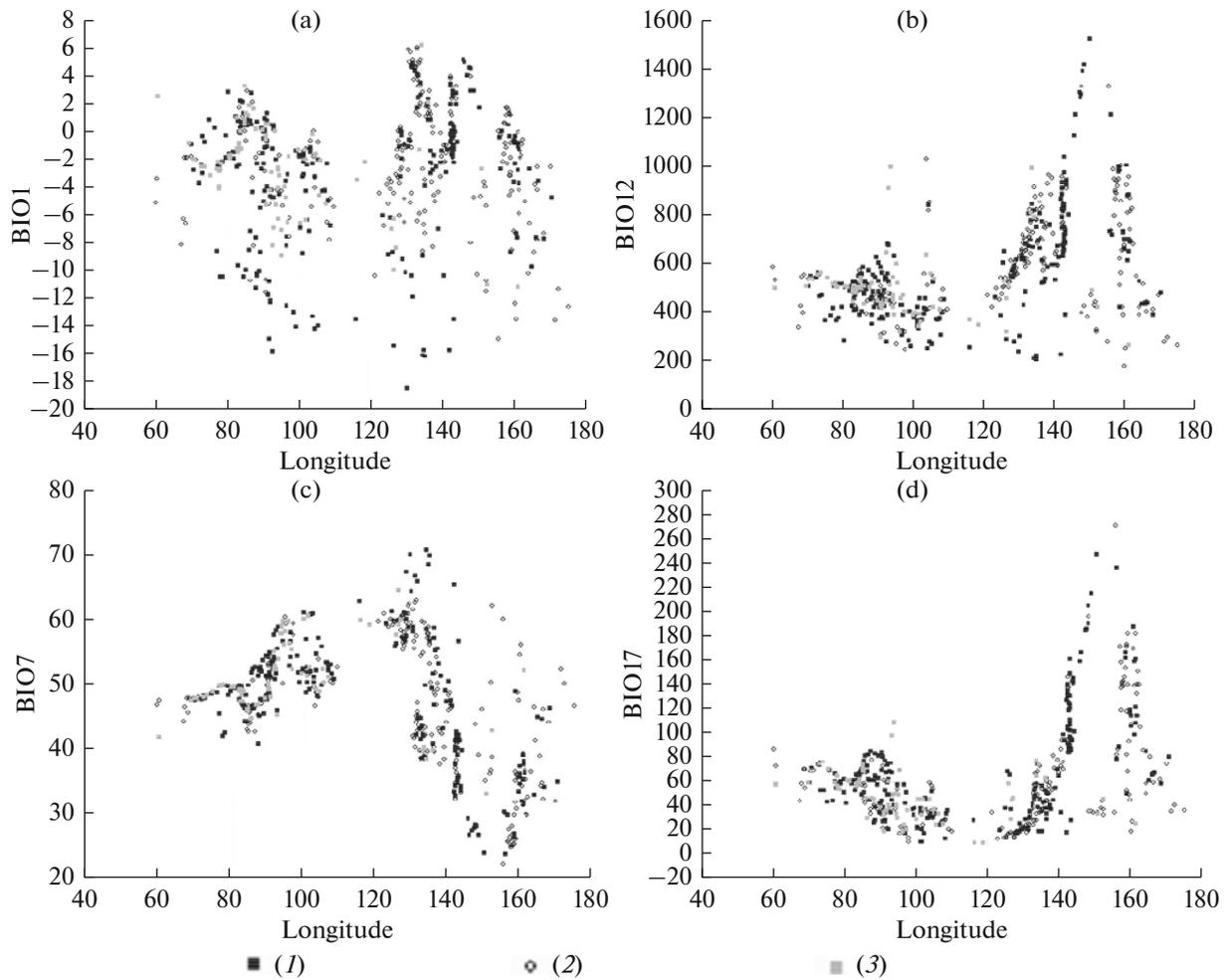


Fig. 2. Dependence of *P. palustris* (1), *P. nemoralis* (2), and *P. intricata* (3) in Asian Russia on longitude ((a) annual mean temperature; (b) annual precipitation; (c) temperature range; and (d) precipitation of wettest period).

Table 1. Main parameters of distribution models of *P. palustris*, *P. nemoralis*, and *P. intricata* in Asian Russia constructed with the use of the MaxEnt algorithm

	<i>Poa palustris</i> , n = 290		<i>Poa nemoralis</i> , n = 229		<i>Poa intricata</i> , n = 97	
<i>n tr/n tst</i>	218/72		172/57		73/24	
AUCtr/AUCtst	0.887/0.871		0.920/0.902		0.922/0.884	
Standard deviation	0.016		0.020		0.036	
Logistic threshold	0.236		0.210		0.273	
Assessment	Percentage contribution	Permutation	Percentage contribution	Permutation	Percentage contribution	Permutation
	BIO12 = 32.6	BIO12 = 25.3	BIO12 = 42.7	BIO1 = 29.7	BIO12 = 36.8	BIO1 = 25.5
	BIO5 = 22.9	BIO1 = 23.6	BIO1 = 15.1	BIO2 = 24.1	BIO1 = 29.7	BIO15 = 22.2
	BIO1 = 20.5	BIO15 = 18.5	BIO5 = 13.5	BIO15 = 23.9	BIO15 = 22.1	BIO8 = 20.1
	BIO15 = 11.1	BIO5 = 14.6	BIO2 = 13.3	BIO5 = 7.3	BIO8 = 5.3	BIO12 = 17.7

n tr is the size of training sampling, *n tst* is the size of testing sampling. AUCtr is the AUC of training sampling and AUCtst is the AUC of testing sampling.

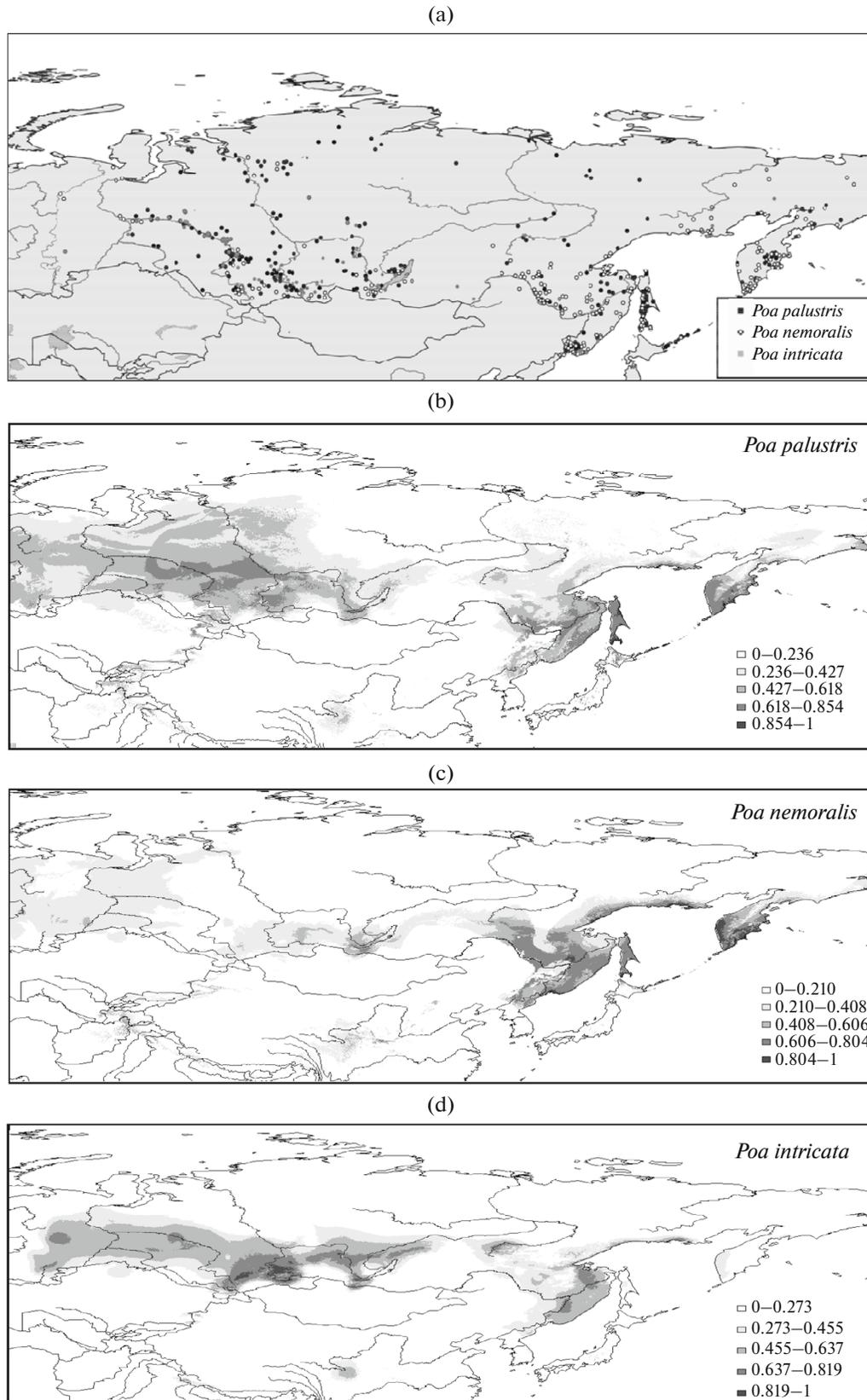


Fig. 3. Models of potential distribution of *P. palustris*, *P. nemoralis*, and *P. intricata* in Asian Russia constructed with the use of the MaxEnt algorithm on the basis of the BIO1, BIO2, BIO5, BIO7, BIO8, BIO12, and BIO15 climatic variables of the modern climate. Locations of (a) the three species, (b) *P. palustris*, (c) *P. nemoralis*, and (d) *P. intricata*.

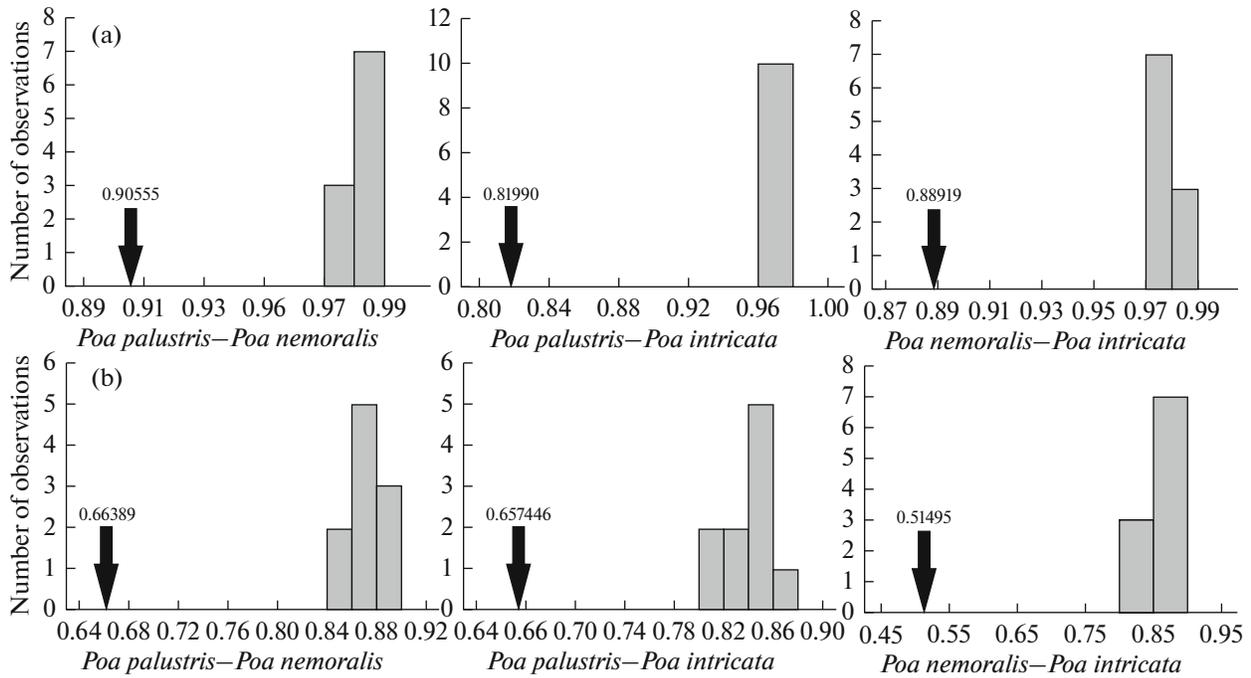


Fig. 4. *I*-test, reflecting the similarity of ecologo-climatic niches. (a) Is the standardized distance by Hellinger. (b) Is the Schoener index.

to reveal the role of each variable in the model construction. The effect of the variables used at the reconstruction of fields of potential distribution of *P. palustris*, *P. nemoralis*, and *P. intricata* in Asian Russia has been assessed by three complementary approaches: percentage contribution, permutation, and the jackknife test. The first, which concerns a direct contribution of variables and significantly depends on the procedure of calculations, shows a similar value of variables for all the three species. A significant role of annual precipitation (32.6% for *P. palustris*, 42.7% for *P. nemoralis*, and 36.8% for *P. intricata*), annual mean temperature (20.5, 15.1, and 29.7%, respectively), and precipitation seasonality (11.1% for *P. palustris* and 22.1% for *P. intricata*) has been revealed. The last parameter is not among the four most important ones for *P. nemoralis* and is replaced by BIO2 (mean diurnal range, 13.3%). Then the difference between the data becomes greater: the four most important parameters for *P. intricata* include BIO8 (mean temperature of wettest quarter, 5.3%). After the permutation (reposition), the assessment of variables changes. The annual mean temperature becomes the most significant for *P. nemoralis* and *P. intricata* (29.7 and 25.5%, respectively), and BIO12 remains the leader for *P. palustris* (annual precipitation, 25.3%). In general, the difference between the priority variables increases (Table 1). The differences in the value of variables for modeling of different species determined by the jackknife test are even greater. For example, the most valuable variables for modeling are represented by BIO1, BIO12, and

BIO15 for *P. palustris* (the variables are given in the order of decreasing value); by BIO12, BIO1, BIO2, and BIO 5f or *P. nemoralis*; and by BIO5, BIO12, BIO8, and BIO1 for *P. intricata*.

The data point to some differences in ecologo-climatic demands of species, but the significant superposition of their areas does not enable one to reject the hypothesis of the identity of their ecologo-climatic niches. In order to check this hypothesis, we used the *I*-test proposed by Warren et al (2008).

As a result of the pair comparison of the ecologo-climatic niches constructed for the three species on the basis of all 19 biologically significant climatic variables, we have received histograms with the total information of ten replicas (tenfold comparison). Red arrows on the plots (Fig. 4) show the value where ecologo-climatic niches of different species overlap. The right diagram shows the distribution of the overlap in replicas. On all plots, red arrows are located at a considerable distance from the diagrams, which testifies that the null hypothesis about the identity of models of the niches should be rejected. At the same time, R. Zink (2015) points out that, if different populations live under various climatic conditions, the *I*-test may be high, but it does not testify to their ecologo-climatic divergence, because they can exist under different conditions as a result of ecological plasticity. The ecological, and in our case, the ecologo-climatic divergence at the genetic level may be revealed by other approaches.

CONCLUSIONS

An analysis of ecologo-climatic niches of *P. palustris*, *P. nemoralis*, and *P. intricata* has revealed the differences between the potential areas of distribution and the role of climatic variables in construction of models. This may testify to differences in climatic preferences and the adaptations of the species.

The test for identity has shown that, despite the overlap of areas, all three species occupy their own ecologo-climatic niches that differ from one other.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

REFERENCES

- Anderson, R.P., Lew, D., and Peterson, A.T., Evaluating predictive models of species' distributions: criteria for selecting models, *Ecol. Model.*, 2003, vol. 162, pp. 211–232.
- Brown, J.L., SDMtoolbox user guide, 2014a. <http://www.sdmtoolbox.org>. Accessed April 18, 2017.
- Brown, J.L., SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic, and species distribution model analyses, *Methods Ecol. Evol.*, 2014b, vol. 5, no. 7, pp. 694–700.
- Clausen, J. and Hiesey, W.M., *Experimental Studies on the Nature of Species. IV. Genetic Structure of Ecological Races*, Washington, DC: Carnegie Inst. Wash., 1958, vol. 57.
- Community Structure and the Niche*, Giller, P., Ed., New York: Springer-Verlag, 1984.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B., Manion, G., Moritz, C., Nakamura, M., et al., Novel methods improve prediction of species' distributions from occurrence data, *Ecogeography*, 2006, vol. 29, pp. 129–151.
- Elton, C.S., *Animal Ecology*, London: Sidgwick and Jackson, 1927.
- ESRI, *ArcGIS Desktop and Spatial Analyst Extension: Release 10.1*, Redlands, CA: Environ. Syst. Res. Inst., 2012.
- Franklin, J., *Mapping Species Distributions: Spatial Inference and Prediction*, Cambridge: Cambridge Univ. Press, 2009.
- Grant, V., *Organismic Evolution*, San Francisco: W.H. Freeman, 1977.
- Grinnell, J., The niche-relationships of the California Thrasher, *Auk*, 1917, vol. 34, pp. 427–433.
- Hiesey, W.M. and Nobs, M.A., Genetic and transplant structure on contrasting species and ecological races of the *Achillea millefolium* complex, *Bot. Gaz.*, 1970, vol. 131, pp. 245–259.
- Hiesey, W.M. and Nobs, M.A., *Interspecific Hybrid Derivatives Between Facultatively Apomictic Species of Bluegrasses and Their Responses to Contrasting Environments*, Carnegie Institution of Washington Publication vol. 636, Washington, DC: Carnegie Inst. Wash., 1982.
- Hijmans, R.J., Cameron, S., and Parra, J., Climate data from Worldclim, 2004. <http://www.worldclim.org>. Accessed September 18, 2017.
- Hijmans, R.J., Guarino, L., Jarvis, A., et al., DIVA-GIS Users manual, version 5.2., 2005. [http://www.Diva-GIS/Diva-GIS.org/DIVA-GIS DIVA-GIS 5_manual.pdf](http://www.Diva-GIS/Diva-GIS.org/DIVA-GIS%20DIVA-GIS%205_manual.pdf). Accessed April 18, 2017.
- Hutchinson, G.E., Concluding remarks, *Cold Spring Harbor Symp. Quant. Biol.*, 1957, vol. 22, pp. 415–422.
- MacArthur, R.H., The theory of the niche, in *Population Biology and Evolution*, Lewontin R.C., Ed., Syracuse: Syracuse Univ. Press, 1968, pp. 159–176.
- Nix, H., A biogeographic analysis of Australian Elapid snakes, in *Atlas of Elapid Snakes of Australia*, *Australian Flora and Fauna Series no. 7*, Longmore, R., Ed., Canberra: Aust. Gov. Publ. Serv., 1986, vol. 7, pp. 4–15.
- Olonova, M.V., *Poa* L.—bluegrass, in *Flora Sibiri* (Flora of Siberia), Novosibirsk, 1990, vol. 2, pp. 163–186.
- Olonova, M.V., Population study of hybrid complexes *Poa palustris* L.—*P. nemoralis* L.—*P. urssulensis* Trin. in the south of Western Siberia, in *Botanicheskie issledovaniya Sibiri i Kazakhstana* (Botanical Studies in Siberia and Kazakhstan), Tr. Gerb. im. V.V. Sapozhnikova, Barnaul, 2001, no. 7, pp. 13–33.
- Olonova, M.V., Review of section Stenopoa of genus *Poa* (Poaceae) in Siberia, *Bot. Zh.*, 2010, vol. 95, no. 6, pp. 869–881.
- Olonova, M.V., Gussarova, G.L., Brysting, A.K. and Mezina, N.S., Introgressive hybridization in mesomorphic bluegrasses, *Poa* section Stenopoa, in western Siberia, *Ann. Bot. Fen.*, 2016, vol. 53, pp. 43–55.
- Ozerskii, P.V., The concept of ecological niche of Elton—Odum: history of the problem, *Funkts. Morfol., Ekol. Zhizn. Tsikly Zhivotn.*, 2013, vol. 13, no. 1, pp. 55–69.
- Peshkova, G.A., Family Poaceae or Gramineae, in *Flora Tsentral'noi Sibiri* (Flora of Central Siberia), Novosibirsk, 1979, vol. 1, pp. 69–139.
- Phillips, S.J., A brief tutorial on Maxent, 2011. <http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc>. Accessed April 18, 2017.
- Phillips, S.J. and Dudik, M., Modeling of species distribution with Maxent: new extensions and a comprehensive evaluation, *Ecography*, 2008, vol. 31, pp. 161–175.
- Phillips, S.J., Anderson, R.P., and Schapire, R.E., Maximum entropy modeling of species geographic distributions, *Ecol. Model.*, 2006, vol. 190, pp. 231–259.
- Probatova, N.S., Family Poaceae or Gramineae, in *Sosudistyie rasteniya sovetskogo Dal'nego Vostoka* (Vascular

- Plants of Soviet Far East), Leningrad, 1985, vol. 1, pp. 89–382.
- Rabotnov, T.A., *Fitotsenologiya* (Phytocenology), Moscow: Mosk. Gos. Univ., 1983, 2nd ed.
- Ramenskii, L.G., Tsatsenkin, I.A., Chizhikov, O.N., and Antipin, N.A., *Ekologicheskaya otsenka kormovykh ugodii po rastitel'nomu pokrovu* (Ecological Evaluation of Fodder Resources by Vegetation Cover), Moscow: Sel'khozgiz, 1956.
- Scheldeman, X. and van Zonneveld, M., *Training Manual on Spatial Analysis of Plant Diversity and Distribution*, Rome: Biodiversity Int., 2010.
- Seledets, V.P. and Probatova, N.S., *Ekologicheskii areal vida u rastenii* (Ecological Range of the Plant Species), Vladivostok: Dal'nauka, 2007.
- Tsatsenkin, I.A., *Ekologicheskie shkaly dlya rastenii pastbishch i senokosov gornyykh i ravninnykh raionov Srednei Azii, Altaya i Urala* (Ecological Scales for the Plants of Pastures and Hayfields of Mountain and Plains Regions of Central Asia, Altai, and Urals), Dushanbe: Donish, 1967.
- Tsvelev, N.N., Role of hybridization in evolution of grasses (Poaceae), in *Istoriya flory i rastitel'nosti Evrazii* (History of Flora and Vegetation of Eurasia), Leningrad, 1972, pp. 5–16.
- Tsvelev, N.N., Genus *Poa* L.) in USSR, *Nov. Sist. Vysshikh Rast.*, 1974, vol. 11, pp. 24–41.
- Tsvelev, N.N., *Poa* L.—bluegrass, in *Arkticheskaya flora SSSR* (Arctic Flora of Soviet Union), Tolmachev, A.I., Ed., Moscow, 1964, no. 2, pp. 112–162.
- Warren, D.L., Glor, R.E., and Turelli, M., Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution, *Evolution*, 2008, vol. 62, pp. 2868–2883.
- Warren, D.L., Glor, R.E., and Turelli, M., ENMTools user manual v. 1.3, 2011. http://www.danwarren.net/enmtools/builds/ENMTools_1.4.3.zip.
- Zink, R.M., Genetics, morphology, and ecological niche modeling do not support the subspecies status of the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*), *Condor*, 2015, vol. 117, pp. 76–86. doi 10.1650/CONDOR-14-27.1

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