Ecological Niche Differentiation from the Example of Bottom Communities of the Middle and Lower Volga Regions

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Abstract—The authors discuss the use of the Greenell concept of ecological niches to analyze the taxonomic structure of communities and their relationship with environmental factors. The modeling of ecological niches was carried out using the results of 30-year studies of macrozoobenthos communities on 90 small and 12 medium-sized plain rivers in the region of the Kuibyshev, Saratov, and Volgograd reservoirs. Geoclimatic indicators, relief characteristics, and hydrochemical assessments of the water quality at sampling points were considered as abiotic factors, where 11 variables with the least collinearity were selected. The multidimensional space of the initial abiotic factors was projected onto the orthogonal axes of the first two principal components; ordination diagrams with plotted points of the presence of species were constructed. The model of the potential ecological niche of each species was represented as an area in the space of latent variables, in which the habitat suitability index Z estimated by the probability density of occurrence corresponds to the given constraints. The authors used the Schoener and Hellinger indices to quantify the proportion of overlapping niches belonging to two different benthos taxa. The matrix of distances between overlapping niches was formed for all possible paired combinations of the 40 most ecologically significant macrozoobenthos species. Cluster analysis of the obtained distance matrix was carried out by the methods of hierarchical agglomeration and fuzzy k-means. In the general multidimensional space of abiotic variables of the region studied, four areas of collective niches for groups of species with maximum distances between their centroids were identified. The analysis of intergroup variation of environmental factors is given, and the characteristic features of each group are discussed: ecological strategy, biological traits, and tolerance level.

Keywords: modeling ecological niches, principal component analysis, environmental suitability, niche overlap, cluster analysis, macrozoobenthos, Lower Volga basin

DOI: 10.1134/S1062359022100302

INTRODUCTION

Modern methods for studying large-scale water ecosystems are based on the active use of GIS-technologies and remote monitoring systems, as well as rapidly expanding public databases summarizing the characteristics of natural and anthropogenic landscapes, the dynamics of climate change, and a wide range of other environmental factors. In recent decades, metods SDM (*Species Distribution Models*, Franklin, 2009; Guisan et al., 2017) and ENM (*Environmental Niche Models,* Peterson et al., 2011), which open up new opportunities for studying the mechanisms of community functioning and their relationship with the living conditions of populations, have become an important instrument of (macro)-ecological and biogeographical studies.

The distribution patterns of populations over the study area are determined by three major groups of variables (Brown et al., 1996; Gaston, 2003; Guisan and Thuiller 2005): (**a**) large-scale ($>10^3$ km^2) environmental factors, such as the average temperature, precipitation, solar radiation, terrain, etc., creating favorable conditions for the emergence, survival, and reproduction of species; (**b**) factors of the biotic environment that determine the full range of interspecific interactions (competition, predation, mutualism, etc.), as well as the availability and dynamics of resource consumption on a scale of up to 10 km^2; (**c**) the ability of species to reproduce and spread due to their own movements or with the help of external influences.

The interest in describing, understanding, and predicting the geographic and ecological distribution of

species has a long history (Grinnell, 1917, 1924; Elton, 1927). The *fundamental Greenell niche* N_F is defined as "the set of all possible vectors in the *n*-dimensional space of group **a** variables for which the internal growth rate of the species is positive and/or the population density exceeds a given threshold" (Soberón, 2007, p. 1118). If we consider a specific territory tied to a grid of geographical coordinates, then the set of J_F cells with values of the variable vectors belonging to N_F is the fundamental area of the species distribution. Based on N_F, the area of J_F can be calculated, but the inverse operation is also theoretically admissible: if J_F is known, then combinations of environment variable vectors can be extracted from its cells to construct N_F. In this regard, the procedures for ENM environmental niche modeling and SDM species distribution modeling largely coincide: at the initial stage, the occurrence of a species in the geographic space is analyzed, then a niche model is built in the space of environmental factors, and, in the case of SDM, the results are again visualized on the map taking into account the possibility of the existence of the species in specific areas (Peterson and Soberón, 2012).

However, the equivalence $N_F \Leftrightarrow J_F$ is valid if we assume that J_F is a fully potential area of distribution of the species, and factors such as the availability of resources, movements of individuals, and interactions between individuals, which determine the processes of Elton's niche, are ignored. J. Hutchinson (Hutchinson, 1957, 1978) defined a fundamental niche as the volume of an *n*-dimensional hyperspace of all internal and external factors **a**−**b** that are necessary for the survival of each species in the absence of other species and an implemented niche as part of a fundamental niche in which the presence of the species was recorded under the conditions of the real competitive exclusion. However, practical modeling of implemented niches is an extremely difficult task. First, the variables of Elton's niche cannot be specified as a set of numbers derived from observational data, since their estimation requires hypotheses about specific forms and models of interactions. The second problem is related to the difference in scales: the mosaic nature of Elton's niche with its small-celled ecological structure often does not affect the size of the Greenell niche. Therefore, according to the @Eltonian Noise Hypothesis@ (Peterson et al., 2011), biotic interactions rarely have a significant impact on the distribution potential of species in large geographical spaces.

Greenell niche modeling has become the main methodology for quantifying the relationship between the structure of ecological communities and environmental factors: for example, a review of the literature by S.M. Melo-Merino et al. (2020) devoted to the biology of marine and inland waters analyzes 328 articles on this topic. One of the important areas is niche segregation, separation, and partitioning, because, using Hutchinson's terminology, niche hyperspaces of some species include parts of such hyperspaces of other species; i.e., they overlap with them. Considering the totality of Greenell niches for the entire community, one must expect that ecosystems with similar environmental conditions can host one or more identical niches that combine ecologically equivalent species, which are often taxonomically unrelated. Another task of differentiation is to assess the volume and boundaries of niches in ecological and geographic spaces, which makes it possible to assess the areas of populations and the degree of eurybiontness of individual organisms.

The goal of this research is to consider the results of differentiation of ecological niches for the example of benthic communities using the results of long-term (1990−2019) studies in the Middle and Lower Volga basin (Zinchenko, 2011; Golovatyuk et al., 2018). Detailed data on the spatial distribution of the biodiversity of the macrozoobenthos and its individual species based on the use of geostatistical methods as well as the MaxEnt and HMSC models are presented in a series of our articles (Zinchenko et al., 2021; Shitikov et al., 2021a, b).

MATERIALS AND METHODS

Hydrobiological samples of the macrozoobenthos were taken in different months of the growing season on 90 small and 12 medium plain rivers that are the tributaries of the Kuibyshev, Saratov, and Volgograd reservoirs, including six rivers of the arid region of the Elton Lake basin (Fig. 1). The middle rivers were divided into approximately the same areas: the upper, middle, lower reaches, and mouth, and each small river was considered as an integral object. Thus, 132 local communities were investigated, at which 1400 samples were taken by standard methods, and total 740 species and macrozoobenthos taxa were distinguished.

The analysis of the environmental factors was carried out taking into account two groups of abiotic variables. The first group included raster geographic data obtained primarily using satellite shooting and presented on general servers. Use was made of layers of the bioclimatic information from the WorldClim world base (Hijmans et al., 2005) on a network of geographical coordinates with a resolution of 2.5 minutes, which included 20 indicators, in particular, various variants of the average air temperature, the volume of precipitation, and the height above sea level. Additionally, the terrain ruggedness index (TRI) was calculated; this is a topographic index showing the average

value of the height difference between the analyzed cell and eight neighboring cells. Preliminary analysis indicates that all bioclimatic indicators are a strongly correlated set of variables. To avoid the effect of collinearity in the construction of models, seven predictors for which a minimum level of the VIF variance inflation factor was not more than 20 were selected (Shitikov and Mastitskii, 2017).

The second group was formed according to the data of monitoring 30 environmental factors, which was simultaneously conducted on the habitats studied and included the hydrological parameters of watercourses, water quality indicators, and the composition of the main chemical ingredients. Based on the results of preliminary testing, four main variables were selected, which are traditionally important for the functioning of the bottom communities: mineralization of water, the content of ammonium nitrogen, saturation with oxygen, and the category of bottom soils (in points from 1 to 6).

Modeling of the niche space was carried out using optimal projection of a multidimensional correlated set of the initial abiotic factors onto the orthogonal axes of the space of small dimension. For this purpose, ordination diagrams were built in the coordinates of the first two principal components (PCA1 and PCA2) and they were calibrated taking into account the nature of the variation of the change in the environmental variables within the area studied. A model of the potential ecological niche was considered as a certain area in the space of latent variables, in which the density of the probability of occurrence of the species or the entire community as a whole corresponds to specified restrictions. These conditions were associated with the @environmental or habitat suitability index@ $Z \in [0, 1]$.

To build the Z response surface, the points of occurrence of analyzed species were plotted on a grid of 100×100 cells that was limited by the minimum and maximum values of the principal components PCA1–PCA2 and determined the multidimensional environmental variability of the territory. Further, the binary variables of the presence/absence were transformed into the relative densities of the two-dimensional distribution by smoothing with *kernel* functions (Broennimann et al., 2012; Di Cola et al., 2017). After calibration of the Z values in the range [0, 1], the potential ecological niche was a certain irregular region in the space of two principal components with the habitat suitability indices $z_{ij} > 0$.

To assess the degree of overlap of two niches belonging to different taxonomic groups visually, ordination diagrams of their pairwise intersection were constructed. To perform quantitative assessment, the
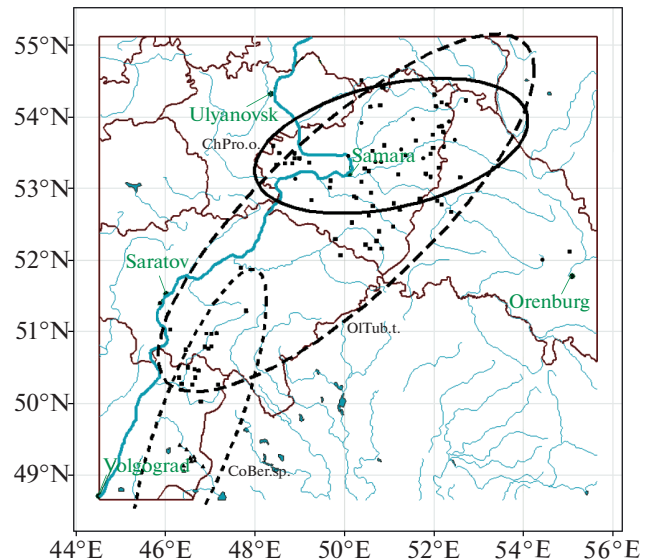
Fig. 1. Cartography of the region studied; detection points and 90% confidence ellipses of some macrozoobenthos species, namely, *Prodiamesa olivacea* (ChPro.o.), *Tubifex tubifex* (OlTub.t.), and *Berosus* sp. (CoBer.sp).

Schoener D and Hellinger I indices were used, which reflect the share of niche overlap in a given space (Warren et al., 2008) and fluctuate between 0 (no overlap) and 1 (complete overlap):

$$D = 1 - 0.5\left(\sum_{ij}\left|z_{1ij} - z_{2ij}\right|\right);$$

$$I = 1 - 0.5\left(\sqrt{\sum_{ij}\left(z_{1ij}^{0.5} - z_{2ij}^{0.5}\right)^2}\right).$$

To analyze the areas of niche overlap by the entire benthic community, 40 macrozoobenthos species were selected from various taxonomic and functional groups represented in at least seven river sections and having a characteristic ecological profile. For each pair of species, the Schoener overlap index was calculated and a matrix of distances $(D - 1)$ between niches in the ecological space was formed. Niche differentiation was carried out using hierarchical clustering using the average link algorithm that maximizes the cophenetic correlation coefficient and the fuzzy k-means method.

The calculations were carried out in the R v.3.6 environment using a special Ecospat package (Di Cola et al., 2017; Shitikov, 2021).

RESULTS

Based on the results of principal component analysis, the two principal axes of maximum variation explained 57.5% of the data variance; moreover, as shown in Fig. 2, the main PCA1 axis correlates posi-
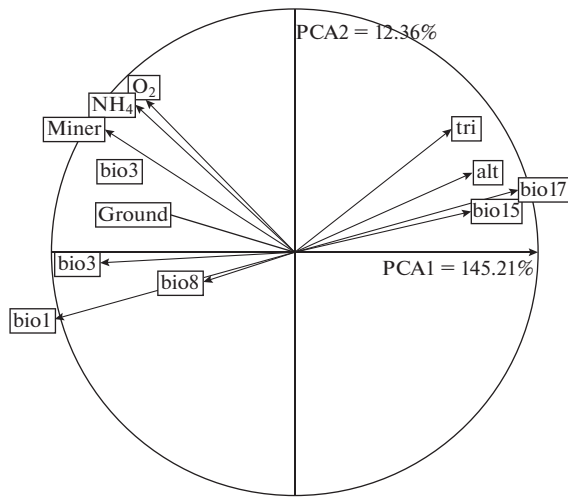
Fig. 2. Correlation circle with decomposing 11 environmental factors along two axes of maximum variation (bio1, average annual temperature; bio3, isothermicity index; bio8, temperature of the wettest quarter; bio15, seasonal precipitation variation; bio17, precipitation of the dry quarter; alt, altitude; tri, terrain roughness index; Ground, soil category; Miner, mineralization; NH_4, ammonium ion content; O_2, oxygen saturation).

tively with the altitude and precipitation and negatively with temperature and salinity. The PCA2 axis is related by us to the content of ammonia ions and oxygen saturation.

For each pair of the 40 species selected, the proportion of niche sharing and the proportion of the total area of ecological space occupied by each species separately were identified—see the examples of two-dimensional and three-dimensional ordination diagrams in the PCA1 and PCA2 coordinates in Fig. 3. In parallel, we calculated the Schoener and Hellinger indices and also performed statistical tests for equivalence and similarity for each pair of niches compared. Additionally, we found out which specific environmental variables caused the difference in ecological niches. Figure 4 shows the graphs of the distribution density on the scales of the most important abiotic factors of occurrence of the species *Prodiamesa olivacea* and *Berosus* sp., which have the greatest "contrast" in terms of their habitat conditions.

Cluster analysis of similar niches by hierarchical methods and using fuzzy sets gave largely identical results—the dendrogram obtained using the average connection algorithm is shown in Fig. 5. The graphs of the distribution density of some environmental factors in the sections of the rivers in which each of the four selected groups of species (I–IV) were found are shown in Fig. 6.

DISCUSSION

The construction of ecological niches and procedures for analyzing their similarity make it possible to expand significantly our understanding of the biology of species and their geographical ranges. For example, it is interesting to compare the configurations of the regions in Figs. 1 and 3, which are occupied by the
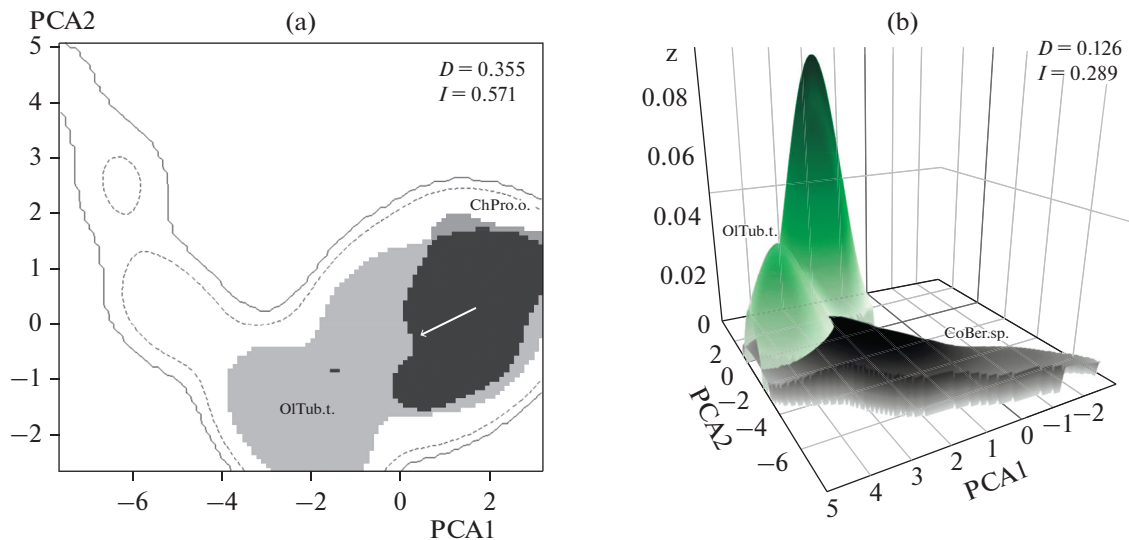

Fig. 3. Ordination PCA diagrams of pairwise overlap of ecological niches of three species, namely, *Prodiamesa olivacea* (ChPro.o.), *Tubifex tubifex* (OlTub.t.), and *Berosus* sp. (CoBer.sp). The values of the niche overlap indices *D* (Schoener) and *I* (Hellinger) are given. (*a*) Contour lines indicate the boundaries of the studied area (dashed, with the removal of 5% of marginal areas). The niches of the two compared species are painted in gray, and the shared area of the ecological space is dark. The end and beginning of the arrow show the position of the centroids of both niches, respectively. (*b*) Three-dimensional diagram; *Z* is the habitat suitability index.
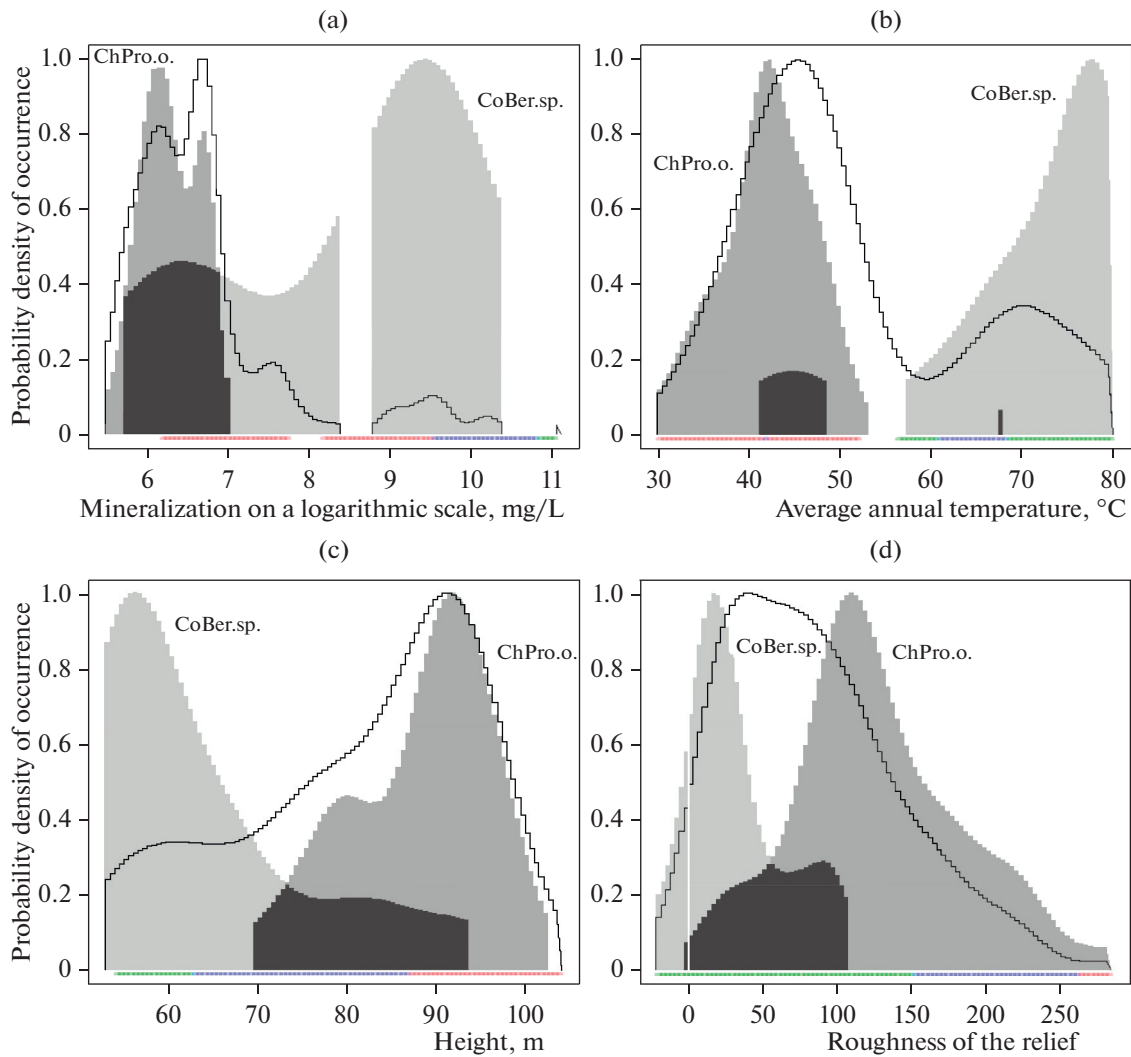
Fig. 4. Graphs of the occurrence distribution density of *Prodiamesa olivacea* (ChPro.o.) and *Berosus* sp. (CoBer.sp) on the abiotic factor scales: *a*, mineralization; *b*, average annual temperature; *c*, height; *d*, roughness of the relief. The dark color shows the area of joint occurrence. The contour line indicates the distribution density curve for all observation points.

species in the ecological and geographical spaces: the species *Tubifex tubifex* is distributed over a large area, but in a rather limited range of environmental factors. In contrast to it, *Berosus* sp. occurs only in the southern part of the region studied, but under the conditions of a large variation in the salinity of watercourses and the content of ammonia nitrogen (see Fig. 4). In this regard, in the second case, the uncertainty of the suitability of environmental conditions assessed by the value *Z* increases significantly.

Cluster analysis has shown that 4−5 characteristic areas that are occupied by overlapping niches of groups of ecologically similar species can be distinguished in the entire available space of environmental factors. There are communities of pelophilic species that form on silted substrates in slow-flowing rivers and in the mouth areas of lowland rivers (*Tubifex tubi-fex*, *Chironomus plumosus@*, *Glyptotendipes gripek-oveny*, etc.—group I); a phytophilic community of fast-flowing small rivers (*Baetis rhodany*, *Orthocladius oblidens*, *Rhaeocricotopus fuscipes*, etc.—group II); and a community of rheophilic species that is characteristic of oligotrophic clean sections of rivers (*Paracladius conversus*, *Prodiamesa olivacea*, *Hydropsyche pellucid-ula*, etc.—classification group III). Group IV on the dendrogram presented in Fig. 4 is formed, (in addition to *Berosus* sp., by a taxon without distinct biotopic preferences), the halophilic species *Chironomus sali-narius*, *Glyptotendipes salinus*, and *Cricotopus salinoph-ilus*, the ecological characteristics of which clearly outline the area of distribution of the community that forms under the conditions of high mineralization of the arid part of the region studied.
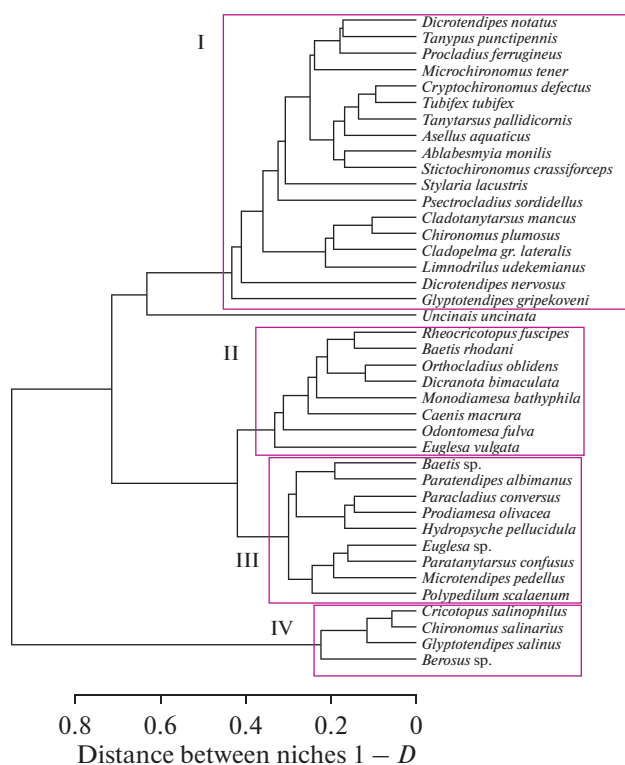
Fig. 5. Dendrogram of hierarchical clustering of ecological niches of 40 macrozoobenthos species using the Schoener overlap index *D*.

One of the computational problems is that many modeling algorithms of the species distribution (Max-Ent, *R*-package virtualspecies, etc.) work only with raster information presented in cells ("pixels") of a uniform grid of geographic coordinates of a sufficiently high resolution. It seems impossible to present in this form the local characteristics of river habitats, such as the composition of chemical ingredients, the hydrological parameters of the watercourse, the type of bottom soil, etc., which are traditionally key for hydrobiology. The ecospat *R*-function package (Broennimann et al., 2012; Di Cola et al., 2017) makes it possible to construct an arbitrarily smooth surface of the environmental suitability index in the axes of two principal components based on the traditional "habitats—environmental variables" table, which allows taking into account the full set of factors.

Modeling of ecological niches and population ranges makes it possible to consider the observed phenomena in a spatial and temporal context: to estimate the rate of spread of invasive species (Di Cola et al., 2017) or reduction in bioproductivity over different time periods; to explore the mechanisms of coexistence of parthenogenetic animal forms (Petrosyan et al., 2020); to identify specific spatial patterns of organization of meta-communities within a large-scale ecosystem; to carry out the selection of statistically significant isolated zones, on the border of which a succession change in species composition occurs, etc. The ENM/SDM models are an effective research tool and allow significantly expanding the biological understanding of the ecology of species and transferring them to a rigorous quantitative basis. All this is of particular importance when conducting complex biospheric studies in the region (aquatic and terrestrial), the need for which is obvious.
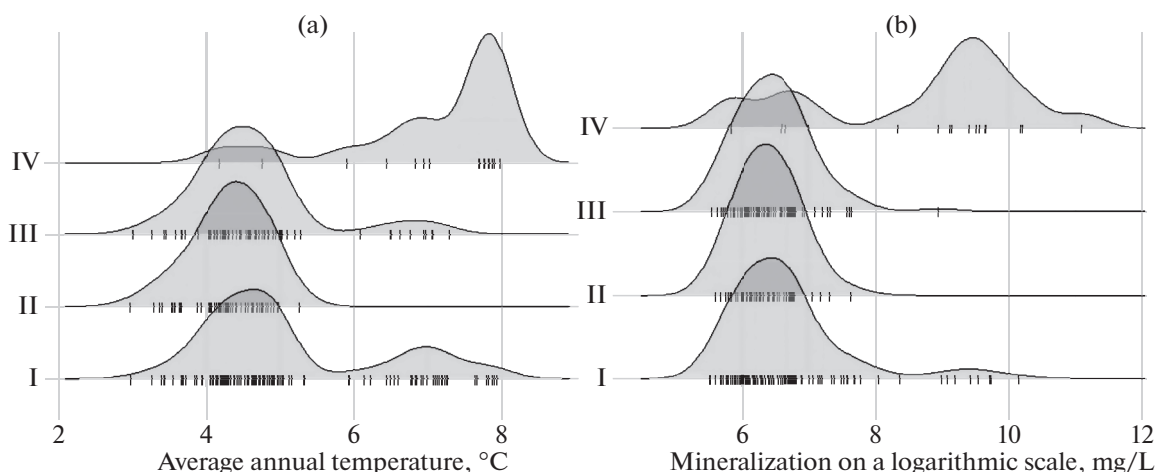
ACKNOWLEDGMENTS

Fig. 6. Distribution density of some environmental factors ((*a*) average annual temperature, (*b*) mineralization) along the river sections where each of the four selected groups of species (I–IV) were found.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

REFERENCES

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., and Guisan, A., Measuring ecological niche overlap from occurrence and spatial environmental data, *Global Ecol. Biogeogr.*, 2012, vol. 21, no. 4, pp. 481−497.
https://doi.org/10.1111/j.1466-8238.2011.00698.x

Brown, J.H., Stevens, G.C., and Kaufman, D.M., The geographic range: size, shape, boundaries, and internal structure, *Annu. Rev. Ecol. Syst.*, 1996, vol. 27, pp. 597−623.

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F.T., D'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, R.G., Mateo, R.G., Hordijk, W., Salamin, N., and Guisan, A., Ecospat: an R package to support spatial analyses and modeling of species niches and distributions, *Ecography*, 2017, vol. 40, no. 6, pp. 1−14.
https://doi.org/10.1111/ecog.02671

Elton, C., *Animal Ecology*, London: Sedgwick and Jackson, 1927.

Franklin, J., *Mapping Species Distributions: Spatial Inference and Prediction*, Cambridge: Cambridge Univ. Press, 2009.

Gaston, K.J., *The Structure and Dynamics of Geographic Ranges*, Oxford: Oxford Univ. Press, 2003.

Golovatyuk, L.V., Shitikov, V.K., and Zinchenko, T.D., Estimation of the zonal distribution of species of bottom communities in lowland rivers of the Middle and Lower Volga basin, *Biol. Bull.* (Moscow), 2018, vol. 45, no. 10, pp. 1262−1268.
https://doi.org/10.1134/S1062359018100126

Grinnell, J., Field tests of theories concerning distributional control, *Am. Nat.*, 1917, vol. 51, pp. 115−128.

Grinnell, J., Geography and evolution, *Ecology*, 1924, vol. 5, pp. 225−229.

Guisan, A. and Thuiller, W., Predicting species distribution: offering more than simple habitat models, *Ecol. Lett.*, 2005, vol. 8, no. 9, pp. 993−1009.
https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan, A., Thuiller, W., and Zimmermann, N.E., *Habitat Suitability and Distribution Models: with Applications in R*, Cambridge: Cambridge Univ. Press, 2017.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A., Very high resolution interpolated climate surfaces for global land areas, *Int. J. Climatol.*, 2005, vol. 25, no. 15, pp. 1965−1978.
https://doi.org/10.1002/joc.1276

Hutchinson, G.E., Concluding remarks, *Cold Spring Harbor Symp. Quant. Biol.*, 1957, vol. 22, pp. 415−427.
https://doi.org/10.1101/SQB.1957.022.01.039

Hutchinson, G.E., *An Introduction to Population Ecology*, New Haven: Yale Univ. Press, 1978.

Melo-Merino, S.M., Reyes-Bonilla, H., and Lira-Noriega, A., Ecological niche models and species distribution models in marine environments: a literature review and spatial analysis of evidence, *Ecol. Model.*, 2020, vol. 415, p. 108837.
https://doi.org/. 2019.108837
https://doi.org/10.1016/j.ecolmodel

Peterson, A.T. and Soberón, J., Species distribution modeling and ecological niche modeling: getting the concepts right, *J. Nat. Conserv.*, 2012, vol. 10, no. 2, pp. 102−107.
https://doi.org/10.4322/natcon.2012.019

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

Petrosyan, V.G., Osipov, F.A., Bobrov, V.V., Dergunova, N.N., Omelchenko, A.V., Varshavskiy, A.A., Daniekyan, F.D., and Arakelyan, M.S., Species distribution models and niche partitioning among unisexual *Darevskia dahli* and its parental bisexual (*D. portschinskii, D. mixta*) rock lizards in the Caucasus, *Mathematics*, 2020, vol. 8, no. 8, p. 1329.
https://doi.org/10.3390/MATH8081329

Shitikov, V.K., Ecological Niches, Their Modern Interpretation and Modeling Using the Ecospat Package, 2021.
https://stok1946.blogspot.com/2021/09/blog-post.html. Accessed September 24, 2021.

Shitikov, V.K. and Mastitsky, S.E., Classification, Regression, and Other Data Mining Algorithms using R, 2017.
https://stok1946.blogspot.com. Accessed September 10, 2021.

Shitikov, V.K., Zinchenko, T.D., and Golovatyuk, L.V., Models of joint distribution of species with benthic communities from the small rivers of the Volga basin as a case study, *Zh. Obshch. Biol.*, 2021a, vol. 82, vol. 2, pp. 143−154.

Shitikov, V.K., Zinchenko, T.D., and Golovatyuk, L.V., Maximum entropy models and spatial distribution of bottom community species on the territory of the Middle and Lower Volga region, *Ross. Zh. Prikl. Ekol.,* 2021b, vol. 2, pp. 10−16.
https://doi.org/10.24852/2411-7374.2021.2.10.16

Soberón, J., Grinnellian and Eltonian niches and geographic distributions of species, *Ecol. Lett.*, 2007, vol. 10, no. 12, pp. 1115−1123.
https://doi.org/10.1111/j.1461-0248.2007.01107.x

Warren, D.L., Glor, R.E., and Turelli, M., Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution, *Evolution*, 2008, vol. 62, no. 11, pp. 2868−2883.
https://doi.org/10.1111/j.1558-5646.2008.00482.x

Zinchenko, T.D., *Ekologo-faunisticheskaia kharakteristika khironomid* (*Diptera, Chhironomidae*) *malykh rek basseina Crednei i Nizhnei Volgi* (*Atlas*) (Ecological and Faunal Characterization of Chironomids (Diptera, Chironomidae) of Small Rivers in Middle and Low Volga Basin (Atlas)), Togliatti: Kassandra, 2011.

Zinchenko, T.D., Shitikov, V.K., and Golovatyuk, L.V., Benthic communities and abiotic factors: analysis of statistical relationship using the instability index and virtual species distribution, *Zh. Sib. Fed. Univ., Ser. Biol.*, 2021, vol. 14, no. 2, pp. 119−132
https://doi.org/10.17516/1997-1389-0344

Translated by L.A. Solovyova

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