Analysis of the Relationship between the Phylogenetic Diversity of Benthic Communities and Degree of Mineralization of Plain Rivers of the Lower Volga River Basin

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Abstract—The statistical background for the relationship between the taxonomic diversity of macrozoobenthos and water mineralization is presented in the example of the benthic communities of plain rivers in the Lower Volga River basin. Significant differences have been found for a complex of 35 indices of species and phylogenetic α- and β-diversity in the tributaries of the Saratov and Volgograd reservoirs compared to the saline rivers of the Elton Lake basin. The hypothesis of phylogenetic niche conservatism [5] is confirmed by a significant effect of phylogenetic overdispersion at low and medium salinity of watercourses and phylogenetic clustering at high water salinity. Mean salinity tolerance has been assessed for each of the 356 species considered; this index was interpreted as the statistical probability of inhabiting the waters of certain mineralization by particular species. A statistically significant phylogenetic signal corresponding to the species traits was revealed by Pagel's lambda and Bloomberg's K tests. Mean salinity tolerance for taxa of various systematic levels has been presented as a cladistic tree.

Ecological communities are the organized associations of interacting species that inhabit a particular geographic region, characterized by a specific set of environmental conditions, during a certain time period [1]. The taxonomic composition of a community depends on the species ability to settle, its ecological tolerance to external factors, and the role it plays in interspecific relations, i.e., on the traits acquired by each species in the course of the general evolutionary history and current biogeographic processes [2]. The observed tendency of transferring the traits from ancestors to descendants, when phylogenetically close species are characterized by similar functional and ecological characteristics [3, 4], has become a hypothesis of phylogenetic niche conservatism [5, 6].

Phylogenetic analysis uses data on the hierarchically ordered structure of kinship relations between taxa (species, genera, families, etc.), presented in the form of a phylogenetic tree [7–9]. In general, a phylogenetic tree consists of a root, nodes, and vertices, the latter correspond to the real experimental objects. The nodes are connected by branches; the length of the latter can be measured, for example, in millions of years from the moment of divergence. Due to the development of molecular methods, this information appears nowadays rapidly for different systematic groups. The main task of phylogenetic analysis is to assess the degree of kinship relations within the tree structure, i.e., whether the tendency of resembling of closely related taxa is more pronounced and statistically significant than that for the taxa randomly extracted from a common tree [10].

The analysis of various aspects of diversity at different levels of ecosystem organization, from molecular to biosphere, is an important issue of modern biology [3]. Species diversity is usually assessed through a large set of heterogeneity indices, which combine the species richness and the probability ratio, as well as through evenness indices that have been developed in order to isolate the component of community equitability as a separate dimension [11, 12]. The objective need to consider phylogenetic differences between species has expanded the concept of diversity and resulted in emergence of a large set of taxonomic and phylogenetic indices [13–18].

Functional diversity is considered as the degree of species variability in the space of their characteristic properties (trait values) associated with morphometric traits, the spectrum limits of responses of certain species to the impact of environmental factors, productivity,

stability, rates of nutrient assimilation, etc. [19, 20]. The concept of a phylogenetic signal is used to analyze the relationship between taxa kinship and species traits [21, 22]. If one projects a phylogenetic tree onto the space of changes of ecological characteristics, then closely related species will be located side by side at a strong phylogenetic signal, i.e., the variability of their traits along the branches of the tree will be relatively small.

Modeling of the spatial distribution of species and biodiversity of communities under the influence of limiting environmental factors is an actual issue of ecology and biogeography. Earlier, the lists of indicator species, evidencing the regular change of the dominant taxa in different climatic zones in the series of reservoirs of the Volga River, have been compiled based on the study of benthic communities of small and medium rivers of the Middle and Lower Volga River basin [23]. The influence of the local geographic gradient on the dynamics of species diversity has been assessed, being evidence for the role of spatial autocorrelation due to the proximity of habitats [24]. The general trends in the formation of the species structure using the concept of meta-communities have been analyzed, including the testing of hypotheses about the consistent occurrence of species, the formation of compact associations of species, etc. [25]. A set of models for the joint distribution of chironomid species (Diptera: Chironomidae) has been developed using a set of indicators that characterize environmental conditions, phylogenetic relationships, spatial autocovariance, and the contribution of interspecies relationships calculated using the association matrix [26].

The study aims to perform a detailed analysis of the structure of benthic communities in regard to phylogenetic concepts and to identify the regularities of the effect of water mineralization, a limiting factor, on the closeness of kinship between species. The statistical distribution along the mineralization gradient of the salinity tolerance of individual species and taxonomic clusters of the highest level is estimated; groups of aquatic organisms with varying degrees of salinity tolerance have been identified.

MATERIALS AND METHODS

The dependence of the phylogenetic structure of benthic communities on water mineralization was analyzed using hydrobiological dataset obtained for lowland rivers in the basin of the Middle and Lower Volga River in different months of the growing season of 1990–2019 [27]. Taking into account the homogeneity of natural and climatic conditions in the entire array, 267 hydrobiological sampling sites were selected on 48 small and medium rivers in the steppe and areas affected by desertification (Fig. 1). At the sampling sites of benthos, environmental factors were measured simultaneously, including water salinity (in g/L). For comparative analysis, the set of observations was divided into two groups: "SV" are the tributaries of the steppe zone of the Saratov and Volgograd reservoirs, and "E" are saline rivers of the arid region of the Lake Elton basin. Both groups were characterized by approximately equivalent sample sizes of statistical units, i.e., macrozoobenthos samples taken according to standard methods and represented by a list of species and their specific abundances (ind./m^2; see Table 1 for details).

For each of the 356 species, a systematic description was carried out at 11 taxonomic levels using the Integrated Taxonomic Information System (ITIS, https://www.itis.gov): Species → Genus → Tribe → SubFamily → Family → SubOrder → Order → SubClass → Class → SubPhylum → Phylum. Tribe has been set as an independent level due to the fact that this gradation is of great practical importance for the species-rich family Chironomidae. On this basis, a matrix of taxonomic distances between each pair of species was sequentially formed and a cladistic tree was constructed in the Newick format.

All stages of data preparation and analysis were performed using packages of the R version 3.6.1 of the statistical environment language. The α-diversity indices for each of the 519 samples was calculated using the Diversity, Evenness, Rarity (DER) function of the EcoIndR package [28]. In total, 31 diversity indices were calculated for various categories: species richness, species rarity, species evenness, taxonomic complexity, and phylogenetic divergence.

The indices of phylogenetic α-diversity were calculated based on cophenetic distance d_{ij}, which was equal to the sum of the lengths of tree branches connecting two arbitrary species i-j, including:

MPD, the mean d_{ij} value for all species; MNTD, the mean distance to the nearest taxon [3, 7]; and Q Rao, Rao's quadratic entropy (a measure of diversity of ecological communities) [29], taking into account the relative abundance of species p_i and p_j.

PSV, the phylogenetic variability of species, which quantified how the relationship between species was associated with a hypothetical neutral trait, characteristic of all species in the community.

PSC, the phylogenetic clustering of species, which increased as the connection between the tops of the tree decreased; PSR, the phylogenetic richness of species; and PSE, species evenness [30].

Null models for estimating the expected distribution of MPD or MNTD values were developed under the process of multiple random permutations of tree nodes after which the value of the tested diversity indicator was calculated for each pseudo-sample. The standardized effect size (SES) was calculated by normalizing the difference between the empirical and zero-model metrics to the standard deviation of the null distribution [10].
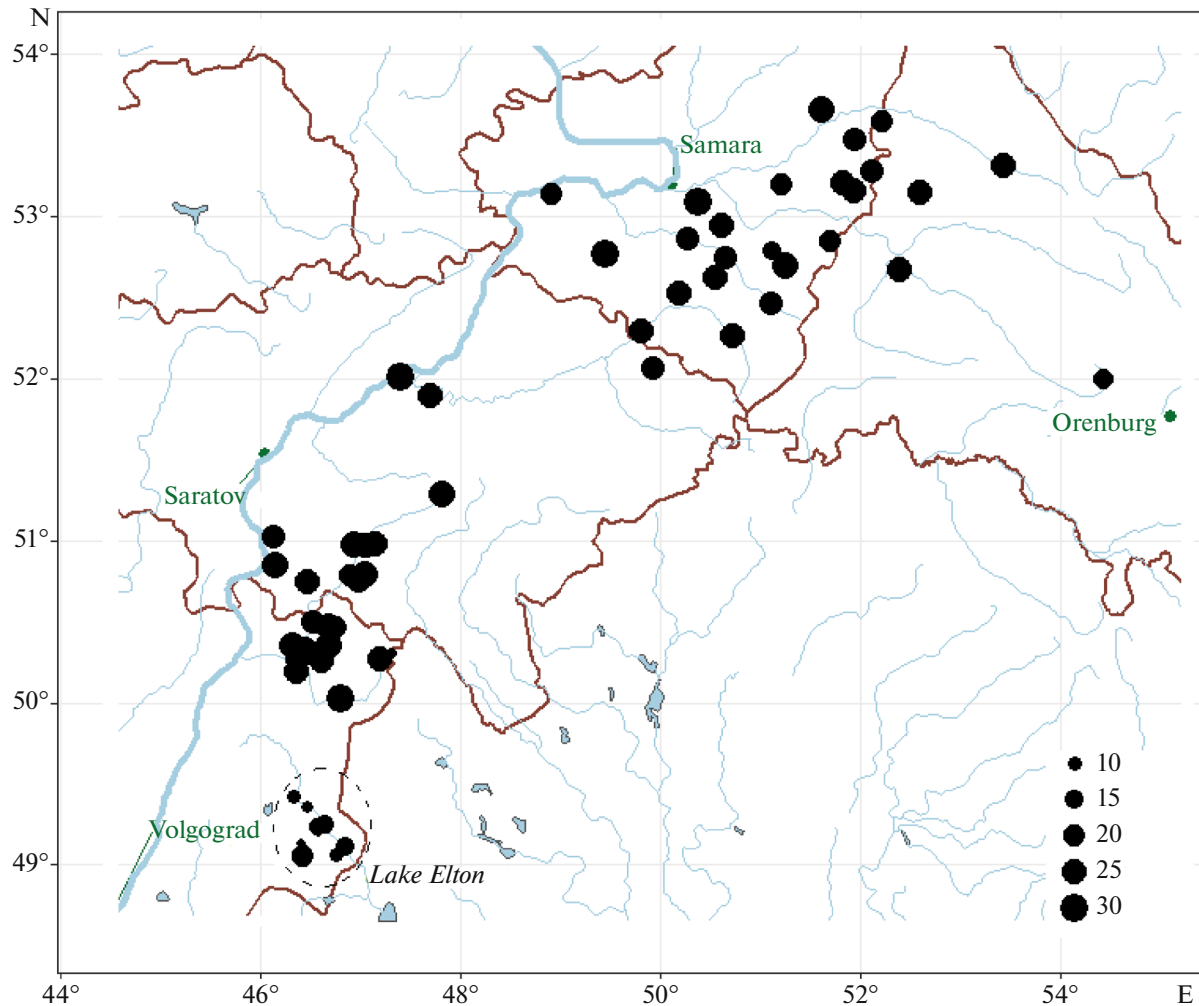
Fig. 1. Study area; the diameter of the circle at the sites of hydrobiological survey is proportional to Q Rao for benthic communities.

For the analysis of phylogenetic β-diversity, the matrices of distances between all combinations of pairs of macrozoobenthos samples were constructed using various metrics: (a) weighted average values of MPD and MNTD; (b) phylogenetic differences of PCD communities based on PSV assessment [31]; and (c) UniFrac or the relative share of unique phylogenetic diversity for two compared communities [32, 33]. These metrics were considered in two ways: (1) taking into account the relative abundance of species, and (2) without using weighted values.

The resulting matrices of phylogenetic distances were compared with the corresponding matrices of the Bray-Curtis and Sørensen distances using the *R* matrix coefficient of the Mantel linear correlation [34]. The linear models of the dependence of the distance matrices on the level of mineralization and subsequent decomposition of the sum of squares of deviations from the centroids of the compared groups were developed using the nonparametric analysis of variance npMANOVA [35].

The phylogenetic diversity indices were calculated in the R packages picante, phyr, and GUniFrac; statistical significance was checked by a randomization test and the mantel() and adonis() functions from the vegan package.

For each species, the mean salinity tolerance (MST) index was calculated, equal to the weighted average value of mineralization X_i (g/L) for n samples in which the species was found:

$$\text{MST} = \sum_n X_i N_i \Big/ \sum_n N_i,$$

where N_i is the transformed value of the abundance, ind./m^2. A similar value of salinity tolerance for tree nodes was calculated as the average MST of the species constituting each group, weighted by their frequency of occurrence in the samples.

The quantitative measure of the phylogenetic signal was estimated according to two statistical parameters, which were equal to zero if any dependence was absent, increasing in accordance with the increase of

Table 1. Mean biodiversity indices of macrozoobenthos in the tributaries of the Saratov and Volgograd reservoirs ("SV") and Lake Elton ("E")

Parameter	Total average	Group mean		t-Statistics	95% confidence interval difference
		"SV"	"E"		
Rivers/sites explored	48/60	41/50	7/10		
Mineralization, g/L (median)	2.7	0.59	15		
Samples taken	519	281	238		
Species registered	356	320	85		
Indices of species heterogeneity					
Number of species per sample	8.383	11.171	5.092	14.96	5.27–6.87
Shannon (1948), bit	1.852	2.470	1.123	22.25	1.22–1.46
Simpson (1949)	0.577	0.726	0.400	18.44	0.291–0.361
Brillouin (1956)	1.269	1.690	0.772	22.11	0.836–0.999
Margalef (1958)	0.955	1.341	0.499	17.17	0.745–0.938
Renyi (1961), $a = 1.5$	1.135	1.536	0.662	21.06	0.792–0.956
Menhinick (1964)	0.195	0.276	0.098	15.15	0.154–0.200
McIntosh (1967)	0.388	0.508	0.247	19.78	0.234–0.286
Berger and Parker (1970)	2.291	2.892	1.581	15.97	1.149–1.472
Hill (1973), $a = 1.5$	3.818	5.228	2.155	18.17	2.74–3.40
Tsallis (1988), $q = 2.5$	3.211	4.305	1.919	17.08	2.11–2.66
Evenness indices, by abundance					
Pielou (1966)	0.642	0.757	0.507	12.99	0.212–0.287
McIntosh (1967)	0.609	0.738	0.458	13.33	0.238–0.321
Heip (1974)	0.472	0.561	0.367	9.33	0.153–0.234
Camargo (1992)	0.094	0.120	0.064	12.28	0.047–0.065
Smith and Wilson (1996)	0.134	0.199	0.058	2.51	0.03–0.252
Taxonomic indices					
Diversity, D	35.34	47.28	21.25	18.57	23.2–28.7
Distinctness, Dstar	58.63	65.28	50.77	8.40	11.1–17.9
Phylogenetic indices					
Diversity, by Faith (1992)	208.63	268.34	138.13	15.35	113–146
Q Rao, by Rao (1982)	17.75	24.10	10.25	20.08	12.4–15.2
Mean paired distance, MPD	35.49	48.20	20.49	20.08	24.9–30.4
Mean distance between closely related taxa, MNTD	35.67	34.75	36.76	−1.34	*−4.96–0.945*
Species variation, PSV	0.583	0.641	0.515	9.46	0.099–0.152
Species richness, PSR	5.177	7.233	2.749	15.58	3.91–5.04
Species evenness, PSE	0.416	0.545	0.264	17.09	0.248–0.312
Species clustering, PSC	0.373	0.359	0.389	−2.75	*−0.051...−0.0086*

Equations for calculating the indices and full references to publications are given in [5]; statistically insignificant relationships are italicized.

the correlation between the degree of taxonomic relationship and the MST index:

— Pagel's lambda [21], approaching 1 if an explicit phylogenetic signal is present; it is based on the compression of internal branches in relation to the apex (at $\lambda = 0$, the tree has the form of a complete polytomy).

— Bloomberg's K [22], based on the Brownian model of random evolutionary drift, which takes place at K = 1; but if K > 1, it is considered that the species are more similar to each other than in the Brownian model.

The statistical significance of the phylogenetic signal was checked by comparing the variance of the observed patterns of independent contrasts (PICs) of the trait with a zero mixing model of taxa labels at the vertices of the phylogenetic tree.

Table 2. Results of the Mantel test and multivariate analysis of variance permMANOVA for groups of macrozoobenthos samples in the tributaries of the Saratov and Volgograd reservoirs ("SV") and Lake Elton ("E") for different matrices of phylogenetic distances

Metric for calculating the distance matrix	Mantel test		permMANOVA	
	r-statistics	p-value	pseudo-F	p-values
MPD taking into account the abundance of species	0.256	0.001	41.153	0.001
MPD unweighted	0.315	0.001	17.2	0.001
MNTD taking into account the abundance of species	0.49	0.001	16.9	0.001
PCD community differences	0.736	0.001	99.4	0.001
Unifrac weighted	0.452	0.001	98.563	0.001
Unifrac unweighted	0.798	0.001	94.244	0.001

A detailed description of the calculation technique, scripts in the R language and examples of calculations are freely available online on the authors' webpage https://stok1946.blogspot.com/2021/06/blog-post.html.

RESULTS

The location of sampling sites and the spatial distribution of quadratic entropy Q Rao over the study area are presented at Fig. 1. The average values of the diversity indices for various categories for the entire meta-community and group averages were calculated for all samples taken in the rivers of the Lake Elton basin (group "E") and tributaries of the Saratov and Volgograd reservoirs (group "SV") (Table 1). A lower level of diversity of benthic communities in the Lake Elton basin with a high level of statistical significance was observed when comparing the t-test means in all metrics, except those for MNTD and PSC. Dynamics of the main indices of species and phylogenetic diversity versus water mineralization (g/L, log-transformed) are presented at Fig. 2. The values of the Mantel correlation coefficient between the matrices of distances of species and phylogenetic diversity are given in Table 2, as well as the results of the permutation test in multivariate analysis of variance npMANOVA of matrices of distances with grouping of samples by "SV" and "E" affiliation.

For a comparative assessment of γ-diversity, the rows of the matrix of species abundance were combined by the groups "SV" and "E," and the unitary metrics of diversity were calculated, i.e., the measure of differences (Unifrac = 0.814) and the phylogenetic analog of the Sørensen similarity index (PhyloSor = 0.312). The measure of the PCD phylogenetic difference was considered as a multiplicative combination of the PCDc compositional component, which was a modification of the Sørensen metric for common species for the two communities, and the PCDp phylogenetic component, reflecting the relationship between mismatched species: PCD = PCDc × PCDp = 1.22 × 1.33 = 1.62.

Statistically significant differences were revealed in groups "SV" and "E" by the magnitude of the standardized size of the SES effect, assessed using the zero richness model with a fixed number of species. In particular, for the weighted MPD, the average SES value was −0.466 for the tributaries of the Volga River, and −1.17, for the rivers of the Lake Elton basin ($t = 7.69$, $p ≈ 0$). These values were −0.045 and −1.98, respectively, for the grouped rows of the species abundance matrix.

For all 356 species, the values of the average salinity tolerance of the MST were calculated, which varied from 0.27 to 30.5 g/L (mean of 3.35 g/L, median of 0.89 g/L). This made it possible to distinguish three groups of aquatic organisms: the species were considered oligohaline (freshwater) at MST < 1 g/L, polyhaline (halophilic), at MST > 10 g/L, and mesohaline or euryhaline, at intermediate values. Below, there is a list of some species from different ecological groups accompanied by an MST index and the species occurrence in samples. The halophilic taxa are represented by Chironomidae, Diptera (*Cricotopus salinophilus* (MST = 20.18/found in 168 samples out of a total of 519), *Chironomus salinarius,* 20.94/117), Ceratopogonidae, Diptera (*Palpomyia schmidti,* 25.92/104), Hemiptera (*Sigara assimilis,* 26.08/9), and Oligochaeta (*Paranais simplex,* 10.11/32). Euryhaline species are presented by Chironomidae (*Procladius ferrugineus*, 1.14/129; *Dicrotendipes notatus*, 1.18/54), Ceratopogonidae (*Sphaeromias pictus*, 5.71/67), Amphipoda (*Gammarus lacustris,* 8.29/33), and Oligochaeta (*Nais elinguis*, 9.17/21). Euryhaline species are presented by Chironomidae (*Tanytarsus pallidicornis*, 0.89/62; *Stictochironomus crassiforceps,* 0.94/45), Ephemeroptera (*Cloeon simile,* 0.42/22), Trichoptera (*Hydropsyche pellucidula*, 0.62/9), and Oligochaeta (*Nais pardalis,* 0.32/10), etc.

Fragments of the phylogenetic tree indicating the group values of salinity tolerance are presented in Fig. 3a (full tree from Phylum to Order) and Fig. 3b (for the most diverse Chironomidae family, from SubFamily to Genus).
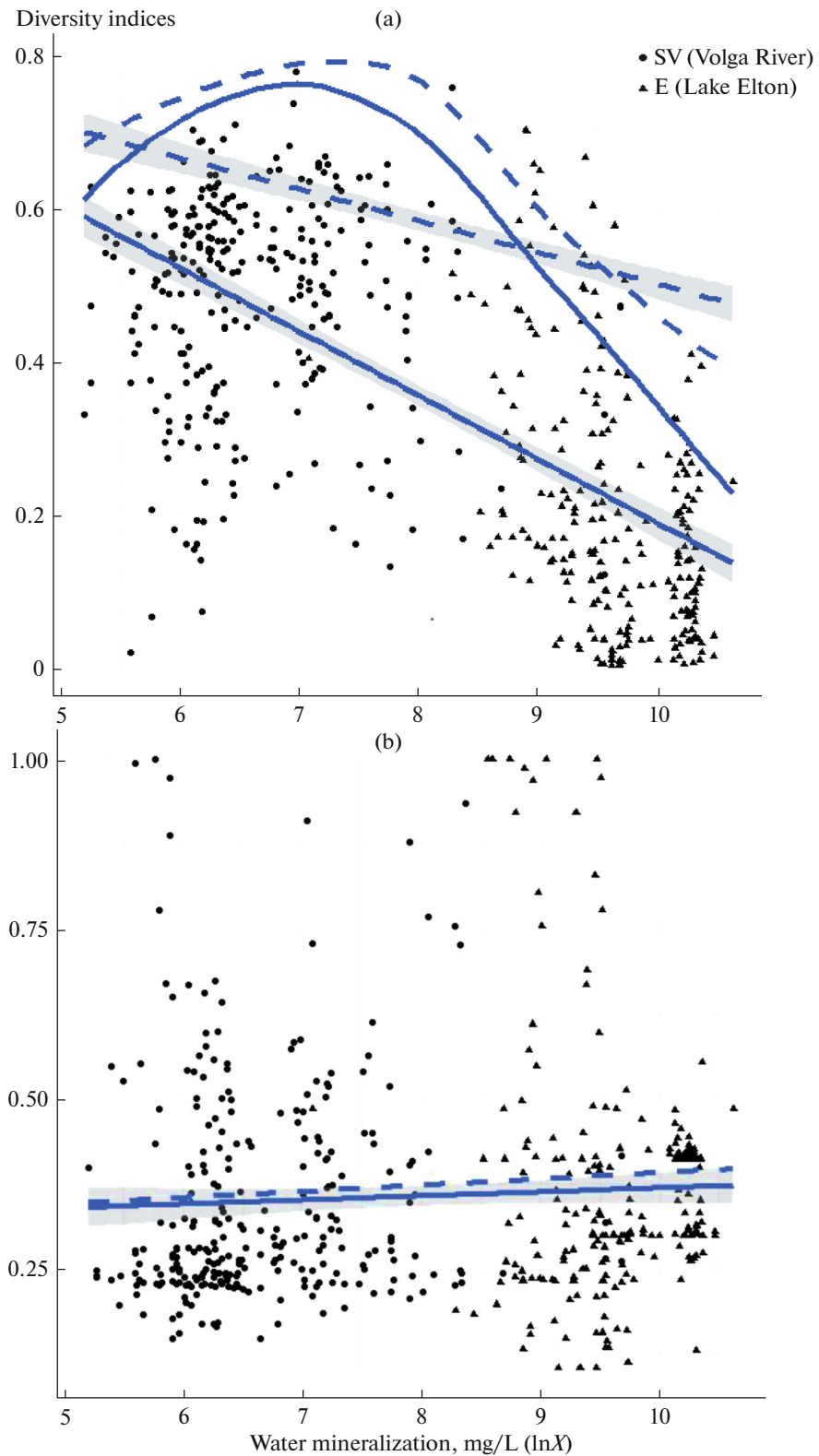
Fig. 2. Dependence of the main indicators of biodiversity on water salinity X (95% confidence intervals are shown in gray): (a) linear models for the mean paired distance, MPD $\times 10^{-2}$ (observation points are shown), and phylogenetic variation of species, PSV (dashed line); nonparametric smoothing curves for the Simpson index and Pielou index (dashed line); (b) linear models for the mean distance of the nearest taxa, MNTD $\times 10^{-2}$ (observation points are shown), and phylogenetic clustering of species, PSC (dashed line).

(a)
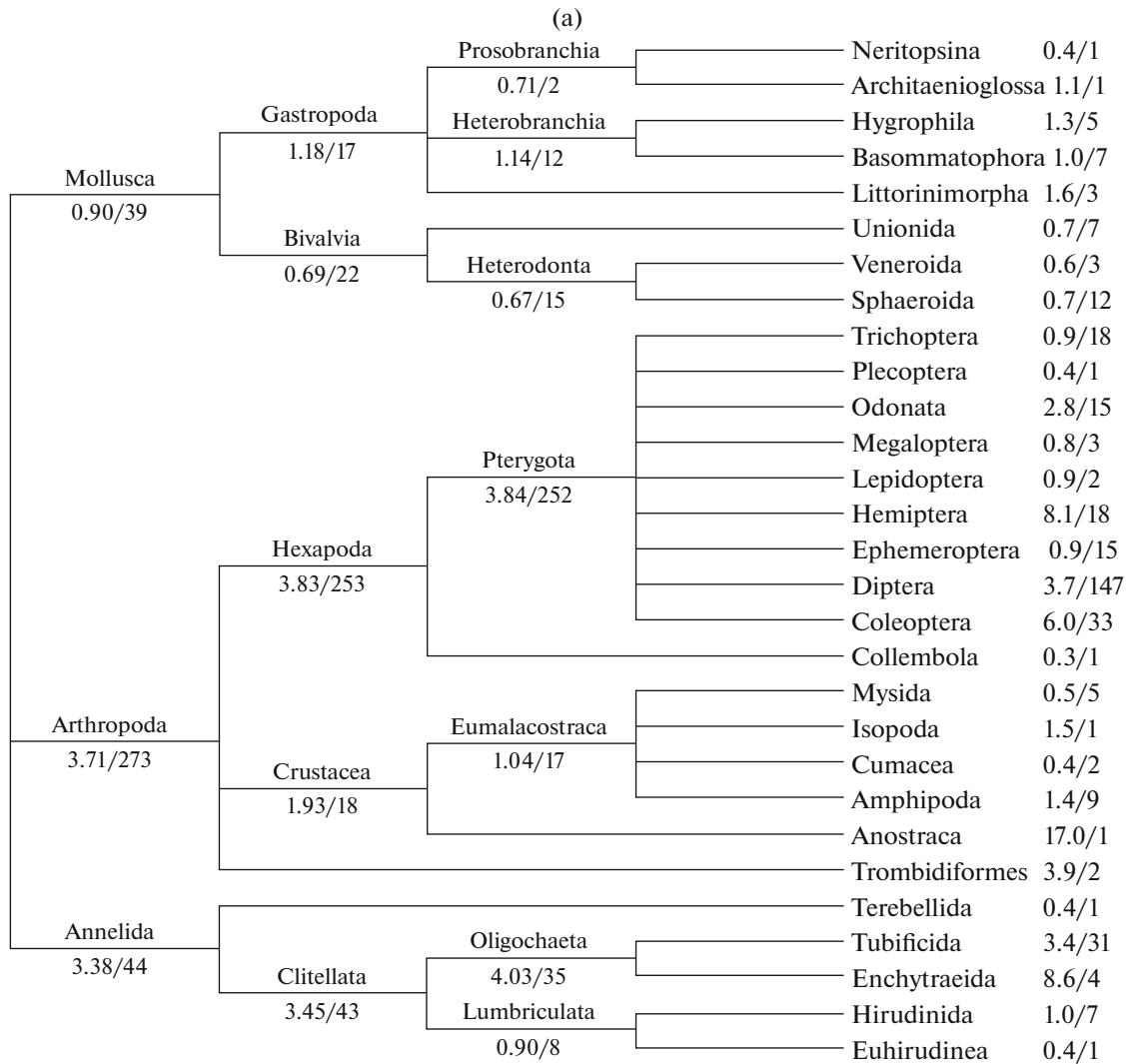
Fig. 3. Cladograms of the taxonomic composition of macrozoobenthos according to the results of the study (mean salinity tolerance/number of species in the clade): (a) common tree from Phylum to Order; (b) fragment of a tree for Chironomidae (Diptera), from SubFamily to Genus.

DISCUSSION

A high statistical significance ($p \approx 0$) was obtained for the relationship between the taxonomic structure of the meta-community and the mineralization of the aquatic environment when assessing the degree of the phylogenetic signal: Pagel's lambda = 0.789, Bloomberg's K = 0.318.

Our analysis of community diversity is inevitably associated with certain assumptions. Strictly speaking, hydrobiological samples, generalized into two groups, are non-random and non-independent, since the tributaries of the Volga River reservoirs occupy a much larger territory than the basin of Lake Elton, which inevitably affects the value of γ-diversity. However, we perform statistical tests solely based on estimates of α-diversity for individual samples, the value of the latter does not depend on the study area.

Formally, we have used not a phylogenetic, but a taxonomic tree (cladogram) in the analysis. Although biological diversity is a result of phylogenesis, many ecological tasks are based not on the evolutionary context, but on traditional biological systematics [36]. Moreover, many hypotheses based on modern phylogenetic models consider the patterns of formation of structures from only the existing species nowadays and are not directly related to evolutionary history [37]. Since the need to consider evolutionary time T is not always obvious in community ecology, it is possible to use the trees with nodes representing specific taxa of different ranks, so the length of each branch becomes 1 [14]. The procedures for analyzing the topology of

(b)

Xenopelopia	1.3/1
Thienemannimyia	0.7/1
Telopelopia	0.5/1
Tanypus	1.1/2
Rheopelopia	0.4/1
Procladius	2.4/3
Paramerina	0.6/1
Macropelopia	0.6/1
Labrundinia	1.2/1
Guttipelopia	0.4/1
Clinotanypus	1.1/2
Apsectrotanypus	0.5/1
Ablabesmyia	1.2/4
Prodiamesa	0.5/1
Monodiamesa	0.6/1
Thienemanniella	1.0/1
Rheocricotopus	0.7/1
Psectrocladius	4.1/4
Parasmittia	17.0/1
Parametriocnemus	0.8/2
Paralimnophies	1.3/1
Paracladius	0.8/1
Orthocladius	0.4/1
Nanocladius	1.7/1
Limnophies	1.2/1
Eukiefferiella	0.6/1
Cricotopus	9.0/9
Corynoneura	2.1/4
Brillia	0.4/1
Acricotopus	0.5/1
Tanytarsus	5.1/3
Stempellina	0.7/1
Rheotanytarsus	1.1/1
Paratanytarsus	2.7/5
Micropsectra	0.7/3
Cladotanytarsus	1.0/1
Xenochironomus	0.9/1
Stictochironomus	0.7/2
Polypedilum	0.6/7
Paratendipes	0.5/1
Paralauterborniella	0.5/1
Paracladopelma	0.5/1
Parachironomus	1.4/1
Microtendipes	0.5/1
Microchironomus	9.8/2
Lipiniella	0.8/1
Lauterborniella	0.3/1
Glyptotendipes	4.1/6
Fleuria	4.2/1
Endochironomus	1.3/3
Dicrotendipes	1.1/2
Cryptotendipes	0.5/1
Cryptochironomus	0.7/2
Cladopelma	1.0/1
Chironomus	5.6/10

Tanypodinae
1.12/20

Prodiamesinae
0.55/2

Orthocladiinae
4.44/30

Chironominae
2.67/59
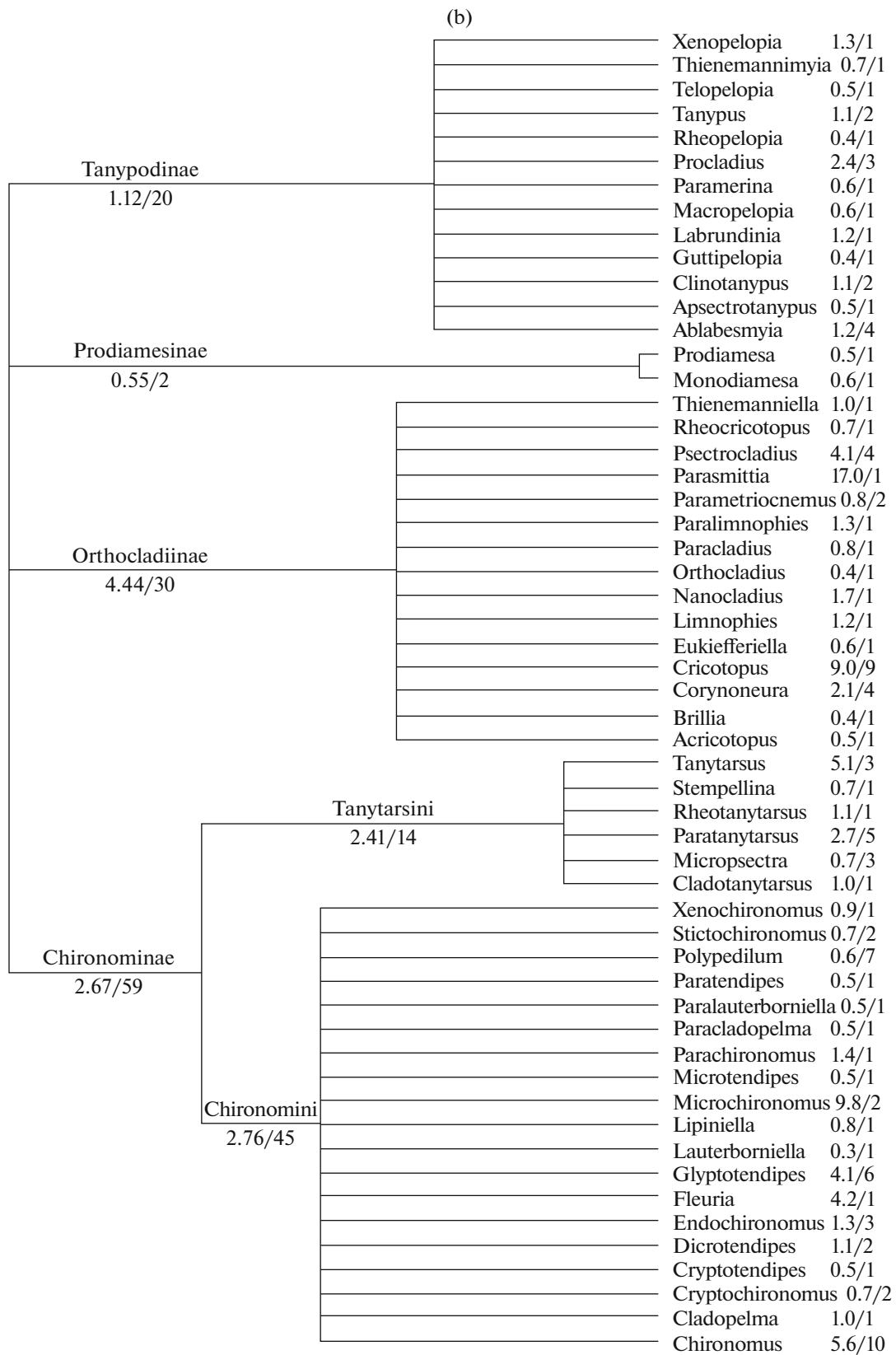
Tanytarsini
2.41/14

Chironomini
2.76/45

Fig. 3. (Contd.).

phylogenetic trees remain correct if time T is replaced by number of taxonomic categories L [18].

Most of the species and phylogenetic metrics synchronously showed a lower level of diversity of benthic communities in the Lake Elton basin (Tables 1, 2) and justify its inversely proportional dependence on water salinity (Fig. 2a). Similar results [38] prompted the authors to state that additional taxonomic, genetic, and functional aspects were excessive to consider when assessing diversity. If one considers the widespread fact of impoverishment of the structure of communities under the influence of extreme environmental factors, then one cannot but agree with this opinion. However, when there is a task of studying subtle dynamic mechanisms, i.e., which groups of species disappear from the community first, or due to which functional properties the productivity decreases, then these aspects inevitably come to the fore.

Both biotic and abiotic factors play a decisive role in the formation of the community structure. When the limiting environmental factor(s) is(are) absent, competitive exclusion processes play a key role, lowering the degree of species relationships in the community compared to a random set of species, since closely related species will compete more strongly with each other in accordance with the principle of phylogenetic niche conservatism. This effect is defined as phylogenetic overdispersion [5], confirmed by high values of diversity indices at low and medium water salinity (Fig. 2a).

If environmental limitations prevail over interspecific competition, then external factors determine the conditions for the formation of the species composition of each specific community and filter out the species that do not meet the environmental requirements (environmental filtering). Then, phylogenetic niche conservatism brings the community to a random set of species (to a lower diversity); this effect is defined as phylogenetic clustering [5]. A very moderate increase in clustering is observed in Fig. 2b; the degree of clustering is estimated by the MNTD and PSC indices. This effect is actually more pronounced, since the value of the indices also depends on the number of species in the community.

According to the assessment of the standardized size of the SES effect using the MPD index, the clustering of communities in the Lake Elton basin results in a significantly lower phylogenetic diversity compared to a random set of species. The negative effect obtained for the tributaries of the Volga River suggests that the entire macrozoobenthos community is characterized by relatively weak competitive exclusion in comparison with other systematic groups.

All phylogenetic indices include two components in one way or another: compositional (list of species) and phylogenetic (the degree of similarity of two trees). Comparison of various β-diversity matrices with the Bray-Curtis or Sørensen distance matrices

(Table 2) makes it possible to estimate their relative proportion: the phylogenetic component of MPD/MNTD is more pronounced than that of Unifrac/PCD. The choice of a specific metric depends on the specific task at hand, for example, when analyzing the influence of the environmental factor, it is preferable to use PCD, which allows decomposition into separate components of PCDc and PCDp.

In real conditions, each species has an indefinite and often multimodal distribution of its ecological properties along the gradient of most environmental factors. The lack of practical ability to model this accurately has led to a case, where the species are characterized by one value of a functional trait, for example, mean or median [39]. Earlier, we have performed a multivariate analysis of the structure of benthic communities depending on the water salinity and have developed the lists of species with different salinity tolerance based on the results of ordination [40].

With a large number of rare species, such calculations become unreliable, and, therefore, we propose here an indicator of the MST, which is interpreted as the statistically based expectation of water mineralization at which the species is most likely to inhabit the watercourse. A statistically significant, albeit rather moderate, relationship between the species MST and the taxonomic structure is obtained when analyzing the phylogenetic signal according to the Pagel's lambda and Bloomberg's K criteria.

The average MST value obtained for systematic clades (Fig. 3) makes it possible to rank groups of aquatic organisms according to the predominant habitat zones associated with the water salinity. For example, this is true for the subfamilies of chironomids: Orthocladiinae, 4.44 g/L > Chironominae, 2.67 > Tanypodinae, 1.12 > Prodiamesinae, 0.55 g/L. However, only certain species of the genera *Cricotopus, Tanytarsus*, and *Chironomus* are reliably halophilic and euryhaline taxa of the first two subfamilies. The groups Ephemeroptera, Plecoptera, and Trichoptera, which are used for the EPT water quality index, are salinity-sensitive taxa according to our study.

We have established a regularity in the growth of the intragroup dispersion of the MST depending on the number of species in the clade. Like the known SAR models, the latter is well approximated by a power function. From a practical point of view, this means that the higher the level of taxonomy is used for biotic assessment of water quality, the greater the uncertainty of the resulting forecast. Since there is a significant scatter of the taxon responding to environmental conditions even at the genus level, then such a prediction using subfamilies may turn out to be erroneous.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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