

Variation of the Epiphytic Lichen Diversity in a Gradient of Atmospheric Pollution: Do Taxonomic, Genetic, and Functional Distances between Species Add any Information?

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Studying the influence of reduced biological diversity on functioning and stability of ecosystems is one of the priorities of modern ecology [1]. Numerous approaches to quantitative estimation of diversity have been developed [2], which even used to be a hindrance to the progress of ecology for some time. Recently, however, researchers succeeded in presenting all of the diversity metrics as special cases of several generalizing relationships [3–5]. This enabled them to focus on the essential issues, rather than to compare mechanically the indices with one another. The paradigm shift going on in quantitative ecology is related to the rejection of the biodiversity concept that takes into account only the number of species and the ratio of their abundances. Biodiversity is considered more broadly when the taxonomic, genetic, morphological, and functional differences between species are also analyzed. Each of these aspects is believed to add some new information that implies not only traditional species diversity [6, 7]. It has been proposed, therefore, to differentiate between *diversity* (in the narrow sense) and *disparity* of the biotic communities [8]. In the former case, all species are assumed to be equivalent, and their contribution into diversity depends only on their abundances; in the latter case, the differences between species are taken into account. The transition from “simple” species diversity to disparity is based on the distances between species, which are the following: (1) taxonomic ones that depend on the species systematic positions and are calculated as the minimal path between two species on the taxonomic tree; (2) genetic

distances calculated on the basis of molecular genetic data, i.e., amino acid or nucleotide sequences in proteins or DNA, respectively; (3) functional distances that are assessed by similarity between the functional groups belonging to different life forms, environmental strategies, trophic groups, etc. [9].

If the distances between species are important for biodiversity assessment, then strong perturbations that disturb ecosystem equilibrium should lead to significant differences between the indices of diversity and disparity. In this study, we aimed to test this hypothesis using the epiphytic lichen communities, which are extremely sensitive to atmospheric pollution of the biotic components [10]. Industrial emissions from a large point source served for studying the effect of the perturbation on the lichen communities. We used the description of the epiphytic lichen cover over the birch trunks (*Betula pubescens* Ehrh. and *B. pendula* Roth) made in 1995–1998 for 208 sample sites uniformly distributed over an area of 40 × 50 km with the Middle Ural Copper Smelter in the center (Revda City, Sverdlovskaya oblast). On the basis of concentrations of heavy metal (Cu, Pb, Zn, Cd) mobile forms in forest litter, we distinguished five zones of the anthropogenic load: the background zone (I, $n = 14$) and zones of poor, moderate, severe, and extremely severe pollution (II, $n = 98$; III, $n = 43$; IV, $n = 29$; V, $n = 24$; respectively). Detailed zoning is described in [11]. Sample sites that contained no lichens ($n = 7$) were excluded from analysis. In each sample site, a lichen cover of 10 at least 60-year-old trees was described using a 10-cell grid of 0.5 m height, and width equal to half of the trunk diameter; scoring of species abundance (from 1 to 10) was performed at two heights (0–50 and 100–150 cm). Afterwards, the abundance was averaged for

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the heights and trees to calculate eight indices (table), which were special cases of Rao’s quadratic entropy [4].

Taxonomic distances were estimated on the basis of the last systematic report [12]. Functional classification is based on 21 traits (species reproductive strategies, life forms, substrate specialization, and secondary metabolite composition) that were used for calculation of Gower’s generalized coefficient [13]. The genetic distances were determined using the nucleotide sequences of ribosomal DNA from GenBank (18S, ITS1, 5.8S, ITS2, 28S). After multiple alignment of the nucleotide sequences with an average length of 596 bp, the evolutionary distances were estimated using the Tamura–Nei nucleotide substitution model. All of the distances obtained were brought to the interval from 0 (the maximum similarity of a pair of species) to 1 (the maximum difference). To verify the hypothesis on the equivalence of diversity indices (i.e., similar trends of their variation in a pollution gradient and equal resolution), we used nonparametric ANOVA (the adjusted rank transform test) [14] and determined the significance of the “zone of pollution × index” interaction. Confidence intervals for the estimates of index informativity were calculated using the bootstrap (10 000 replications). All calculations were performed using the Rv.2.15.3 software.

Forty-three species of epiphytic lichens were found in the area of investigation. The taxonomic and genetic distances were closely correlated (Mantel’s rank-order correlation coefficient $r_m = 0.532$, $p \ll 0.001$, $n = 903$). This is to be expected because the distances reflect the evolutionary relationships of species, albeit in different degree. In contrast, the functional distances depend on neither taxonomic, nor genetic

Relationship between the indices of diversity

Condition for interspecific distances	Condition for species abundance	
	$p_i \neq \text{const}$	$p_i = \text{const}$
$d_{ij}^{(x)} \neq \text{const}$	$D_x = \sum_{i < j} d_{ij}^{(x)} p_i p_j$	$I_x = \frac{\sum_{i < j} d_{ij}^{(x)}}{S^2}$
$d_{ij}^{(x)} = \text{const}$	$D_0 = 1 - \sum_{i=1}^S p_i^2$	$1/S$

p_i and p_j , the proportion of abundance for the species i and j ; $d_{ij}^{(x)}$, the distance between the species i and j [0; 1]; x , the type of distances between species ($x = t, g, f, t$, taxonomic, g , genetic, f , functional). D_x , Rao’s quadratic entropy; I_x , intensive entropy; S , number of species; D_0 , the complement of Simpson’s index.

ones ($r_m = 0.114$, $p = 0.083$ and $r_m = 0.042$, $p = 0.292$, respectively).

Along the pollution gradient, the values of all indices decreased: smoothly from zone I to zone IV and sharply from zone IV to zone V (Fig. 1). In the flat segment of the trend changes in the indices of species abundance were more pronounced: unlike in the other group, not only zone V, but also zone IV differed significantly from zones I and II.

The direction of changes along the pollution gradient was similar for all indices: interaction between the zone and the index type was nonsignificant in all cases ($F(4; 392) = 0.734 - 2.064$, $p = 0.339 - 0.909$). The indices did not differ significantly in informativity,

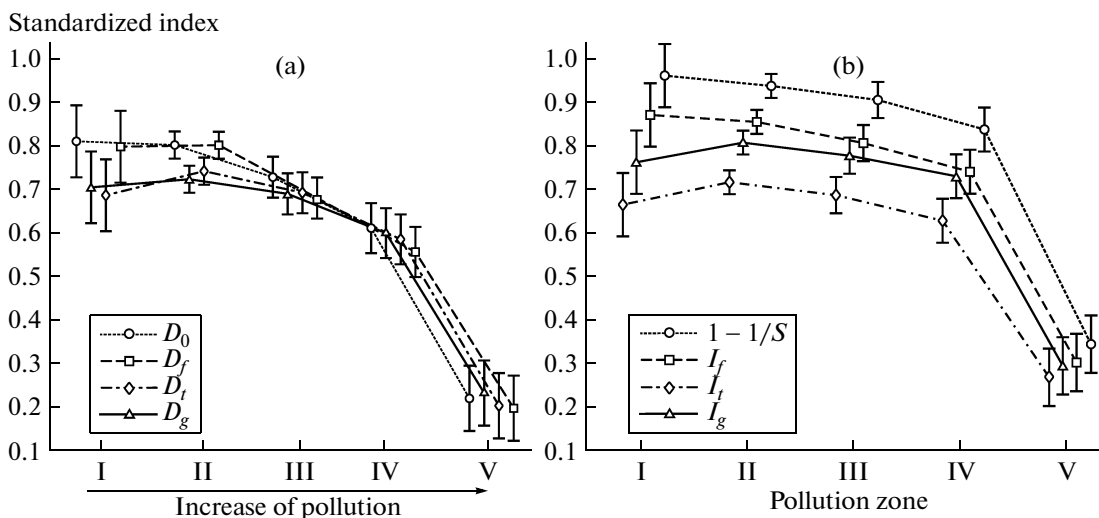


Fig. 1. Variation of diversity indices of the epiphytic lichen communities in a pollution gradient: (a) indices that take into account species abundance; (b) indices that do not take into account abundance. The mean ± 95% confidence interval is indicated; accounting unit is the sample site.

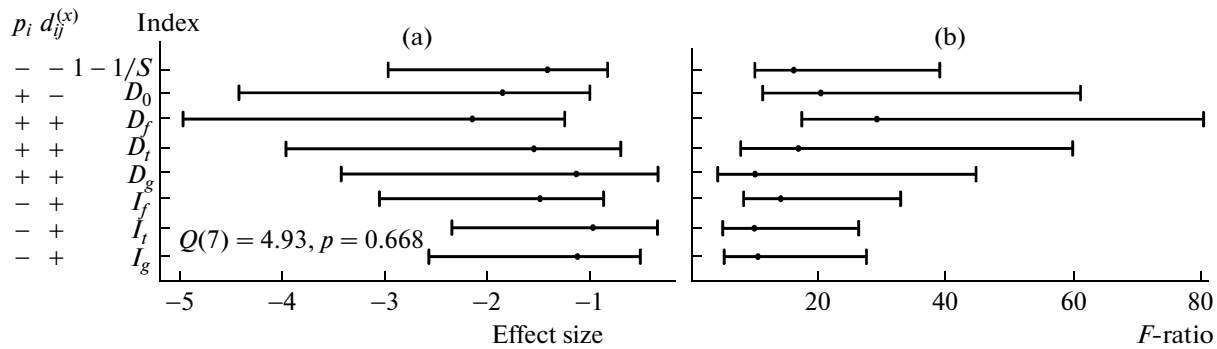


Fig. 2. Informativity of diversity indices of the epiphytic lichen communities in a pollution gradient: (a) the effect size (Q , test for the effect homogeneity); (b) Fisher's ratio. The components taken or not into account by the index (+ and –, respectively): p_i , species abundance; $d_{ij}^{(x)}$, the distance between species. Horizontal lines indicate 95% confidence interval.

which was assessed either as the effect size (Cohen's d for two contrast levels of pollution, Fig. 2a), or as Fisher's F ratio (for the entire gradient, Fig. 2b).

Similar trends found in variation of different indices were rather unexpected. In terms of the prevailing view on the high probability of co-extinction of closely related species, we expected that genetic and taxonomic diversity drops down less dramatically than the species diversity. We also expected that, with increasing toxic load, the functional diversity changes either more slowly, or, in contrast, much more rapidly than the species diversity. The assumption on a smoother decrease in the functional diversity supports modern ideas about the functional redundancy of communities [15], which are based on the fact that the number of groups is much lower than the number of species (in our case, 43 species can be grouped into four to six clusters according to the functional distances). The opposite scenario—a sharp drop of functional diversity—is expected if a loss of entire functional clusters occurs because of a close relationship between species sensitivity to pollution and the functional traits.

Thus, our results suggest that a loss of one or another lichen species with increasing pollution is equally probable and does not depend on the groups formed according to similarity of genetic, taxonomic, or functional traits of the species. All of the indices studied give practically similar information on the changes in the state of lichen communities in a pollution gradient. Therefore, considering different aspects of a community disparity gives no advantage in the accuracy of the diagnosis over Simpson's index and species richness.

It should be emphasized that our results can be specific for the object and the pollution gradient studied here. In addition, the construction of taxonomic and genetic trees with a higher resolution needs a larger number of species than in the communities studied; note also that the functional roles of many morpho-

logical and physiological traits of lichens still remain unclear. Hence, more large-scale testing of the original hypothesis is required not only for other biotic objects (multispecies communities should be preferred), but also for other areas and types of perturbing factors.

Nevertheless, to answer the question put in the title, we can conclude that analysis where distances between species were taken into account fails to give more information on changes in diversity under the influence of anthropogenic factors. Simple traditional indices are less laborious and more informative; those ones which takes species abundance into account are more sensitive to the rate of changes under moderate loads.

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