http://dx.doi.org/10.1016/j.ecolind.2014.03.011

Ecological Indicators Volume 45, October 2014, Pages 28–36

The role of phytoplankton diversity metrics in shallow lake and river quality assessment

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Abstract

Ecological water quality problems are frequently connected to increment of phytoplankton productivity and overdominance of some phytoplankton species. Metrics that show monotonously increasing or decreasing tendencies along stressor gradients is recommended for ecological state assessment. Diversity metrics are influenced by various physical disturbances and show high within-year variability; thus, there is no agreement on the usefulness of these metrics as state indicators.

To test the usefulness of phytoplankton diversity in ecological state assessment we investigated the productivity-diversity relationships for lakes and rivers in the Carpathian Basin (Hungary). We demonstrated that the shape of productivity-diversity relationship depends on the investigated water body type. Regarding lakes, hump-shaped relationship was found for all computed metrics. Parallel with the increase in phytoplankton productivity values, diversity metrics showed monotonously increasing tendencies in rhithral and decreasing tendencies in large potamal rivers. We found no systematic relationship in the case of small lowland rivers.

Changes of diversity metrics calculated for species and functional groups showed similar tendencies within the types, only the slopes of regression lines differ each other.

The use of diversity metrics as ecological state indicators should be restricted to water body types where diversity decreases or increases monotonously with phytoplankton biomass. Regarding the lakes the use of diversity metrics is not recommended for ecological state assessment. In rhithral and large potamal river assessment, application of diversity metrics should be strongly considered. We demonstrated that diversity metrics can be useful components of multimetric indices proposed to use by the Water Framework Directive.

Key words: potamal rivers, rhithral rivers, species diversity, functional diversity, contradictory trends

1. Introduction

Diversity is indisputably one of the most frequently used quantitative descriptors of communities. Diversity metrics are capable of describing system properties such as complexity, stability, and functioning of ecosystems (Hacker and Gaines, 1997); therefore, they became parts of several multimetric indices used for biological quality assessment (Hering et al., 2006; Stoddard et al., 2008; Carvalho et al., 2013). Applicability of diversity-based approaches needs a clear relationship between stressors and diversity metrics as response variables (European Commission, 2010). The nature of these relationships depends on the types of the anthropogenic disturbances and the responses of biological assemblages. In highly diverse natural assemblages human-caused environmental changes result in a decrease both in functional and species diversity (Gabriels et al., 2010). In the case of benthic diatoms, assemblages exhibit opposite responses to nutrient enrichment. Sonneman et al. (2001) demonstrated that sites with low nutrient concentrations were more species-rich than mildly enriched sites. In contrast Stevenson et al. (2008) found that species diversity of stream phytobenthos increases with phosphorus enrichment. These examples indicate that prior to the application of diversity metrics as ecological indicators the possibilities and limitation has to be investigated.

Due to central role in the aquatic food chain, phytoplankton is one of the biological quality elements that have to be monitored and assessed in Europe (European Commission, 2000). Based on quantitative and qualitative characteristics of phytoplankton several types of metrics have been elaborated and used in Europe: e.g. biomass, sensitivity/tolerance, composition and bloom metrics (Carvalho et al., 2013). Among the various water quality problems, eutrophication is indisputably a phenomenon that is closely related to phytoplankton issues. Nutrient enrichment coincides with enhanced phytoplankton production and impoverishment of floristic composition in lakes and large potamal rivers as well (Schmidt, 1994; Thorp et al., 1998; Wehr and Descy, 1998; Borics et al., 2007; 2013; Stanković et al., 2012). Several human induced alterations of the aquatic ecosystems result in the overdominance of some phytoplankton taxa (Naselly-Flores et al., 2003), which cause the decrease of diversity; therefore, diversity indices as state indicators seem plausible ecological assessment measures.

Phytoplankton diversity is influenced by the fluctuation of the resources (Sommer, 1984) and not by their absolute quantity; thus, diversity metrics cannot be studied by the traditional stressor-metric relationships, as it is proposed in technical guidance (European Commission, 2010), and has been done in the nutrients-sestonic chl-a and nutrients-sensitivity metrics relations. Instead of that, we investigated the changes of diversity along phytoplankton productivity, which is the most robust phytoplankton metric used for quality assessment (Carvalho et al., 2013).

Diversity is frequently studied as a function of productivity in the case of plants, animals or microbes (Adler et al., 2011; Grime, 2001; Chase and Leibold, 2002; Borics et al., 2012; Fridley et al., 2012; Skácelová and Lepš, 2013). Besides its theoretical importance, the shape of this relationship provides useful information on the practical use of diversity metrics as state indicators. Ecological state assessment should be based on clear relationship between the stressor(s) and the indicator metrics, i.e., the metrics should exhibit monotonously increasing or decreasing tendencies with increasing anthropogenic loads (European Commission, 2010). As phytoplankton productivity can be considered as a proximate measure of anthropogenic loads (Borics et al., 2013), investigation of the productivity-diversity relationships, in an indirect way, inform us about the role of diversity in phytoplankton-based ecological state assessment.

The specific objective of this study is to investigate the usefulness of diversity metrics in phytoplankton-based water quality assessment, and to set the limits of their application. Thus, we tested the following hypotheses:

- The shape of the phytoplankton productivity-species diversity curves depends on water body types.
- Functional diversity metrics are more sensitive measures of productivity than those calculated for species data.

2. Material and methods

2.1. Data

For the analyses phytoplankton and chlorophyll-a (chl-a) data were provided by the Hungarian national water quality monitoring system. Data of 25 lakes and 71 rivers were used for the investigations. Lake samples were from the photic layer (2.5×Secchi depth) of the lakes. In the case of the very shallow lakes (Z_{max} < 2m) the whole water column was sampled. River samples were collected from the immediate surface layer of the thalweg. There were monthly samplings in the growing season. Samples were fixed by Lugol's solution on the spot. Algal counting was performed using the Utermöhl's settling procedure (Lund et al., 1958). Algae were identified to species level. Standard geometric models (Hillebrand et al., 1999) were used to calculate phytoplankton biovolumes. Sestonic chl-a as a surrogate measure of phytoplankton productivity was used to analyse phytoplankton productivity-diversity relationships.

2.2 Applied metrics

We characterize the diversity of phytoplankton by four diversity indices (species richness, Shannon index, Simpon index, Berger-Parker index); each of these indices is a member of the Rényi diversity index family (eq. 1) (Rényi 1960, Tóthmérész, 1998). This is a so-called one-parametric diversity index family: the diversity of an assemblage is characterized by a (scale-dependent) diversity profile instead of a numerical value (see Fig. 1). By increasing the value of scale parameter (α), the contribution of abundant species to the diversity of the assemblage increases, and the contribution of rare species decreases. This is a solution of the classical index choice problem: one may wish the index to be sensitive to the composition of the abundant species but relatively indifferent to that of the rare ones (Peet, 1974). Diversity profiles can be used in a graphical form to visualize the diversity relations of an assemblage as shown by Fig. 1 for the assemblages A and B based on Rényi diversity index family (Tóthmérész, 1995). We have used the following α values: 0, 1, 2, ∞. When the value of the scale parameter is 0, then the value of the Rényi diversity is the logarithm of the number of species (eq. 2). It is extremely sensitive to the presence of rare species: a species present as a single individual has the same contribution to HR(0) as the most abundant species. When the value of the scale parameter is 1, Rényi diversity is identical to the Shannon index of diversity (eq. 3). It is less sensitive to the rare species than HR(0). When the value of the scale parameter is 2, the Rényi diversity is equivalent to the Simpson diversity (eq. 4), and it is more sensitive to the frequent species than to the rare ones. HR(∞) is the logarithm of the relative abundance of the commonest species, and ignores the others (eq. 5); it is usually mentioned as Berger-Parker diversity (Berger and Parker, 1970).

eq.1 $$HR_{\alpha} = \frac{1}{1-\alpha}\log\sum_{i=1}^{S} p_i^{\alpha} \text{ where } \alpha \geq 0 \text{ and } \alpha \neq 1,$$

eq.2 $$HR_0 = \log S,$$

eq.3 $$\lim_{\alpha\to 1} HR_{\alpha} \equiv HR_1 = -\sum_{i=1}^{S} p_i \log p_i ,$$

eq.4 $$HR_2 = -\log\sum_{i=1}^{S} \mathrm{p}_{\mathrm{i}}^2 ,$$

eq.5 $$HR_{\infty} = -\log(\max p_i).$$

To study functional diversity, species were assigned to functional groups based on the literature (Reynolds et al., 2002; Borics et al., 2007; Padisák et al., 2009). Functional diversity was defined as diversity of functional groups in the samples. All diversity calculations were based on algal biovolumes.

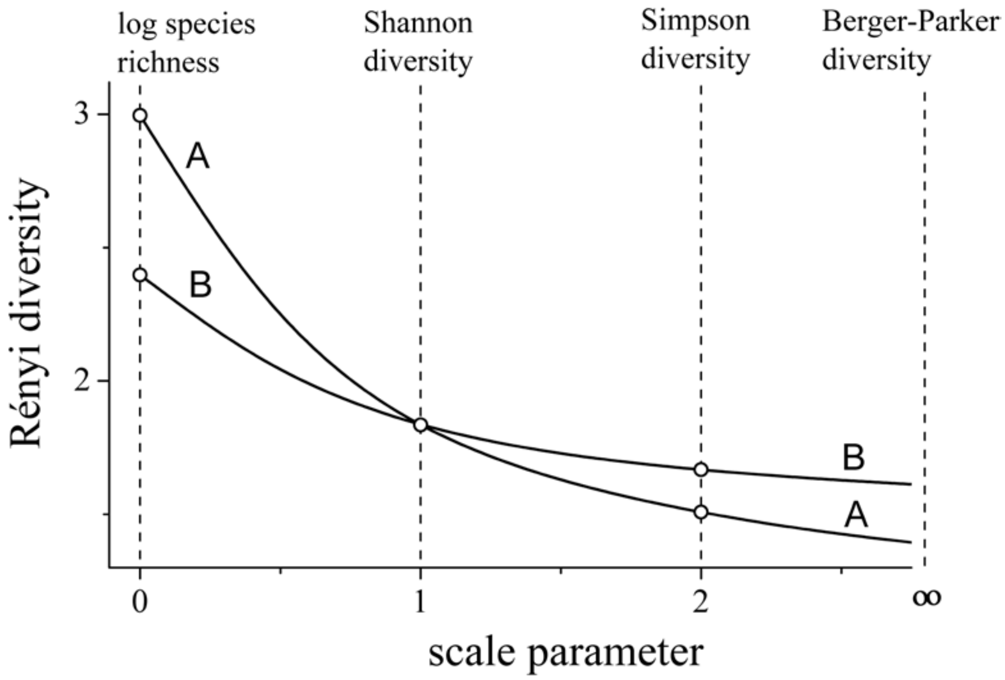

Fig. 1
Diversity profiles of the one-parametric Rényi diversity index family for two hypothetical assemblages, denoted by A and B. Vertical dotted lines denotes the particular values of the scale parameter (measured along the x-axis) which provides classical diversity index statistics, like number of species, Shannon, Simpson, and Berger-Parker index of diversity.

2.3 Data analysis

We hypothesised that phytoplankton productivity-diversity relationship depends on the type of water bodies; therefore, three river types were studied. A: rivers of the mountain and hilly region, and lowland rivers with coarse sediment (rhithral rivers); B: small lowland rivers with fine sediments; C large potamal rivers. We had one lake group: the shallow eutrophic lowland lakes.

A linear regression model was used to study the relationship between chl-a and diversity metrics in rivers. To reduce skewness of chl-a data, logarithmic transformation was used. In the case of lakes where the relationship was nonlinear, to reveal the general shape of the relationship General Additive Model was used with the Gamma distribution of the response variable (GAM, Hastie and Tibshirani, 1990), and stepwise selection of complexity using the Akaike information criterion (AIC). The GAM algorithm selects the best shape of given complexity (defined by degree of freedom) using the AIC. In our model the Gamma distribution and the canonical log link-function is used by the CANOCO 4.5 package (ter Braak and Šmilauer, 2012). The coefficient of determination for the fitted relationship was calculated according to Nagelkerke (1991).

3. Results

Phytoplankton productivity covered the whole trophic spectrum (ranging between 1.0 and ~300 μgl^{-1} values) in all water types. We observed three distinct patterns regarding the productivity-diversity relationship: monotonously increasing, decreasing and hump shaped relationship. All the relationships were characterised by high variability. In rivers the analyses revealed contradictory trends.

In the group of rhithral rivers all diversity metrics HR_0, HR_1, HR_2 and HR_∞ showed steadily increasing tendency with chl-a values. The regression line was less steep for species diversity (Fig. 2 a-d) than for functional diversity (Fig. 2 e-h) values (Table 1).

Table 1 Summary of the linear regression models ($HR_{0-\infty}$: diversity metrics (see in the methods); n: number of data; R^2: proportion of the variance explained; p: level of significance).

	Species based		Kodon based	
Type	R^2	p	R^2	p
1 rithral (n=109)				
HR_0	0.1754	< 0.01	0.1138	< 0.01
HR_1	0.0408	0.0352	0.1798	< 0.01
HR_2	0.0221	0.1227	0.1711	< 0.01
HR_∞	0.0203	0.1398	0.1442	< 0.01
2 small (n=1197)				
HR_0	0.0638	< 0.01	0.0760	< 0.01

HR_1	0.0034	0.0434	0.0119	< 0.01
HR_2	0.0103	< 0.01	0.0065	< 0.01
HR_∞	0.0105	< 0.01	0.0044	0.0224
3 potamal (n=310)				
HR_0	0.0415	< 0.01	0.0686	< 0.01
HR_1	0.1936	< 0.01	0.0028	0.3505
HR_2	0.2452	< 0.01	0.0036	0.2901
HR_∞	0.2393	< 0.01	0.0024	0.3896

In the river group B (small lowland rivers) the plane numbers of species and functional groups (HR_0) (Fig. 3 a, e) showed slightly increasing tendency with production. The other three metrics (HR_1, HR_2, HR_∞) showed slight increases when the calculations were based on functional groups (Fig. 3 f-h) and decrease when they were based on species data (Fig. 3 b-d). In large potamal rivers the H_0 metrics (the plane number of species and functional groups) showed slightly increasing tendencies (Fig. 4 a, e). Opposite (decreasing) tendencies could be observed for the other three metrics (HR_1 HR_2 HR_∞,) (Fig. 4 b-d, f-h). Steepness of the regression line was considerably higher when diversity metrics were calculated for species data.

In lakes, the hump-shaped form of relationship was revealed for the HR_0, HR_1 and HR_2 diversity metrics calculated for species data (Fig. 5 a-d). Diversity peaked in the chl-a ~ 60-80 μgl^{-1} interval. In case of functional diversity the unimodal relationship could be found only for the H_0 metric (Fig. 5 e), i.e. for the plane number of functional groups, which peaked at chl-a ~100 μgl^{-1} concentration range. The other metrics did not show significant relationships with productivity (Table 2).

Table 2 Summary of the GAM s obtained by stepwise selection. ($HR_{0-\infty}$: diversity metrics (see in the methods); n: number of data; df: degrees of freedom of the model complexity; R^2: proportion of the variance explained; p: level of significance; F: F value of the model at the given df).

Lakes (n=669)	Species based				Kodon based			
	df	F	p	R^2	df	F	p	R^2
HR_0	5	13.62	< 0.01	0.090	5	8.08	< 0.01	0.044
HR_1	4	4.16	< 0.01	0.024	2	2.01	0.1344	0.004
HR_2	3	2.85	0.0375	0.013	1	2.80	0.0929	0.003
HR_∞	2	2.6	0.0841	0.007	1	2.86	0.0897	0.004

4. Discussion

There are various shapes of productivity diversity relationships published in the literature, but the most frequent examples show that diversity is either concave-down, or increasing function of productivity (Cardinale et al., 2009). The shape of the relationship depends on the scale of investigations (Chase and Leibold, 2002), and on whether plants or animals are studied (Mittelbach et al., 2001). In this study we used four metrics, which represented diversity at a wide scale, from emphasising the importance of rare taxa (logarithm of the number of species, and Shannon), to giving higher weight to dominant taxa (Simpson, and Berger-Parker indices). This kind of approach is particularly applicable to assemblages, which show high within-year variation in terms of the dominance of the species. Our results demonstrated that all metrics in which dominance of taxa were considered showed similar changes along the productivity gradient. These metrics were sensitive to water body types. The logarithm of species richness, by contrast, showed slight increasing tendency in every case. We found that all productivity-diversity relationships were characterised by high variation. Consistent with previous results (Skácelová and Lepš, 2014) productivity seemed to determine the upper values of diversity metrics, low values were found in the entire productivity range. However, exceptions to this general rule did occur, because productivity determined both the upper and lower limits of the plane numbers of species and functional groups (HR_0) both in rhithral (Fig. 2 a, e) and potamal (Fig. 4 a, e) rivers.

In the present study we demonstrated that phytoplankton productivity-diversity relationship depends on water-body type. The monotonously increasing tendency in rhithral rivers is explained by their naturally oligotrophic character. These rivers in natural state are characterised by low diversity phytoplankton dominated by tychoplanktonic elements, i.e. benthic taxa that occasionally carried into the plankton by physical disturbances (Rojo et al., 1994; Leland, 2003; Stankovic et al., 2012). Although, nutrient and light conditions in these rivers would enable phytoplankters to develop larger populations, because of lack of inocula and short residence time (Borics et al., 2007), phytoplankton abundance in pristine rivers remains low. The clear rhithral rivers are highly susceptible to species invasions. Phytoplankton composition in these water currents is quite sensitive to that of the inlets, which continuously enrich the phytoplankton. Phytoplankton abundance of the inlets (ponds or reservoir effluents) can highly exceed that of the rivers; therefore, despite the dilution effect, the inlets basically determine the phytoplankton composition and diversity in the recipient rivers. Along the river the phytoplankton is continuously enriched by various elements, and finally, eclectic species rich assemblages will develop even at high biomass range.

The small lowland rivers are the most threatened water bodies worldwide. Their watersheds are on the heavily populated and intensively used lowlands, which are seriously impacted by anthropogenic influents (van Dam et al., 2007; Várbíró et al., 2012). In pristine state these water currents were macrophyte dominated, and the phytoplankton must have been dominated by tychoplanktonic and metaphytic elements. Several of the lowland rivers in our database were affected by human induced disturbances which masked the natural processes and the real shape of biomass-diversity relationship. The steepness of regression lines (both for species and functional group data) was quite low in case of HR_1, HR_2, HR_∞, thus, we can conclude that there was no relationship between the variables.

The large potamal rivers provide hospitable environment for several phytoplankton species. Due to nutrient retention of the river basins concentrations of nutrients are relatively high in these rivers even in natural state, and the residence time is long (Kronvang et al., 1999); thus, everything is optimal to the development of high biomass phytoplankton assemblages. Composition of the plankton is strongly influenced by competition among the plankton members, and this leads to the development of a characteristic assemblage called potamoplankton. The potamoplankton is mostly dominated by centric diatoms and chlorococcaleans not only in the vegetation period (Bothár and Kiss, 1990; Várbíró et al., 2007), but in winters too (Kiss and Genkal, 1993). This assemblage can also be enriched by the influents, but this impact is of lesser importance, because of the very large water discharge of the rivers in this category. Decreasing tendency for the plane number of species (HR_0) and at functional level cannot be observed, which implies that although physical constraints might change considerably along the large rivers, the competition does not act at this level.

The contrasting shape of biomass-diversity relationships found in rhithral and potamal rivers is not a "lack of data problem", where the increasing or decreasing tendency can be explained by the fact that data available covers only one tail of the otherwise hump-shaped relationship. The opposite trends can be explained by differences in the strength of contradictory processes e.g. colonisation and competitive exclusion. Both in the case of rhithral and potamal rivers, the whole trophic spectrum was considered in this study, from the oligotrophic to hypertrophic states. The productivity gradient also covered the whole trophic spectrum when lakes were studied.

In accordance with previous findings (Skácelová and Lepš, 2013), where the calculations were based on species data the observed hump-shaped relationship became flattened towards the HR_0, HR_1, HR_2, HR_∞ direction. It means that those indices in which higher weight is given to the dominant taxa are less sensitive to the productivity. Regarding the functional diversity the hump shaped character was observed exclusively for the plane number of functional groups (HR_0). The lack of significant relationships we found in the case of the other metrics was due to the high number of small naturally eutrophic water bodies in the database. These lakes are characterised by high functional diversity values even under hypertrophic conditions (Borics et al., 2012).

We hypothesized that functional diversity metrics show more pronounced changes along productivity. We found that this is not true for all types. Metrics calculated from functional groups and species data showed different sensitivity depending on the type of water bodies. Differences were more pronounced in case of rhithral and potamal rivers. In rhithral rivers the functional diversity, in potamal rivers species diversity showed more pronounced relationship with productivity. Differences are attributable to the different intensity of the underlying mechanisms, impact of inlets and species competition.

The apparent similarity, which exists between phytoplankton dynamics in potamal rivers and in shallow lakes (Reynolds et al., 1994) would imply that this similarity should appear in the shape of the productivity-diversity curves. Differences in the productivity-diversity curves suggest that intensity of the underlying processes along the productivity scale is different in lakes and large potamal rivers. However, at higher productivity range, diversity showed decreasing tendency both in the case of lakes and large potamal rivers. Borics et al. (2012) demonstrated that in shallow lakes dominance of the good light competitor bloom-forming cyanobacteria exert strong negative impact both on functional and species diversity at high biovolume range, while dominance of other groups has much less consequences for the diversity of assemblages. In large potamal rivers light deficiency also plays crucial role in phytoplankton succession (Vörös et al., 2000; Sellers and Bukaveckas, 2003). The high biomass riverine assemblages are dominated mostly by diatoms, which taxa due to their plastic physiological properties can cope with fluctuating light conditions (Lavaud and Lepetit, 2013).

The decisive role of physical disturbances in supporting diversity (Connell, 1978; Padisák et al., 1988; Hambright and Zohary, 2000) and the unimodal character of the phytoplankton productivity-diversity relationship in lakes (Skácelová and Lepš, 2013) raise the question of whether and to what extent diversity metrics can be used for water quality assessment.

Regarding the lakes we think that diversity metrics should not be used for ecological state assessment because of the following reasons:

1. We demonstrated the unimodal character of the productivity-diversity relationship, but productivity determines only the maxima of the diversity metrics and not the actual value of the metrics in case of a particular lake. Values close to the theoretical minima of the given metrics might occur along the whole productivity gradient, which result in a huge amount of scatter of data.
2. The hump shaped relationship means that low diversity values are expected both at low and high productivity; thus, low diversity values might occasionally refer to good or bad ecological state.

For these reasons in lake quality assessment only sensitivity/tolerance indices should be used as composition metrics. On the other hand, the use of diversity metrics as state indicators seems a plausible approach for rivers. In rhithral rivers a significant increase of diversity may indicate nutrient load and/or undesirable hydromorphological modification of the watershed. In large potamal rivers the decreasing tendency indicates nutrient input and/or impoundment.

In these river types, besides the well known biomass and composition metrics, diversity metrics can be incorporated into a multimetric index, which approach otherwise is strongly supported by the WFD (European Community, 2000). Because of the contrasting trends observed in rhithral and potamal rivers (for HR_1, HR_2 and HR_∞ metrics), development of detailed river typology and correct classification of rivers are of crucial importance.

As compared with biomass and sensitivity/tolerance metrics that are considered robust measures of the actual state of waters, diversity metrics have higher uncertainties (Carvalho et al., 2013). On the other hand, when longer time periods are evaluated, changes in diversity (mostly changes in plane number of species) provide important information about the mechanisms that drive the systems into positive or negative directions. Impoverishment of the microflora caused by acidification or nutrient enrichment in the last decades (Almer et al., 1974; Ruggiu et al., 1998) was a striking indicator of the undesirable processes. Long-term studies on phytoplankton diversity are also important in highlighting the trends in species invasions (Kaštovský et al., 2010).

Our results are summarized as follows. We propose to use diversity metrics to assess the actual state of waters in the case of rhithral, and large potamal rivers. Regarding the lakes, phytoplankton diversity metrics should be used for ecological state assessment when long term trends are evaluated.

Acknowledgements

This work was funded by the OTKA Grant K104279 and by the Bolyai János fellowship of the Hungarian Academy of Sciences. The work was supported by TÁMOP-4.2.2_B-10_1-2010-0024, and TAMOP-4.2.2.C-11/1/KONV-2012-0010 projects. We would like to thank to Ministry of Rural Development to make the data available for the analyses.

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Fig. 2

Relationship between phytoplankton productivity (expressed in chl-a μgL^{-1}) against species (a-d) and functional diversity (e-h) in rhithral rivers. Diversity is expressed in four indices of the Rényi's diversity series: HR_0 is the logarithm of species richness, HR_1 is the Shannon-wiener diversity, HR_2 is the Simpson dominance index and HR_∞ is the proportion of the most abundant species, known as the Berger-Parker (BP) index. Lines fitted by ordinary least squares regression.

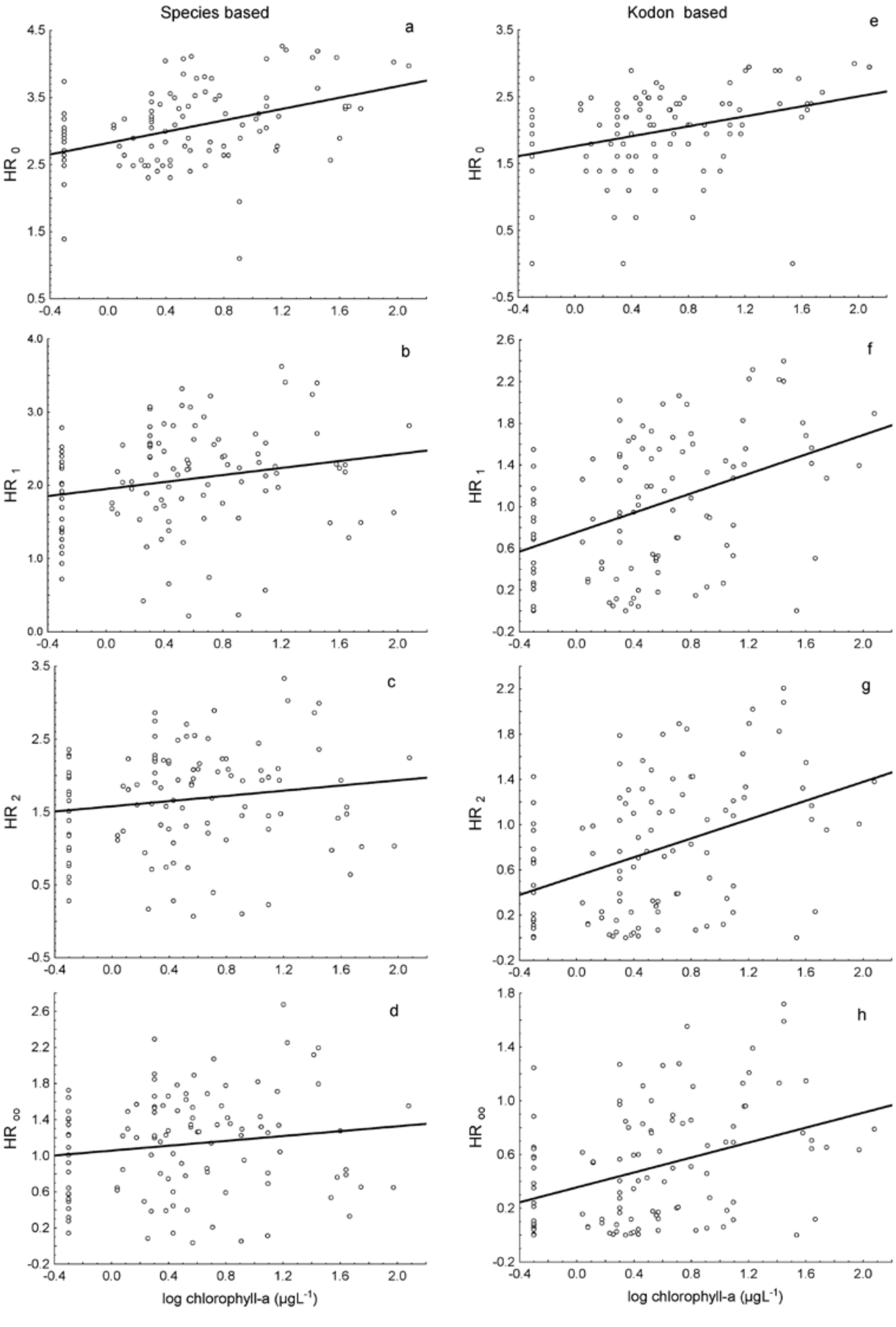

Fig. 3

Relationship between phytoplankton productivity (expressed in chl-a μgL^{-1}) against species (a-d) and functional (e-f) diversity in small lowlands rivers of fine sediments. (Abbreviations as in Fig. 2.)

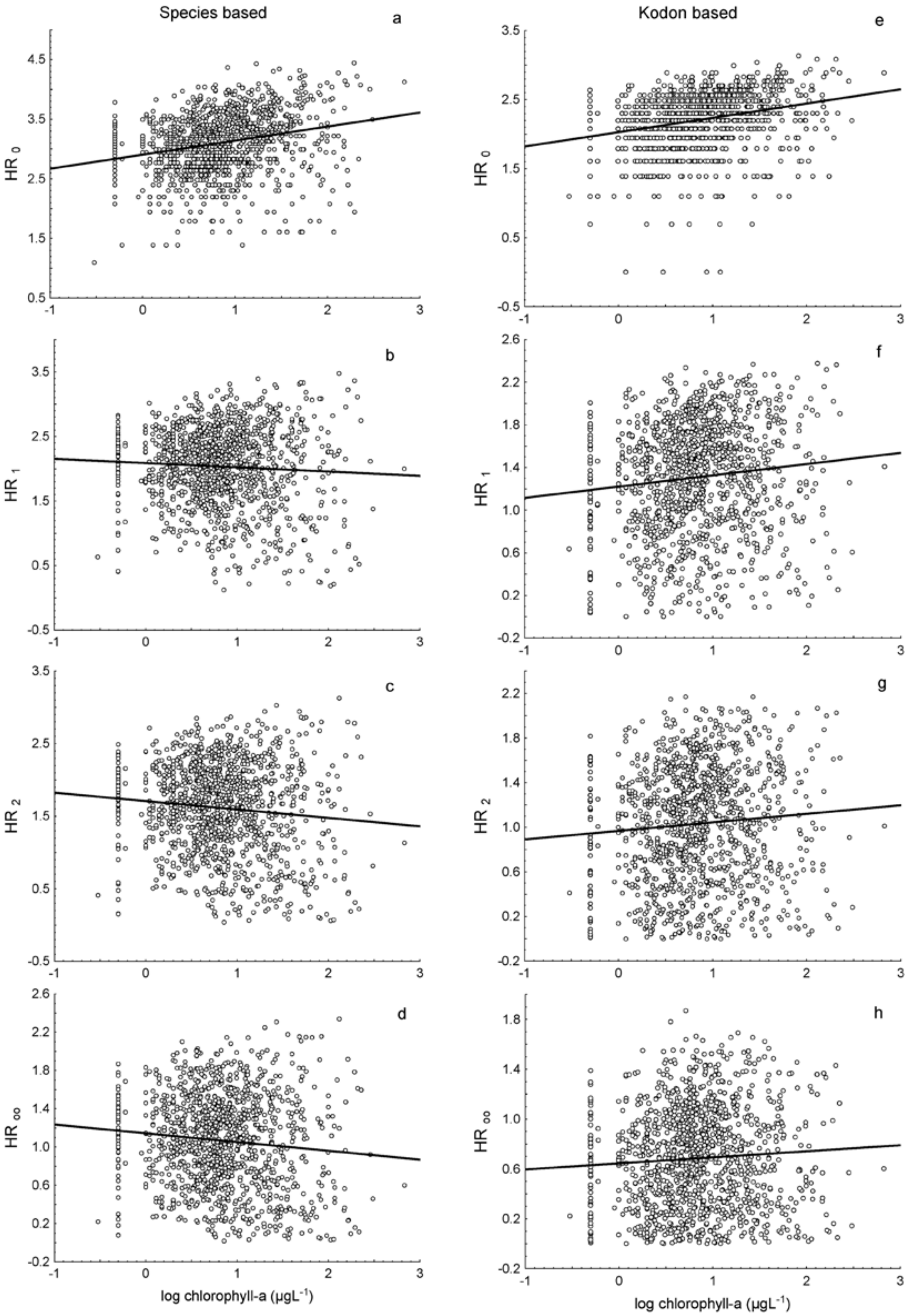

Fig. 4

Relationship between phytoplankton productivity (expressed in chl-a μgL^{-1}) against species (a-d) and functional (e-f) diversity in large potamal rivers. (Abbreviations as in Fig. 2.)

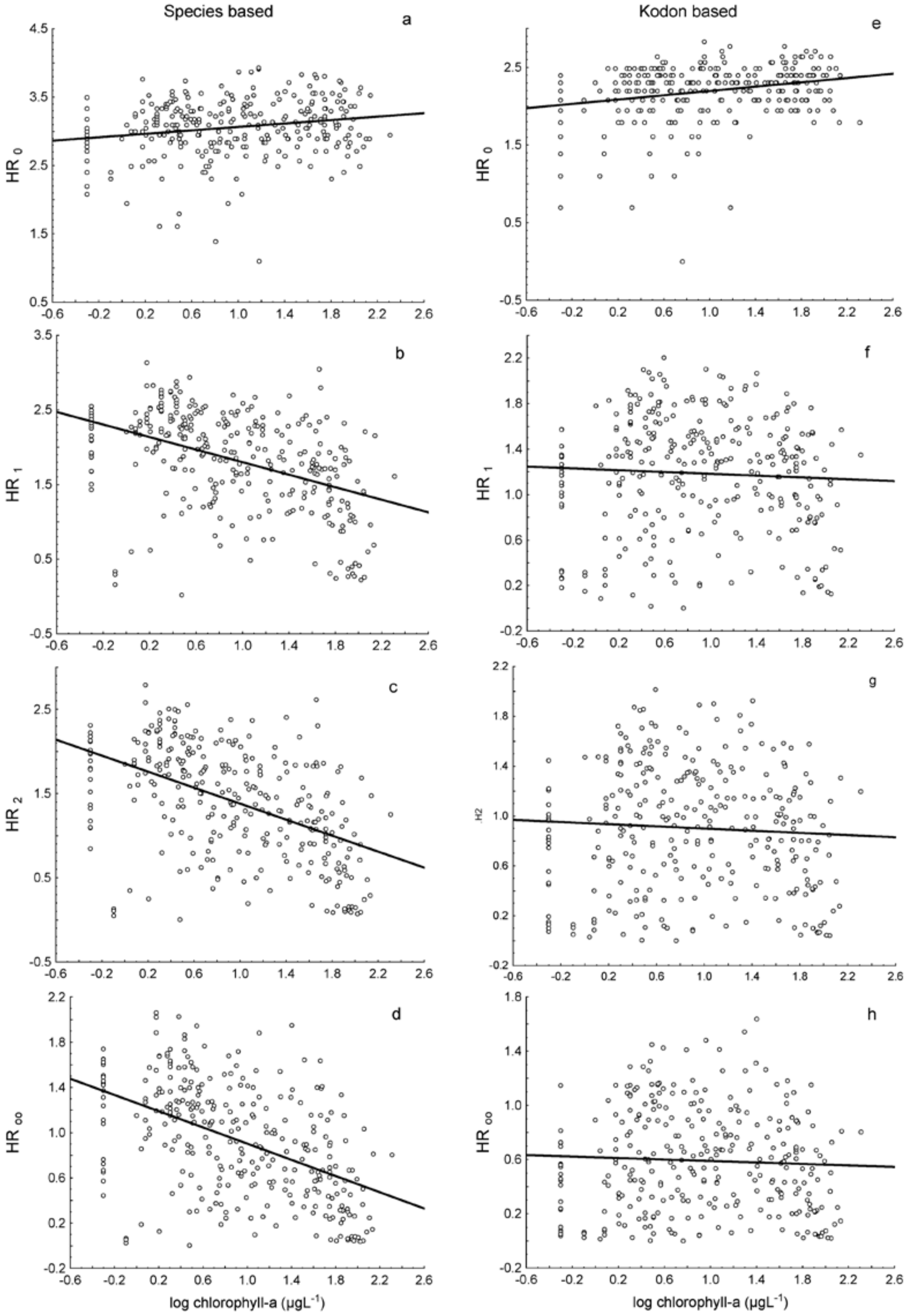

Fig. 5

Relationship between phytoplankton productivity (expressed in chl-a µgL^{-1}) against species (a-d) and functional (e-f) diversity in shallow lakes. (Abbreviations as in Fig. 2.) Regression line fitted by GAM.