

The relationship between species richness and taxonomic distinctness in freshwater organisms

Jani Heino¹

Finnish Environment Institute, Research Programme for Biodiversity, P.O. Box 413,
FIN-90014 University of Oulu, Finland

Janne Soininen and Jyrki Lappalainen

Department of Biological and Environmental Sciences, P.O. Box 65, FIN-00014 University of Helsinki, Finland

Risto Virtanen

Department of Biology, Botanical Museum, P.O. Box 3000, FIN-90014 University of Oulu, Finland

Abstract

Taxonomic distinctness is a newer biodiversity measure that emphasizes the average taxonomic relatedness between species in a community. We examined whether species richness (SR) and taxonomic distinctness (TD) were significantly related and whether they showed similar environmental relationships in regional data sets for various groups of freshwater organisms, ranging from lake mollusks and fishes to stream diatoms and invertebrates. We found that the relationship between SR and TD varied widely, ranging from significantly negative through nonsignificant to significantly positive. In general, SR and TD were related to different environmental gradients, although the particular environmental variables accounting for biodiversity patterns varied among data sets and, more importantly, even between different data sets for the same organism groups. SR and TD can provide complementary views of the variability of biodiversity. These findings thus underline the importance of considering a set of different measures in the assessment of community-level biodiversity, as well as considering this variability when determining anthropogenic effects in freshwater ecosystems.

Describing the variability of biodiversity presents enormous challenges to biologists, and these challenges concern not only the cost and effort needed to conduct extensive surveys but also how to evaluate the value of biodiversity most relevantly and efficiently. Being the simplest measure of biodiversity, species richness has traditionally attracted the most attention (Gaston 1996), and general patterns of species richness have been revealed for major organism groups across large geographical gradients (e.g., Willig et al. 2003; Hillebrand 2004) and also among local ecosystems within regions (e.g., Heino et al. 2005). However, as a measure of biodiversity, species richness can easily be criticized on the grounds that it does not account for phylogenetic, taxonomic, and functional variability among species in a community. Thus, increasingly, other measures of biodiversity have been developed to account for the deficiencies of species richness alone (e.g., Vane-Wright et al. 1991; Faith 1992; Humphries et al. 1995).

One of the promising new indices of biodiversity is that

of taxonomic distinctness devised by Clarke and Warwick (1998). Taxonomic distinctness does not measure the number of species per se but rather the taxonomic relatedness of species in a community. When using species presence–absence data, this is done by defining the path length along the taxonomic hierarchy of each species pair in the community and then averaging across all species pairs. A major benefit of this index over species richness is its virtual independence of sampling effort (Magurran 2003). Furthermore, contrary to taxonomic distinctness, species richness may be more sensitive to underlying variation in natural environmental factors (e.g., habitat heterogeneity), thus potentially generating confounding effects if one is interested in the influences of anthropogenic perturbations on communities. However, to our knowledge, no study has rigorously examined the conjecture that the strength of the relationship of species richness and taxonomic distinctness to natural environmental gradients varies among these two measures of biodiversity (but for marine fish, see Hall and Greenstreet 1998; Rogers et al. 1999). Thus, if they respond to the same environmental gradients and are thereby strongly correlated to each other, they may be redundant with regard to biodiversity evaluation and conservation planning. By contrast, if they respond to different environmental gradients, they also may describe biodiversity differently, being valuable independent measures in conservation evaluation. The latter hypothesis seems intuitive in a situation in which the increase in species richness is not related to an increase in species from higher taxonomic levels, as opposed to a situation in which the increase in species richness is the consequence of an increase in the taxonomic breadth of the community.

¹ Corresponding author (jani.heino@ymparisto.fi).

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Table 1. Descriptive statistics for the data sets used in this study. LSR, local species richness per lake or stream. Taxonomic levels refer to the number of levels at which all species in a data set are joined in the taxonomy.

Data set	Number of sites	Number of species	LSR mean	LSR SD	LSR range	Taxonomic levels	Distinctness mean	Distinctness SD	Distinctness range
Lake mollusks	21	30	9.57	6.27	2–22	6	3.38	0.84	1.00–4.33
Littoral insects	21	86	22.24	7.37	8–37	5	3.65	0.09	3.42–3.83
Lake fish I	97	23	12.60	3.27	2–20	5	3.59	0.13	3.23–4.00
Lake fish II	83	10	4.81	1.06	3–7	5	3.81	0.21	3.00–4.00
Stream invertebrates I	27	87	34.56	9.13	15–48	7	4.29	0.15	4.06–4.66
Stream invertebrates II	34	190	38.06	9.39	21–60	7	3.94	0.21	3.50–4.40
Stream diatoms I	47	232	48.91	14.52	19–85	5	2.74	0.09	2.52–2.92
Stream diatoms II	55	141	35.27	10.27	14–55	5	2.80	0.13	2.56–3.08
Stream bryophytes	29	48	9.62	3.71	3–15	8	4.97	0.68	3.00–6.33

Although the community-environment relationships of many groups of freshwater organisms are increasingly well studied (e.g., Malmqvist and Mäki 1994; Magnuson et al. 1998; Soininen et al. 2004), less attention has been directed to more comparable aspects of biodiversity: for example, species richness and taxonomic distinctness. The existing information on the biodiversity patterns of freshwater organisms indicates, however, that certain generalities are to be expected along environmental gradients. For example, invertebrate and fish species richness usually increases with the size of a stream or a lake (e.g., Tonn and Magnuson 1982; Allen et al. 1999), either increases, decreases or shows a unimodal relationship to nutrient concentrations (e.g., Jepsen et al. 2000; Chase and Ryberg 2004), and decreases with increasing acid stress (e.g., Townsend et al. 1983; Petchey et al. 2004). However, the strength of the relationship between species richness and environmental gradients is often context dependent, varying in relation to the most important limiting factors within a region, among taxonomic groups, and between regions (e.g., Dodson et al. 2000; Heino et al. 2003*b,c*). Such patterns are to be expected for other measures of biodiversity as well.

Our objectives were to examine the responses of species richness and taxonomic distinctness in several freshwater organism groups to underlying environmental gradients and to test whether these two measures of biodiversity are redundant in communicating the value of sites. Our analyses were based on nine data sets, ranging from stream diatoms and bryophytes to lake mollusks and fishes. Our research was aimed at extending the taxonomic distinctness studies on marine organisms (e.g., Hall and Greenstreet 1998; Price et al. 1999; Rogers et al. 1999) and fish parasites (Poulin and Mouillot 2003) to freshwater organisms. Contrary to most previous studies, however, we did not consider directly the effects of anthropogenic influences on species richness and taxonomic distinctness. Rather, our main aims were to examine (i) whether species richness and taxonomic distinctness are significantly correlated and thus largely redundant and (ii) whether these measures of biodiversity respond similarly to primarily natural environmental gradients, an issue thus far largely neglected. Thus, this study should be regarded as one examining biodiversity patterns in the context and constraints of regional limnology, as opposed to studies spanning broad geographical gradients or anthropogenically stressed ecosystems.

Materials and methods

Data sets—Our analyses were based on nine regional data sets of streams and lakes that included both species lists and several environmental variables. In the following paragraphs, we will shortly describe the study areas, environmental variables, sampling methods, and taxonomic details of each data set. Most of the data sets comprised surveys of sites within a single drainage system, whereas some of them spanned across ecoregions and several drainage systems. However, even in the latter cases, dispersal limitation is supposed to be of minor importance as a result of largely similar species pools (e.g., stream diatoms in northern Finland and lake fishes in southern Finland), and biodiversity patterns should thus be primarily controlled by environmental gradients. For delineations of the ecoregions to which we refer, see Heino et al. (2002). Descriptive statistics for each data set are shown in Table 1, and locations of the study areas are shown in Fig. 1. See our original publications for descriptions of study regions, sampling methods, and environmental variables measured.

1. *Lake mollusks*—This data set, comprising freshwater clams and snails of the littoral of 21 lakes, was derived from the literature (Aho 1966). The lakes are located within southern Finland (centered on 61°26'N, 23°40'E). Major environmental gradients of relevance to the organisms include lake size and water chemistry. Taxonomic levels include species, genus, family, order, class, and phylum.

2. *Littoral insects*—The study area is located in the Koutajoki drainage system in northeastern Finland (centered on 66°21'N, 29°20'E). The data comprise surveys of littoral insects in 21 headwater lakes. The major environmental gradients of potential relevance to the organisms are lake size and habitat structure. Taxonomic levels include species, genus, family, order, and class.

3. *Lake fishes I*—The fish data were based on a postal questionnaire sent to the regional fishing associations in 1998 (Lappalainen and Malinen 2002). Most of the 97 lakes surveyed are situated in southern Finland (centered on 62°10'N, 24°36'E). Major gradients of importance to fishes are lake size and productivity. Taxonomic levels include species, genus, family, order, and class.

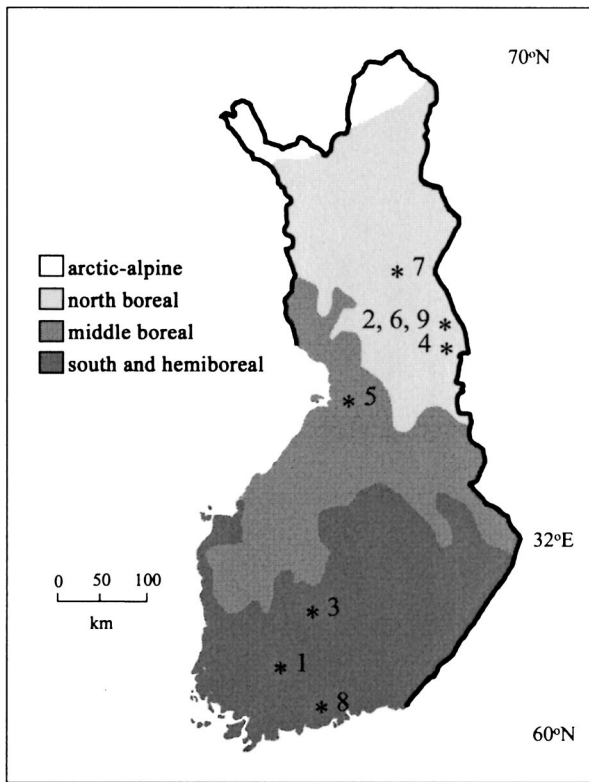


Fig. 1. Map of Finland indicating the centers of the areas of each survey included in this study: 1. lake mollusks, 2. littoral insects, 3. lake fishes I, 4. lake fishes II, 5. stream invertebrates I, 6. stream invertebrates II, 7. stream diatoms I, 8. stream diatoms II, and 9. stream bryophytes. Also shown are ecoregion delineations of Finland.

4. *Lake fishes II*—This data set comprised 84 lakes in Kuusamo in northeastern Finland (centered on 66°N, 29°E). The fish data were based on a postal questionnaire sent to every household in the study area to inquire about lake-specific fish, fish yields, and fishing gear in 1976 (Myllymaa and Ylitolonen 1980). Major gradients of importance to fishes include lake size and productivity. Taxonomic levels comprise species, genus, family, order, and class.

5. *Stream invertebrates I*—A survey of 27 stream sites was conducted in the River Kiiminkijoki drainage system (centered on 65°N, 26°E) in northern Finland (Heino et al. in press). The major environmental gradient of relevance to the organisms is stream size. Taxonomic levels include species, genus, family, order, class, phylum, and kingdom.

6. *Stream invertebrates II*—The study area is located in the Koutajoki drainage system in northeastern Finland (centered on 66°21'N, 29°20'E). The 34 stream sites surveyed for the present study represent typical first- to third-order headwater streams and small rivers in the area. The sites were surveyed in September 2002. Refer to Heino et al. (2003a) for the measurement of environmental variables and invertebrate sampling. Major environmental gradients of relevance to the organisms include stream size and habitat

structure. Taxonomic levels comprise species, genus, family, order, class, phylum, and kingdom.

7. *Stream diatoms I*—A set of 47 near-pristine streams was sampled in northern and eastern Finland (centered on 66°3'N, 27°3'E), spanning several drainage systems in the mid-boreal and north-boreal ecoregions in Finland (Soininen et al. 2004). Major environmental gradients of relevance to the organisms include acidity, nutrients, and shading. Taxonomic levels comprise species, genus, family, order, and class.

8. *Stream diatoms II*—Another set of 55 streams was sampled for diatoms in the hemiboreal and south boreal ecoregions in southern Finland (centered on 60°4'N, 25°E) (Soininen and Könönen 2004). The major environmental gradients of relevance to the organisms are nutrients and shading. Taxonomic levels include species, genus, family, order, and class.

9. *Stream bryophytes*—A set of 29 streams (first to fourth order) was surveyed for bryophytes in the Koutajoki drainage system in northeastern Finland (centered on 66°21'N, 29°20'E). For a description of the sampling methods, refer to Muotka and Virtanen (1995). Environmental variables of importance to bryophytes include habitat structure and water chemistry. Taxonomic levels include species, genus, family, order, subclass, class, division, and kingdom.

Additional taxonomic levels (e.g., subgenera, tribes, subfamilies) could have been used for some data sets. However, because these levels are prone to constant revision, we decided to concentrate on those taxonomic levels that have remained more or less unchanged in the long term. Taxonomy followed Nilsson (1996, 1997) for insects, Krammer and Lange-Bertalot (1986–1991) for diatoms, and Ulvinen et al. (2002) for bryophytes, and we also consulted ITIS (<http://www.itis.usda.gov/index.html>) to check a recent higher level taxonomy for each organism group and data set.

Statistical methods—Clarke and Warwick (1998) devised three indices describing the taxonomic diversity of communities by utilizing path lengths between individuals or species grouped by their taxonomic relatedness. The first two of these indices use abundance data, whereas they both reduce to a simpler form when only presence–absence data are used. Thus, for the presence–absence data, taxonomic distinctness (TD) is calculated as:

$$TD = \frac{\sum \sum_{i < j} \omega_{ij}}{s(s-1)/2}$$

where the summation is taken over all species i, j , ω_{ij} is the weight given to the path length linking species i and j in the taxonomy, and s is the number of species present. This index thus describes the average path length between any two randomly chosen species present in the community (Clarke and Warwick 1998; Rogers et al. 1999). Taxonomic distinctness indices for each site and data set were calculated using PAST version 1.28 (Hammer et al. 2004), a program designed for paleontologists, but it is also highly suitable for biodiversity

Table 2. Correlations between species richness and taxonomic distinctness for the different data sets. Pearson's partial *r* denotes the correlation between species richness and taxonomic distinctness when environmental variables were controlled for. Thus, if partial correlations are significant, species richness and taxonomic distinctness respond to differing, primarily uncorrelated environmental factors.

Data set	Pearson's <i>r</i>	<i>p</i>	Partial <i>r</i>	<i>p</i>	Spearman's <i>r</i>	<i>p</i>
Lake mollusks	0.349	0.121	-0.046	0.877	0.267	0.242
Littoral insects	0.466	0.033	0.299	0.434	0.533	0.013
Lake fish I	-0.524	<0.001	-0.598	<0.001	-0.549	<0.001
Lake fish II	-0.153	0.167	-0.132	0.269	-0.349	<0.001
Stream invertebrates I	-0.435	0.023	-0.507	0.014	-0.268	0.176
Stream invertebrates II	0.076	0.668	0.183	0.404	0.098	0.580
Stream diatoms I	0.567	<0.001	0.524	0.001	0.618	<0.001
Stream diatoms II	0.019	0.891	-0.001	0.997	0.014	0.919
Stream bryophytes	-0.007	0.970	-0.167	0.494	-0.084	0.665

research in general. Species diversity was simply the number of species detected in a lake or a stream.

We used correlation analyses to examine the relationships between species richness and taxonomic distinctness. Partial correlations, where we controlled for environmental variables, were also calculated between species richness and taxonomic distinctness. To model environmental relationships of these two measures of biodiversity, we used Pearson correlation and stepwise regression analysis with forward selection ($\alpha = 0.05$) and backward elimination ($\alpha = 0.10$) of independent variables, although only the latter results are shown for all data sets. Furthermore, quadratic relationships between the biodiversity measures and potentially important variables in this context (pH, nutrients) were also examined, but in practice, these quadratic models did not appreciably differ from the linear results or were not significantly related to the response variables. Thus, for simplicity, we here examine only linear relationships. Prior to regression analyses, all variables were first checked using Shapiro–Wilks and Lilliefors tests, and, if necessary, appropriate transformations were used to improve normality and remove heteroscedasticity. Analyses were run using SPSS version 10.0 (SPSS 1999).

Results

Both species richness and taxonomic distinctness varied either widely or moderately within each data set, with the former being related to the total number of species in a data

set and the latter to the number of taxonomic levels in the analysis (Table 1). However, no general patterns were detected when species richness and taxonomic distinctness were correlated in each data set (Table 2). Rather, the correlation between these two measures of biodiversity ranged from significantly positive (stream diatoms I, littoral insects) to nonsignificant (lake fish II, stream invertebrates II), to highly negative (lake fish I, stream invertebrates I). The correlation between species richness and taxonomic distinctness did not change appreciably when the environmental variation among sites was controlled for (i.e., environmental variables were treated as covariables in partial correlation analysis (Table 2)). These patterns were likely related to slightly or widely differing environmental relationships of these two measures of biodiversity. This was exemplified by the data set on lake mollusks (Table 3). Although the environmental gradients in this data set were rather strong, species richness and taxonomic distinctness showed slightly different correlations to key abiotic variables. More importantly, water hardness and conductivity, two key variables in determining the distributions of freshwater mollusks (e.g., Briers 2003), were either strongly (species richness) or nonsignificantly (taxonomic distinctness) related to these measures of molluscan biodiversity.

Further evidence of the differing environmental drivers of species richness and taxonomic distinctness were found in stepwise regression analyses. In general, the final models, after forward selection and backward elimination of independent variables, were highly contrasting for these two measures of biodiversity. Thus, species richness of lake mollusks was best accounted for by a model including lake area and water hardness, whereas taxonomic distinctness showed a positive relationship to pH. The species richness of littoral insects showed a negative relationship to organic material, but in the models of both species richness and taxonomic distinctness, moss cover was positively related to biodiversity. The species richness of lake fishes (I) showed positive relationships to lake area and conductivity, whereas taxonomic distinctness was significantly related to several variables themselves related to the trophic status of lakes (Table 4). By contrast, in the other data set of lake fishes (II), species richness was nonsignificantly related to environmental variables, whereas taxonomic distinctness was positively related to chemical oxygen demand. The two measures of bio-

Table 3. Example of the responses of species richness and taxonomic distinctness to environmental gradients: Pearson correlations between environmental variables and species richness and taxonomic distinctness of lake mollusks.

Variable	Richness	Distinctness
Lake area (log)	0.417†	0.183
pH	0.567**	0.776**
Alkalinity	0.620**	0.433*
Hardness	0.670**	0.399
Conductivity	0.682**	0.421‡‡
Color	-0.600**	-0.746**
KMnO ⁴ consumption	-0.512*	-0.633**

* $p < 0.05$, ** $p < 0.01$; † $p = 0.060$; ‡‡ $p = 0.057$.

Table 4. Best regression models (after forward selection and backward elimination of independent variables) for species richness and taxonomic distinctness for the different data sets.

Data set	Dependent	Model	R^2	F	p
Lake mollusks	Richness	$y = -11.281 + 8.691 (\log \text{ area}) + 14.428 (\text{hardness})$	0.731	24.491	<0.001
Lake mollusks	Distinctness	$y = -3.899 + 1.159 (\text{pH})$	0.601	28.669	<0.001
Littoral insects	Richness	$y = 41.568 - 4.856 (\text{detritus}) + 5.390 (\text{moss})$	0.616	14.443	<0.001
Littoral insects	Distinctness	$y = 3.623 + 0.074 (\text{moss})$	0.208	4.995	0.038
Lake fish I	Richness	$y = 4.999 + 1.720 (\log \text{ area}) + 3.028 (\log \text{ conductivity})$	0.206	12.165	<0.001
Lake fish I	Distinctness	$y = 3.572 - 0.195 (\log \text{ turbidity}) + 0.164 (\log \text{ oxygen}) - 0.130 (\log \text{ conductivity})$	0.419	22.352	<0.001
Lake fish II	Richness	No significant variables entered	—	—	—
Lake fish II	Distinctness	$y = 0.629 + 0.059 (\log \text{ COD})$	0.231	24.287	<0.001
Stream invertebrates I	Richness	$y = 63.905 + 6.212 (\log \text{ width}) + 26.291 (\arcsin \text{ moss}) - 14.362 (\log \text{ particle})$	0.629	12.989	<0.001
Stream invertebrates I	Distinctness	No significant variables entered	—	—	—
Stream invertebrates II	Richness	No significant variables entered	—	—	—
Stream invertebrates II	Distinctness	$y = 4.116 - 0.390 (\log \text{ TP}) + 0.013 (\text{depth})$	0.345	8.171	0.001
Stream diatoms I	Richness	$y = 51.205 + 0.194 (\text{moss}) - 15.086 (\log \text{ conductivity})$	0.246	7.163	0.002
Stream diatoms I	Distinctness	$y = 2.957 + 0.157 (\log \text{ TP}) - 0.126 (\log \text{ Fe}) - 0.01 (\text{shading})$	0.370	8.430	<0.001
Stream diatoms II	Richness	$y = 75.647 + 20.033 (\log \text{ TP}) - 10.620 (\text{pH})$	0.271	9.684	<0.001
Stream diatoms II	Distinctness	$y = 2.955 + 0.241 (\log \text{ width}) - 0.190 (\log \text{ color})$	0.317	12.093	<0.001
Stream bryophytes	Richness	$y = -0.423 + 13.059 (\log \text{ particle})$	0.215	7.389	0.011
Stream bryophytes	Distinctness	$y = 13.163 - 1.082 (\text{pH})$	0.189	6.302	0.018

diversity of stream invertebrates showed varying environmental relationships in the two data sets analyzed. In the first data set (I), species richness was strongly related to stream size, moss cover, and particle size, whereas taxonomic distinctness was nonsignificantly related to any explanatory variable. In the second data set (II), species richness did not show a significant relationship to any variable, whereas taxonomic distinctness was significantly accounted for by a model incorporating total phosphorus and depth. Similarly to stream invertebrates, stream diatom biodiversity showed differing environmental relationships in the two data sets analyzed. In the first data set (I), species richness was best accounted for by a model including moss cover and conductivity, whereas taxonomic distinctness was related to total phosphorus, iron, and shading. In the second data set, species richness was accounted for by a model including total phosphorus and pH, whereas taxonomic distinctness was primarily related to stream size and water color. Finally, stream bryophyte species richness was positively related to particle size, and taxonomic distinctness was negatively related to pH. In summary, there were no general differences in the coefficient of determination of the regression models for species richness and taxonomic distinctness, but, rather, the former was better explained in some data sets, while the latter showed stronger environmental relationships in others (Table 4). More importantly, both measures of biodiversity varied strongly along environmental gradients, regardless of organism group or data set.

Discussion

The relationships between species richness and taxonomic distinctness of freshwater communities, comprising such diverse groups as stream diatoms, stream bryophytes, stream invertebrates, littoral insects, lake mollusks, and lake fishes,

ranged from negatively significant through nonsignificant to positively significant, with little evidence of association with either taxonomic group or the number of taxonomic levels in a data set. Furthermore, the relationships to environmental gradients of these two measures of biodiversity also varied widely, with either the same factors or highly dissimilar ones accounting for the variability in biodiversity. These findings thus indicate a high level of contingency in biodiversity patterns along environmental gradients, which was likely related to organism group, between-region differences in the ranges of environmental factors of importance to the biota, as well as the characteristics of the biota itself (i.e., what kind of species are available in the regional species pool, or taxonomic variability). These findings also underline the importance of considering different measures of biodiversity in the evaluation of sites for conservation planning at the regional scale.

Although one of the main aims of ecological research is to search for general, repeated patterns in nature, as well as to reveal the processes behind the patterns, this aim is not easy to accomplish. Contingency and context-dependency are common problems hindering the efficiency of generalizations in community ecology, conservation biology, and regional limnology. Typically, regions differ from each other in species composition, taxonomic variability, and functional composition as a result of historical effects and climatic constraints (Brown and Lomolino 1998; Heino 2001), setting the limits within which the local communities are assembled (Tonn 1990; Poff 1997). Although the filtering process undoubtedly is in action in each and every region, the factors responsible for such filtering may not remain unchanged among regions. For example, regions themselves differ in the constraints set by the regional limnology for the biota (i.e., ranges in abiotic conditions among water bodies vary between regions and drainage systems, leading to the im-

portance of different environmental filters in different regions). Our finding that species richness in the two stream diatom data sets showed significant responses to differing environmental gradients may indeed indicate that the relative influence of different environmental factors varies in different regions, concurring with former findings for lake fish (Magnuson et al. 1998) and stream invertebrates (Heino et al. 2003b). Similarly, the range in environmental conditions along which the biota is surveyed per se may affect our perception of the importance of different environmental gradients in accounting for biodiversity. Our finding that the two stream invertebrate data sets revealed differing species richness–environmental relationships strongly supports this reasoning, because the first data set comprised a longer gradient in stream size (first to fifth order) than the other one, which was largely restricted to headwater streams (first to third order). Also, taxonomic distinctness showed differing environmental relationships in the data sets for stream diatoms and stream invertebrates, which was likely related to the regional context-dependency.

One could a priori assume either a positive or a negative relationship between the species richness and taxonomic distinctness of communities. In the former case, an increase in species richness is associated with species from highly differing taxonomic levels (e.g., families and orders), whereas in the latter case, increase in species richness is mainly attributable to congeneric species. Both positive and negative relationships bear an interesting relationship to the environmental filtering of species within regions. In the former case, the environmental preferences of species may be directly related to increased habitat heterogeneity and availability of resources, with heterogeneous environmental conditions allowing taxonomically diverse species to coexist. In other words, taxonomically, as well as ecologically, distinct species may be adapted to differing conditions, and, therefore, heterogeneity in conditions leads to high biodiversity, both in terms of species richness and taxonomic distinctness. By contrast, in the latter case, the negative relationship results from a decrease in average taxonomic distinctness between species, because the increase in species richness is attributable to related species. Such an increase may also be related to habitat heterogeneity, with ecologically largely similar, congeneric species being either adapted to slightly different niches or able to avoid direct competition in heterogeneous conditions (see also discussion by Leibold 1998; Chase and Leibold 2003). We found both negative and positive relationships between species richness and taxonomic distinctness in our data sets, although it is difficult to assess whether these relationships were related to variation in habitat heterogeneity among lakes or streams. However, our finding that the species richness and taxonomic distinctness of lake fishes, for example, were negatively correlated indicates that habitat heterogeneity or productivity may be related to the patterns of coexistence of congeneric and confamilial species. Lakes with a high number of species and low taxonomic distinctness were typically dominated by several members of a single family (Cyprinidae), whereas low-richness lakes usually comprised one or two species from several families (e.g., Percidae, Esocidae, Salmonidae, Cyprinidae). This pattern was also strongly related to environmental gradients,

with species richness increasing with lake size and conductivity, whereas taxonomic distinctness was related to factors portraying lake productivity and perhaps was also associated with an increase in habitat heterogeneity in terms of increasing macrophyte cover and diversity from oligotrophic to mesoeutrophic conditions (Rørslett 1991). As high-productivity lakes in boreal and temperate regions are typically dominated by cyprinids (e.g., Tammi et al. 1999; Jeppesen et al. 2000), instead of species divided equally among several families and orders, productivity may actually decrease taxonomic distinctness, while species richness may either increase or remain unchanged with productivity compared to lower productivity conditions. The pattern was rather different in the other species-poor fish data set, however; in fact, an opposite pattern was found for one data set of stream diatoms, in which species richness and taxonomic distinctness were positively related. Thus, in this case, the increase in diatom species richness was primarily attributable to additional species unrelated to those found in more species-poor assemblages, although the environmental variables responsible for variability in biodiversity varied among these two measures.

An interesting pattern was also shown by stream bryophytes. Species richness and taxonomic distinctness were not correlated, and their variability was attributable to different environmental gradients. Not unexpectedly, the species richness of stream bryophytes showed a positive relationship to particle size; large particles supposedly provide a stable substrate for bryophytes, thereby facilitating the occurrence of even the most disturbance-prone species, and also providing suitable habitats for both strictly aquatic and semiaquatic species (Muotka and Virtanen 1995; Virtanen et al. 2001). By contrast, taxonomic distinctness was not correlated to particle size, but instead showed a rather curious negative relationship to stream pH. While such a negative relationship between pH and biodiversity might at first glance seem counterintuitive, there is actually a good reason to expect it to be a rather common phenomenon. In highly alkaline streams (pH > 8), there may be an increase in a few alkaline-tolerant species that often appear to belong to few related species (see Hedenäs and Kooijman 2004), whereas in circumneutral streams (pH \pm 7), one is likely to encounter broader sets of taxonomically unrelated species, including species typical of more acidic conditions. Thus, the average taxonomic distinctness of bryophytes may actually be reduced in alkaline waters that are, contrary to acidic conditions, otherwise thought to represent highly amenable conditions for a high biodiversity of aquatic organisms (e.g., Hildrew and Giller 1994; Heino et al. 2003c, 2005; Petchey et al. 2004). Accordingly, our finding that the taxonomic distinctness of lake mollusks increased with pH lends support to this latter conjecture.

Because there were no general relationships between species richness and taxonomic distinctness, or their environmental relationships, efficient biodiversity assessment should preferably be based on several different indices of community biodiversity. In addition to providing complementary information about the biodiversity value, different measures may also have further pros and cons. For example, although species richness is severely sensitive to sampling effort, the

measure of taxonomic distinctness is virtually uninfluenced by the sampling effort (Clarke and Warwick 1998; Warwick and Clarke 1998; Magurran 2003). Although each of our data sets was based on exactly similar sampling effort among sites, all data sets analyzed undoubtedly suffered from undersampling, and increased sampling effort would have yielded more species, both locally and regionally. The problem is not that severe if a similar proportion of potentially available species was sampled at each site, but in practice, it is likely that some sites would likely have yielded proportionally more species with further sampling. This is a concern, most likely with regard to clearly small, highly speciose diatoms and invertebrates. Such among-site biases might potentially affect biodiversity assessment based on species richness alone. By contrast, the index of average taxonomic distinctness between species may not be severely affected by insufficient sampling, as the missed species are either unlikely to be highly unrelated to those species already found or do not considerably affect the average index value. Furthermore, while species richness describes only the number of different units of organism present, it explains little about the phylogenetic (e.g., Faith 1992) or functional diversity (e.g., Petchey and Gaston 2002) of communities, measures that are highly influential if species' relatedness and ecosystem functioning are of prime interest to conservation planning and environmental assessment in particular situations (e.g., Brown et al. 2002; Price 2002). However, as species richness is the simplest and most easily comparable measure of biodiversity across studies (Gaston 1996), one should not abandon species richness in conservation-oriented studies, as long as the sampling effort is standardized among sites.

An issue largely beyond the scope of this article involved the effect of anthropogenic disturbance on biodiversity patterns, and we thus limited our study to least-impacted sites within the regions. However, our present findings are of importance to the assessment of anthropogenic effects on biodiversity on two grounds. First, because species richness typically varies widely across natural environmental gradients, one should take such background variability into consideration and, if possible, account for it statistically when the main interest lies in detecting changes in biodiversity due to anthropogenic effects. Second, although the index of taxonomic distinctness has been suggested to be less sensitive than species richness to differences in habitat types, and to thereby be more amenable to detecting actual degradation due to anthropogenic effects (Warwick and Clarke 1995, 1998), our findings strongly indicate that this measure of biodiversity also varies along stream and lake gradients for all of the organism groups studied. Thus, it is highly unlikely that a site can be determined to be degraded or not degraded based only on the measure of taxonomic distinctness, without regard to the underlying natural environmental gradients. A comparison of a site's taxonomic distinctness value to that derived randomly from a regional list of species may be helpful in this regard, however, as has been shown to be the case for marine communities (Clarke and Warwick 1998). For freshwater organisms, these issues will be addressed more fully in a forthcoming article.

Freshwater research that can be considered conservation-

oriented lags behind that directed to terrestrial and marine ecosystems (Abell 2002), both in the number of studies and perhaps also in the quality of research. The few studies that exist have primarily related biodiversity patterns to the underlying environmental gradients (e.g., Allen et al. 1999; Heino et al. 2005), although most of these studies have been conducted for the purpose of defining variability in biodiversity across reference conditions for bioassessment (e.g., Heino et al. 2003a; Johnson et al. 2004). Although the aims of conservation and bioassessment are somewhat divergent (but *see* Linke and Norris 2003), with the former trying to find the most valuable sites for conservation planning, and the latter trying to separate impacted sites based on reference conditions, the data for both types of studies come largely from similar sources. Regional surveys of multiple freshwater sites thus provide the raw material for both fields of study, and the data can be effectively used in guiding the conservation of valuable sites and generating networks of such sites, as well as in addressing phenomena of interest to freshwater biodiversity conservation in general. As such, our study adds to the literature on freshwater conservation through its examination of the ways in which different kinds of biodiversity measures behave along natural environmental gradients. Our main points here are that (i) freshwater conservation planning should not be based on a single measure of biodiversity (e.g., species richness), but rather should preferably take into consideration other characteristics of communities, including the phylogenetic and functional status of their constituent species; (ii) Although near-pristine sites and the landscapes within which they are embedded are undoubtedly the foci of most conservation efforts (e.g., Angermeier and Schlosser 1995), there is much contingency and context-dependency along environmental gradients in the actual conservation value of sites, based on different measures of biodiversity. Thus, it appears that no general guidelines can be provided with regard to the variability of different measures of biodiversity along environmental gradients.

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