



Do different facets of littoral macroinvertebrate diversity show congruent patterns in a large lake system?

K. T. Tolonen^{1,2,4}, A. Vilmi¹, S. M. Karjalainen³, S. Hellsten³ and J. Heino¹

¹Finnish Environment Institute, Natural Environment Centre, P.O. Box 413, FI-90014 Oulu, Finland

²Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014 Jyväskylä, Finland (Current address)

³Finnish Environment Institute, Freshwater Centre, P.O. Box 413, FI-90014 Oulu, Finland

⁴Corresponding author. E-mail addresses: kimmo.t.tolonen@jyu.fi and kttolonen@gmail.com

Keywords: Biodiversity, Congruence, Facets of biodiversity, Lake ecosystems, Littoral zone.

Abstract: Modern biodiversity research focuses on multiple diversity facets because different indices may describe different ecological and environmental processes, as well as the effects of varied disturbances of natural and anthropogenic origins. We investigated littoral macroinvertebrate diversity in a large boreal lake system and specifically explored congruence of indices within and between the three diversity facets: species diversity, functional diversity and taxonomic distinctness. First, we found that the indices of taxonomic distinctness were the most sensitive indicators of eutrophication. Second, we observed that most correlations between the indices within the same diversity facet, and between the indices of functional and species diversity, were relatively strong. However, the indices of taxonomic distinctness ($\Delta+$ and $\Lambda+$) were weakly associated with other metrics of diversity, emphasising the importance of taxonomic distinctness as a complementary dimension of biodiversity. Therefore, our observations support the importance to examine multiple facets for mapping biodiversity or for assessing the effects of anthropogenic disturbances on biological communities.

Abbreviations: TP – Total Phosphorus, S – Species richness, J' – evenness, H' – Shannon diversity, Δ – taxonomic diversity, $\Delta+$ – taxonomic distinctness and $\Lambda+$ – variation in taxonomic distinctness.

Introduction

A modern perspective in ecology highlights multidimensionality of biodiversity, thus focusing on multiple facets of diversity (Devictor et al. 2010, Naeem et al. 2012, Purschke et al. 2013, Monnet et al. 2014). Here, we focus on three of these facets: species diversity, functional diversity and taxonomic distinctness. Species diversity is based on the numbers and relative abundances of species, including traditionally used measures of species richness, evenness and composite indices merging these separate dimensions of species diversity (e.g., Shannon index, Shannon 1948). Functional diversity refers to the ecological functions performed by species. Functional diversity is thus a key to understand, and a proxy for, ecosystem functioning (Litchman and Klausmeier 2008, Naeem et al. 2012). Taxonomic distinctness indices based on information from different taxonomic levels can be used as proxies of phylogenetic diversity (Warwick and Clarke 1995, Clarke and Warwick 2001). Therefore, taxonomic distinctness represents aspects related to the evolutionary history of species (Winter et al. 2013, Heino et al. 2015).

Current aquatic environmental assessment systems emphasize biotic elements of ecosystems, which are often summarized as ecological status and biodiversity indices. Species diversity indices have been shown to be sensitive in detecting impacts of anthropogenic stress, and a linear negative relationship with a stressor has often been detected (Guerold et

al. 2000, Jeppesen et al. 2000, Johnston and Roberts 2009). However, unimodal humped relationship of species richness has been observed to be common along the eutrophication gradient (Jeppesen et al. 2000, Ludsins et al. 2001). The use of species diversity indices in the ecological quality assessments has, however, been criticised due to their sensitivity to natural environmental gradients, which may impair sensitivity of species diversity indices to detect anthropogenic impacts (e.g., Warwick and Clarke 1998). Functional diversity has also been used in the bioassessment of freshwater ecosystems (e.g., Bonada et al. 2006). Advantages of using functional diversity measures include that they may allow rather straightforward comparison between studies based on different sets of species in different regions (e.g., Gallardo et al. 2011). Functional diversity also has lower sensitivity to sampling effort than species diversity (e.g., Bady et al. 2005), although a potential disadvantage is that functional diversity metrics are often redundant with species diversity metrics (e.g., Gallardo et al. 2011). Finally, taxonomic distinctness indices have commonly been used in the assessment of environmental pollution in marine environments (Warwick and Clarke 1995, Warwick and Clarke 1998, Leonard et al. 2006), and an increasing trend is to apply them to address similar problems in freshwater ecosystems (Abellán et al. 2006, Leira et al. 2009). In freshwater systems, however, the utility of taxonomic distinctness indices has been shown to be variable (e.g., Heino et al. 2007).

Congruence between different diversity indices is important when selecting metrics for environmental assessment. When evaluating impacts of specific environmental stressor (e.g., eutrophication), the use of only a single, typically the most sensitive indicator metric among the correlated variables may increase accuracy and precision of the assessment (e.g., Klemm et al. 2002). However, different stressors are effective in different water bodies and regions, and ecosystems are often impacted by several, sometimes even unknown stressors, which can often act synergistically (Folt et al. 1999, Matthaei et al. 2006). Our knowledge on the complexity of species interactions, effects of abiotic environmental conditions, and impacts of multiple human activities on ecosystems is also insufficient. Hence, the multidimensional approach combining several metrics may be more suitable for multi-purpose monitoring of ecosystems (Fore et al. 1996, Friberg et al. 2011). Furthermore, different facets of biodiversity have been observed to mismatch spatially, which is a challenge for conservation planning (Devictor et al. 2010). Therefore, the use of complementary and uncorrelated diversity indicators may provide a more comprehensive view of the whole complexity of biodiversity (Wilsey et al. 2005, Heino et al. 2008, Gallardo et al. 2011, Lyashevskaya and Farnsworth 2012).

We focused on multiple diversity facets and indices of biodiversity in a large boreal lake system. We first examined relationships of the diversity indices representing different diversity facets to a nutrient gradient. Based on earlier studies, we expected unimodal humped relationship of species richness (e.g., Jeppesen et al. 2000) and declining negative relationship for taxonomic distinctness indices (e.g., Δ^+) (e.g., Leonard et al. 2006) along the nutrient gradient. Second, we examined the congruence between diversity metrics within and between different diversity facets to evaluate complementarity of different indicator metrics. Therefore, we investigated if different diversity indices and facets are highly inter-correlated and, therefore, one diversity index, e.g., most commonly used species richness, is sufficient indicator to locate 'hotspots' or 'coldspots' of overall macroinvertebrate di-

versity. Alternatively, in the case of weak congruence among the indices and facets of diversity, we need complementary measures of diversity to identify biodiversity hotspots with highest conservation importance and to sufficiently understand anthropogenic threats to biota. The study was conducted using an extensive set of sampling sites covering the whole perimeter of the large lake system.

Material and methods

Study lake

The large Kitkajärvi lake system (305 km²) consists of several distinct sub-basins (Fig. 1), and drains through the River Koutajoki system to the White Sea. Lake Kitkajärvi has been a nutrient-poor lake with mesotrophic production of phytoplankton, moderate alkalinity and clear water in the past (Kankaala et al. 1984). During last decades, some parts of the lake system have, however, suffered eutrophication due to anthropogenic activities, which include forest clear-cutting, ditching, agriculture, loading of treated municipal wastewaters, and increased number of summer houses along the shoreline (Vilmi et al. 2015).

Field sampling and laboratory processing of macroinvertebrates

In September 2013, littoral macroinvertebrates were sampled at 81 stony bottom sites covering all sub-basins along the entire perimeter of Kitkajärvi lake system. Macroinvertebrates were sampled on shores with stony substratum using a kick-net with 0.5 mm mesh-size. At each site, a pooled sample of six kick samples, each along the 1-m stretch with 30 s kicking effort, were taken at 20-50 cm depth. This represented 6 m and 3 minutes sample size in total at each site. Samples were sieved using 0.5 mm mesh and preserved in alcohol in the field. In the laboratory, the samples

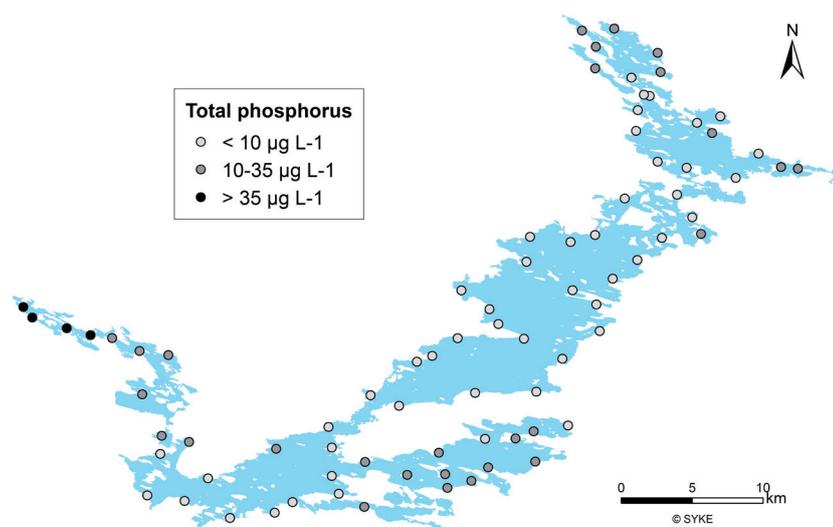


Figure 1. Map of Kitkajärvi lake system with the location of sampling sites along the lake perimeter. Total phosphorus status of the sites indicated by different symbols.

were sorted and animals were identified usually to species or genus, including the species-rich family Chironomidae, and individuals were counted. However, for the Oligochaeta, only a few common taxa were identified to species level. Water mites (Hydracarina) were not identified to lower level. All the phases of field and laboratory work were conducted by the same persons.

Indices of different diversity facets

We examined 9 indices describing species, functional and taxonomic facets of local diversity of littoral macroinvertebrates. Species diversity indices studied were: (1) species richness (S), which was the observed number of taxa at each site; (2) Pielou's evenness (J') or equality of the proportional abundances of species (Pielou 1966) and (3) Shannon's diversity (H') related to both the number of species and division of individuals among species (Shannon 1948).

We studied functional diversity based on three functional trait groups: body size, substrate association and feeding mode. Using the length-weight relationships obtained from the literature (Smock 1980, Meyer 1989, Benke et al. 1999), we calculated potential maximum size (dry weight mg) of the aquatic stage of species, where the 13 classes observed were the Log_2 transformed dry weights rounded down to the nearest whole number (-6, -5, -4, ..., 4, 5 and 6) following Rasmussen (1993). Second, functional trait group "substrate association" included five "traits": swimmers, crawlers, burrowers, semisessile and sessile. Third, species were classified by functional feeding group with the traits: scrapers, piercers, collector-gatherers, filterers, commensals, parasites and predators (e.g., Merritt and Cummins 1996, Tachet et al. 2010). Functional trait classifications of observed species are earlier reported in Tolonen et al. (2017). We calculated three indices related to functional diversity. (4) Functional richness (FR) was the number of combinations of the classes based on the three functional trait groups. (5) Functional evenness (FE) and (6) Functional diversity (FD) were based on the Pielou's evenness (J') and the Shannon diversity (H') indices, respectively, calculated using different combinations of the traits of three functional trait groups.

We examined three taxonomic distinctness indices, which are proxies of true phylogenetic diversity (Clarke and Warwick 2001, Winter et al. 2013). Since a comprehensive enough phylogeny of freshwater macroinvertebrates based on true phylogenetic relationships does not exist yet, we used taxonomic distance based on the path lengths in the Linnean taxonomic trees. This included seven taxonomic levels (i.e. species, genus, family, suborder, order, class and phylum). Fixed taxonomic distances were used for all consecutive pairs of taxonomic levels. Taxonomic distinctness measures were calculated using Primer software (version 6.1.13, Clarke and Gorley 2006). (7) Taxonomic diversity (Δ) is the average path length between random pairs of individuals in the sample whether they belong to the same or different species (Warwick and Clarke 1995). (8) Taxonomic distinctness ($\Delta+$) is the average path length between random pairs of species in the sample (Clarke and Warwick 1998). Finally, (9) varia-

tion in taxonomic distinctness ($\Lambda+$) is the variation in pairwise path lengths of $\Delta+$ and reflects the unevenness of the taxonomic tree (Clarke and Warwick 2001). We adopted the terminology used in the above-mentioned references and previous bioassessment studies (Leonard et al. 2006, Leira et al. 2009), where these indices have generally been called "taxonomic diversity" and "taxonomic distinctness". However, it should be noted, that Δ , $\Delta+$ and $\Lambda+$ are conceptually measuring phylogenetic diversity rather than taxonomic diversity of an assemblage (Winter et al. 2013, Heino et al. 2015).

Statistical analyses

The relationships of the diversity indices with total phosphorus (TP), a water chemistry variable describing human impacts in the lake system, were examined by regression analysis. In order to meet assumptions of the regression analyses (e.g., distribution normality and homoscedasticity of residuals), the total phosphorus was log_{10} -transformed. Akaike information criterion (AIC, Akaike 1974) was used to find the best model between the linear and quadratic functions in the regression analyses. Congruence within and between the species diversity, functional diversity and taxonomic distinctness facets was examined using Pearson correlation analysis.

Results

Shannon diversity, functional diversity, Δ and $\Delta+$ were curvilinearly associated with the total phosphorus (TP), which accounted for from 8 to 31% of the variation in these diversity variables (Figure 2). Of these indices, $\Delta+$ tended to be lower in eutrophic than in oligotrophic conditions. Species richness, functional richness and $\Lambda+$ were positively linearly correlated with the TP concentration, which explained 10 to 23% of the variation in these diversity indices. Evenness and functional evenness were not significantly ($\alpha = 0.05$) correlated to TP.

In the pairwise comparison between species diversity indices, Shannon diversity correlated significantly ($r \geq 0.65$, $P < 0.001$) with both species richness and evenness (Fig. 3). On the other hand, species richness and evenness were not associated with each other ($P = 0.968$). Among functional metrics, functional diversity was strongly correlated with functional richness and evenness, while the latter variables were not significantly inter-correlated. Among the taxonomic distinctness indices, Δ and $\Lambda+$ were not significantly correlated, while $\Delta+$ and $\Lambda+$ were relatively strongly correlated.

Most pairwise correlations between species diversity and functional diversity facets were significant ($r = 0.44$ to 0.93 , $P < 0.001$), with the exception of the association between species richness and functional evenness, and that between species evenness and functional richness. Very strong correlations were observed between species richness and functional richness, species evenness and functional evenness, and between Shannon diversity and functional diversity ($r \geq 0.83$) (Fig. 3). Relationships of taxonomic distinctness with species diversity and functional diversity facets were weaker

than that between the latter two facets. Significant ($P \leq 0.008$) relationships of species diversity and taxonomic distinctness included weak negative ($r = -0.30$) and positive ($r = 0.29$) associations of Δ^+ and Λ^+ with species richness, respectively, and stronger positive associations of Δ with species evenness and Shannon diversity. The significant ($P < 0.001$) relationships between the indices of taxonomic distinctness and functional diversity included only strong positive correlations of Δ with functional evenness and functional diversity.

Discussion

Among the studied diversity facets, taxonomic distinctness indices were the most sensitive indicators of eutrophication in our study lake system with monotonically decreasing

(Δ^+), unimodal (Δ) or with linearly increasing (Λ^+) relationships with the nutrient concentrations. The relationships of species and functional diversity indices with the phosphorus gradient were positively linear, unimodal or not significant. Among the species and functional diversity indices, we observed unimodal humped associations of Shannon diversity and functional diversity with nutrients. On the other hand, species and functional richness were positively linearly correlated with the nutrient gradient. At the local scale, as was the case in this study, the types of diversity-productivity relationships in aquatic ecosystems may be highly variable and context dependent (Mittelbach et al. 2001, Witman et al. 2008). However, the humped diversity-productivity association may be the most common type of relationship in lakes, especially at the local scale (Dodson et al. 2000, Chase and

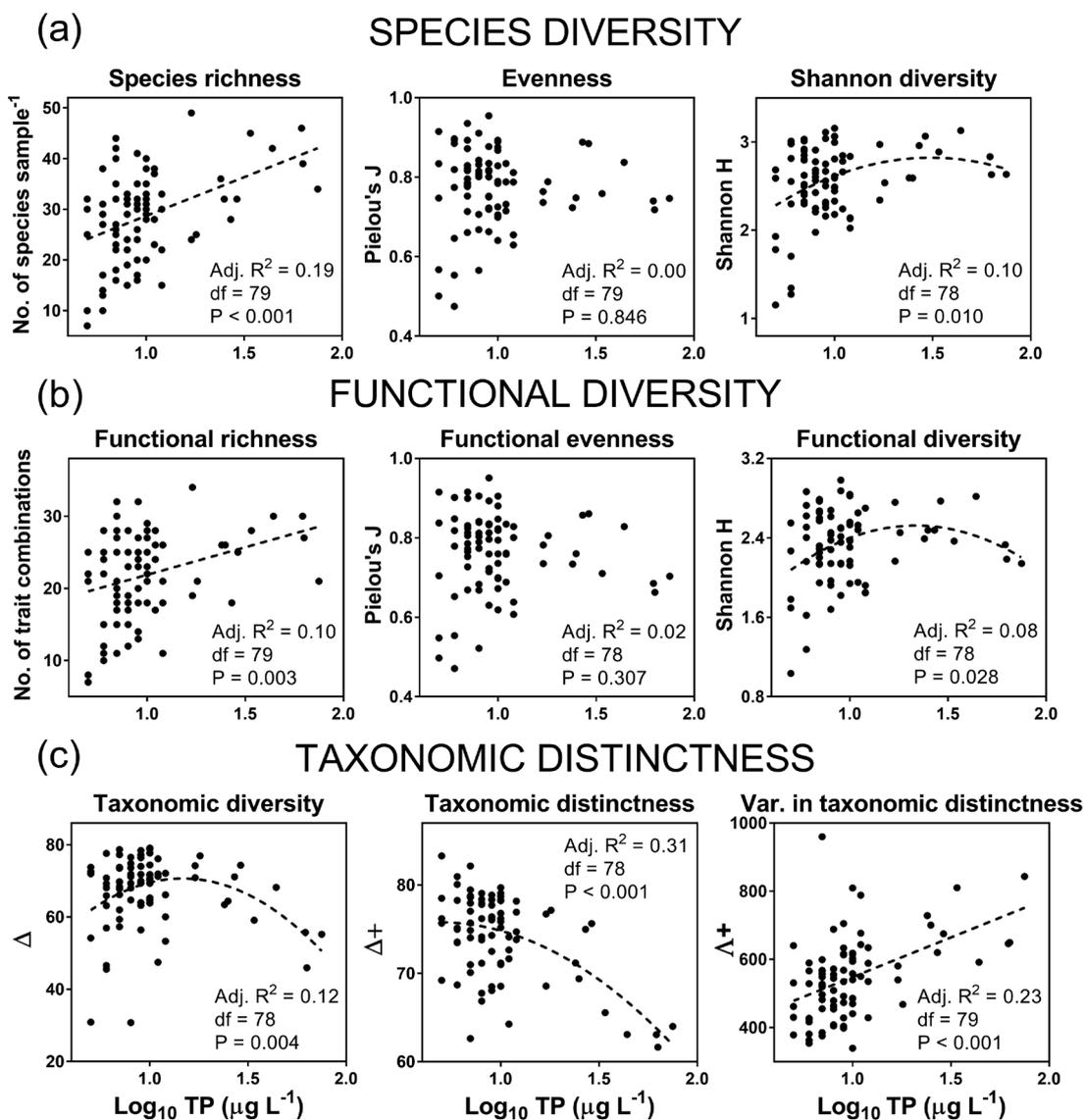


Figure 2. Relationships of the indices of **a)** species diversity, **b)** functional diversity and **c)** taxonomic distinctness to the total phosphorus (TP) gradient in the Kitkajärvi lake system.

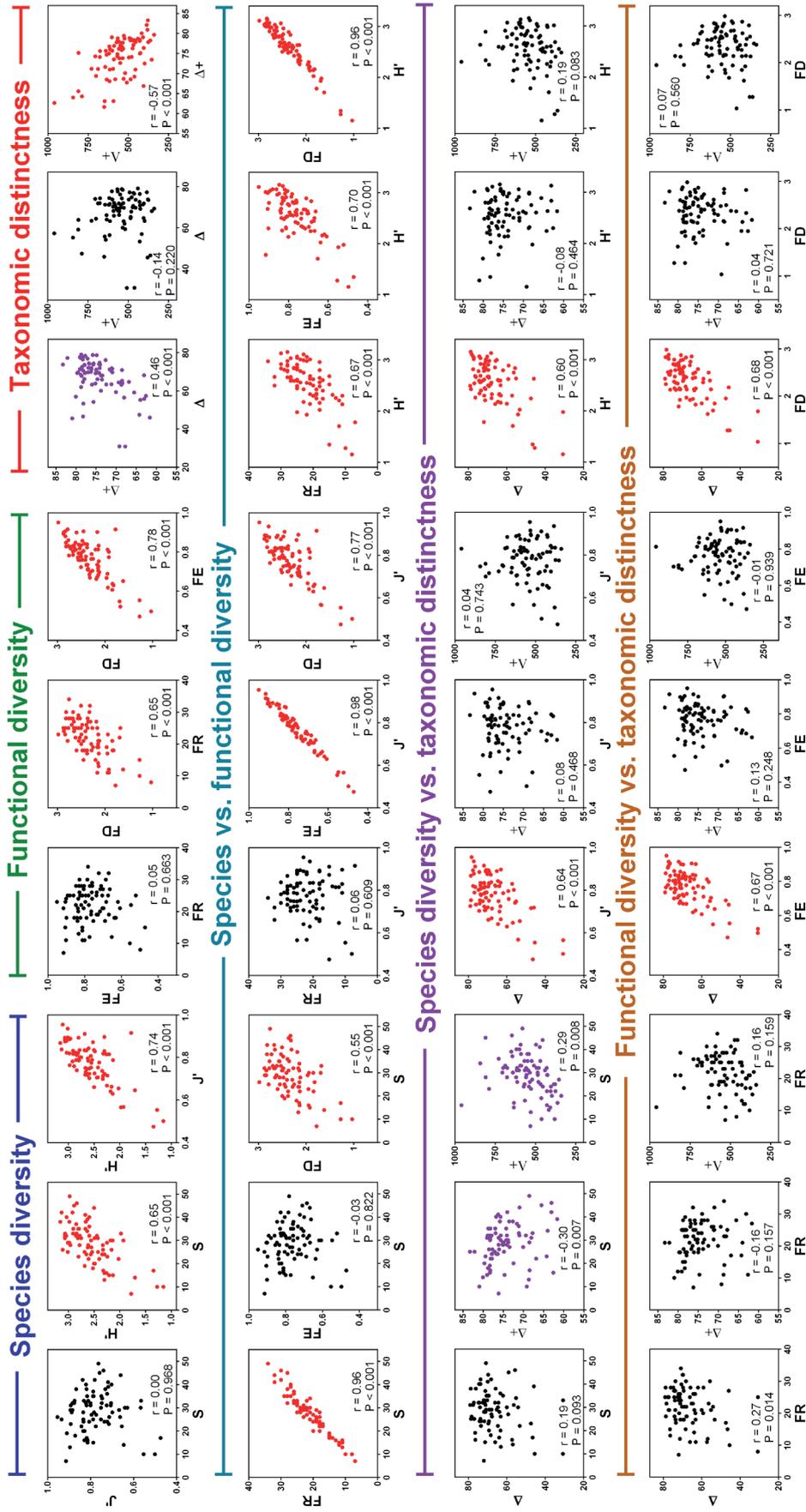


Figure 3. Congruence between the indices of the three diversity facets. In the individual scatter plots, non-significant ($P > 0.05$), weak but significant ($P = 0.05 - 0.001$, $r < 0.5$) and strongly significant ($P < 0.001$, $r \geq 0.5$) relationships are indicated by black, purple and red dots, respectively. S = species richness, Δ = taxonomic diversity, Δ+ = taxonomic distinctness and Δ+ = variation in taxonomic distinctness.

Leibold 2002, Chase and Ryberg 2004, Penning et al. 2008, Korhonen et al. 2011). Contrary to some earlier observations, which have shown that Pielou's evenness index may be a sensitive indicator of pollution in marine environments (Johnston and Roberts 2009), we did not observe a significant association between evenness and nutrient concentrations in our freshwater study system.

Congruence within each diversity facet was variable. Within the species diversity facet, Shannon diversity correlated strongly with species richness and evenness. These observed associations among species diversity indices are consistent with the earlier observations based on these indices (Heino et al. 2007, Mérigot et al. 2007, Gascón et al. 2009, Gallardo et al. 2011). Within the functional diversity facet, a corresponding pattern to species diversity indices was observed, i.e. functional diversity was strongly associated with functional richness and evenness. Within the taxonomic distinctness facet, relatively strong negative relationship was observed between $\Delta+$ and $\Lambda+$. Earlier observations regarding the association between $\Delta+$ and $\Lambda+$ have been contradictory, with earlier studies reporting significant positive (Heino et al. 2007, Leira et al. 2009, Gallardo et al. 2011), significant negative (Gascón et al. 2009) and non-significant (Mérigot et al. 2007) relationship between these indices.

Congruence of the indices among the diversity facets varied. We observed that congruences between species and functional diversity indices were particularly strong, which agrees with the earlier observations on the relationships between the indices of these two diversity facets (Heino 2008, Gallardo et al. 2011). Therefore, functional diversity may be a redundant facet, when compared to the species diversity facet (Van den Brink 2011). On the other hand, the relationships between taxonomic distinctness and species or functional diversity indices were weak or non-significant, if Δ is not taken into account (see also Heino et al. 2007, Gascón et al. 2009, Gallardo et al. 2011). This index was correlated with evenness, Shannon diversity, functional evenness and functional diversity, which agrees with the earlier observations (Heino et al. 2007, Gascón et al. 2009). These observations also suggest that indices of the taxonomic distinctness ($\Delta+$ and $\Lambda+$) may represent different dimension among diversity facets, and may provide additional information about biodiversity and ecosystem conditions if compared to the other studied facets (Heino et al. 2008, Gallardo et al. 2011).

We observed that measures of taxonomic distinctness were the most sensitive indicators of lake eutrophication among the studied diversity indices. It is striking that our results from a highly connected lake ecosystem were rather similar to those from sets of individual stream (e.g., Heino et al. 2007) and wetland (e.g., Gascón et al. 2009) sites, which suggest some generalities in the congruence within and between diversity facets. Our observations thus support the fact that sensitivity of taxonomic distinctness as an indicator of anthropogenic disturbances should also be investigated more thoroughly in freshwater ecosystems. Our results also support the importance of using multiple facets of diversity in environmental assessment and biodiversity analysis. These observations imply that, as a proxy of phylogenetic diversity,

taxonomic distinctness may be a robust and uncorrelated biodiversity dimension among the diversity facets to be applied in bioassessment and biodiversity mapping.

Acknowledgements: This study was financially supported by the European Regional Development Fund of the European Union and by Maj and Tor Nessling Foundation. S. Hellsten was supported by the MARS project funded under the 7th EU Framework Programme, Theme 6 (Environment including Climate Change), Contract No. 603378. We thank M. Manninen, S. Latvala, O. Murtovaara, R. Paavola, J. Leppälä, Y. Kivinen, T. Laamanen and S. Kunnas for their valuable help during different stages of the study.

References

- Abellán, P., Bilton, D.T., Millán, A., Sánchez-Fernández, D. and Ramsay, P.M. 2006. Can taxonomic distinctness assess anthropogenic impacts in inland waters? A case study from a Mediterranean river basin. *Freshwater Biol.* 51: 1744–1756.
- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723.
- Bady, P., Dolédec, S., Fesl, C., Gayraud, S., Bacchi, M. and Schöll, F. 2005. Use of invertebrate traits for the biomonitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity. *Freshwater Biol.* 50: 159–173.
- Benke, A.C., Huryn, A.D., Smock, L.A. and Wallace, J.B. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *J. North Am. Benthol. Soc.* 18: 308–343.
- Bonada, N., Prat, N., Resh, V.H. and Statzner, B. 2006. Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. *Annu. Rev. Entomol.* 51: 495–523.
- Chase, J.M. and Leibold, M.A. 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* 416: 427–430.
- Chase, J.M. and Ryberg, W.A. 2004. Connectivity, scale-dependence, and the productivity-diversity relationship. *Ecol. Lett.* 7: 676–683.
- Clarke, K.R. and Warwick, R.M. 1998. A taxonomic distinctness index and its statistical properties. *J. Appl. Ecol.* 35: 523–531.
- Clarke, K.R. and Warwick, R.M. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series* 216: 265–278.
- Clarke, K.R. and Gorley, R.N. 2006. Primer v6: User Manual/Tutorial. Primer-E Ltd. 190 pp.
- Devictor, V., Mouillot, D., Meynard, C., Jiquet, F., Thuiller, W. and Mouquet, N. 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13: 1030–1040.
- Dodson, S.I., Arnott, S.E. and Cottingham, K.L. 2000. The relationship in lake communities between primary productivity and species richness. *Ecology* 81: 2662–2679.
- Folt, C.L., Chen, C.Y., Moore, M.V. and Burnaford, J. 1999. Synergism and antagonism among multiple stressors. *Limnol. Oceanogr.* 44: 864–873.
- Fore, L.S., Karr, J.R. and Wisseman, R.W. 1996. Assessing invertebrate responses to human activities: evaluating alternative approaches. *J. North Am. Benthol. Soc.* 15: 212–231.

- Friberg, N., Bonada, N., Bradley, D.C., Dunbar, M.J., Edwards, F.K., Grey, J., Hayes, R.B., Hildrew, A.G., Lamouroux, N., Trimmer, M. and Woodward, G. 2011. Biomonitoring of human impacts in freshwater ecosystems: the Good, the Bad and the Ugly. *Adv. Ecol. Res.* 44: 1–68.
- Gallardo, B., Gascón, S., Quintana, X. and Comín, F.A. 2011. How to choose a biodiversity indicator - redundancy and complementarity of biodiversity metrics in a freshwater ecosystem. *Ecol. Indic.* 11: 1177–1184.
- Gascón, S., Boix, D. and Sala, J. 2009. Are different biodiversity metrics related to the same factors? A case study from Mediterranean wetlands. *Biol. Conserv.* 142: 2602–2612.
- Guerold, F., Boudot, J-P. Jacquemin, G., Vein, D., Merlet, D. and Rouiller, J. 2000. Macroinvertebrate community loss as a result of headwater stream acidification in the Vosges Mountains (N-E France). *Biodivers. Conserv.* 9: 767–783.
- Heino, J. 2008. Patterns of functional biodiversity and function-environment relationships in lake macroinvertebrates. *Limnol. Oceanogr.* 53: 1446–1455.
- Heino, J., Alahuhta, J. and Fattorini, S. 2015. Phylogenetic diversity of regional beetle faunas at high latitudes: patterns, drivers and chance along ecological gradients. *Biodivers. Conserv.* 24: 2751–2767.
- Heino, J., Mykrä, H. and Kotanen, J. 2008. Weak relationships between landscape characteristics and multiple facets of stream macroinvertebrate biodiversity in a boreal drainage basin. *Lands. Ecol.* 23: 417–426.
- Heino, J., Mykrä, H., Hämäläinen, H., Aroviita, J. and Muotka, T. 2007. Responses of taxonomic distinctness and species diversity indices to anthropogenic impacts and natural environmental gradients in stream macroinvertebrates. *Freshwater Biol.* 52: 1846–1861.
- Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T. and Landkildehus, F. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biol.* 45: 201–218.
- Johnston, E.L. and Roberts, D.A. 2009. Contaminants reduce the richness and evenness of marine communities: a review and meta-analysis. *Environ. Pollution* 157: 1745–1752.
- Kankaala, P., Hellsten S. and Alasaarela, E. 1984. Primary production of phytoplankton in the oligohumic Kitka lakes in northern Finland. *Aqua Fennica* 14: 65–78.
- Klemm, D.J., Blocksom, K.A., Thoeny, W.T., Fulk, F.A., Herlihy, A.T., Kaufmann, P.R. and Cormier, S.M. 2002. Methods development and use of macroinvertebrates as indicators of ecological conditions for streams in the Mid-Atlantic Highlands Region. *Environ. Monitor. Assess.* 78: 169–212.
- Korhonen, J.J., Wang J. and Soininen, J. 2011. Productivity-diversity relationships in lake plankton communities. *PLoS ONE* 6: e22041.
- Leira, M., Chen, G., Dalton, C. Irvine, K. and Taylor, D. 2009. Patterns in freshwater diatom taxonomic distinctness along an eutrophication gradient. *Freshwater Biol.* 54: 1–14.
- Leonard, D.R.P., Clarke, K.R., Somerfield, P.J. and Warwick, R.M. 2006. The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessment. *J. Environ. Manage.* 78: 52–62.
- Litchman, E. and Klausmeier, C.A. 2008. Trait-based community ecology of phytoplankton. *Ann. Rev. Ecol. Evol. Syst.* 39: 615–639.
- Ludsin, S.A., Kershner, M.W., Blocksom, K.A., Knight, R.L. and Stein, R.A. 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecol. Appl.* 11: 731–746.
- Lyashevskaya, O. and Farnsworth, K.D. 2012. How many dimensions of biodiversity do we need? *Ecol. Indic.* 18: 485–492.
- Matthaei, C.D., Weller, F., Kelly, D.W. and Townsend, C.R. 2006. Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biol.* 51: 2154–2172.
- Mérigot, B., Bertrand, J.A., Gaertner, J-C., Durbec, J-P., Mazouni, N. and Manté, C. 2007. The multi-component structuration of the species diversity of groundfish assemblages of the east coast of Corsica (Mediterranean Sea): variation according to the bathymetric strata. *Fish. Res.* 88: 120–132.
- Merritt, R.W. and Cummins, K.W. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company. 862 pp.
- Meyer, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. *Archiv für Hydrobiologie* 117: 191–203.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. and Gough, L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- Monnet, A-C., Jiguet, F., Meynard, C.N., Mouillot, D., Mouquet, N., Thuiller, W. and Devictor, V. 2014. Asynchrony of taxonomic, functional and phylogenetic diversity in birds. *Global Ecol. Biogeogr.* 23: 780–788.
- Naeem, S., Duffy, J.E. and Zavaleta, E. 2012. The functions of biological diversity in an age of extinction. *Science* 336: 1401–1406.
- Penning, W.E., Dudley, B., Mjelde, M., Hellsten, S., Hanganu, J., Kolada, A., van den Berg, M., Maemets, H., Poikane, S., Phillips, G., Willby, N. and Ecke, F. 2008. Using aquatic macrophyte community indices to define the ecological status of European lakes. *Aquat. Ecol.* 42: 253–264.
- Pielou, E.C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. *J. Theoret. Biol.* 10: 370–383.
- Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S.G., Durka, W., Kühn, I., Winter, M. and Prentice, H.C. 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *J. Ecol.* 101: 857–866.
- Rasmussen, J.B. 1993. Patterns in the size structure of littoral zone macroinvertebrate communities. *Can. J. Fish. Aquat. Sci.* 50: 2192–2207.
- Shannon, C.E. 1948. A mathematical theory of communication. *The Bell System Technical J.* 27: 379–423.
- Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biol.* 10: 375–383.
- Tachet, H., Richoux, B., Bournaud, M. and Usseglio-Polatera, P. 2010. Invertébrés d'eau douce. CNRS éditions.
- Tolonen, K.T., Vilmi, A., Karjalainen, S.M., Hellsten, S., Sutela, T. and Heino, J. 2017. Ignoring spatial effects results in inadequate models for variation in littoral macroinvertebrate diversity. *Oikos*. DOI: 10.1111/oik.03587
- Van den Brink, P.J., A.C. Alexander, A.C., Desrosiers, M., Goedkoop, W., Goethals, P.L.M., Liess, M. and Dyer, S.D. 2011. Trait-based approaches in bioassessment and ecological risk assessment: strengths, weaknesses, opportunities and threats. *Integrated Environ. Assess. Manage.* 7: 198–208.
- Vilmi, A., Karjalainen, S.M., Landeiro, V.L. and Heino, J. 2015. Freshwater diatoms as environmental indicators: evaluating the

- effects of eutrophication using species morphology and biological indices. *Environ. Monitor. Assess.* 187: 243–252.
- Warwick, R.M. and Clarke, K.R. 1995. New ‘biodiversity’ measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* 129: 301–305.
- Warwick, R.M. and Clarke, K.R. 1998. Taxonomic distinctness and environmental assessment. *J. Appl. Ecol.* 35: 532–543.
- Wilsey, B.J., Chalcraft, D.R., Bowles, C.M. and Willig, M.R. 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology* 86: 1178–1184.
- Winter, M., Devictor V. and Schweiger, O. 2013. Phylogenetic diversity and nature conservation: where are we? *Trends Ecol. Evol.* 28: 199–204.
- Witman, J.D., Cusson, M., Archambault, P., Pershing, A.J. and Mieszkowska, N. 2008. The relation between productivity and species diversity in temperate-arctic marine ecosystems. *Ecology* 89: S66–S80.

Received September 29, 2016

Revised May 16, 2017

Accepted May 23, 2017