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

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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.


Introduction

A modern perspective in ecology highlights multidimensionality of biodiversity, thus focusing on multiple facets of diversity (Devictor et al. 2010, Naem 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, Naem 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 observed to be common along the eutrophication gradient (Jeppesen et al. 2000, Ludsin 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 multipurpose 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 (De victor 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, Lyashevska 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 diversity. 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 clearcutting, 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.](image-url)
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 weight-length 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, semisessiles and sessiles. 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 (Δ+) is the average path length between random pairs of species in the sample (Clarke and Warwick 1998). Finally, (9) variation in taxonomic distinctness (Λ+) is the variation in pairwise path lengths of Δ+ 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, Δ+ and Λ+ 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 Δ+ 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, Δ+ tended to be lower in eutrophic than in oligotrophic conditions. Species richness, functional richness and Δ+ 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 (α = 0.05) correlated to TP.

In the pairwise comparison between species diversity indices, Shannon diversity correlated significantly (r ≥ 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 Λ+ were not significantly correlated, while Δ+ and Λ+ 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 ≥ 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 \(\Delta^+\) and \(\Lambda^+\) with species richness, respectively, and stronger positive associations of \(\Lambda\) 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 \(\Delta\) 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 \((\Delta^+\), unimodal \((\Delta)\) or with linearly increasing \((\Lambda^+\)) 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](image_url). 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, $J'$ = evenness, $H'$ = Shannon diversity, $\Delta =$ taxonomic diversity, $\Delta^+ =$ taxonomic distinctness and $\Lambda^+ =$ 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 $\Delta^-$. 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 $\Delta$ 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 $\Delta^-$) 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.

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References


Vlimi, A., Karjalainen, S.M. Landeiro, V.L. and Heino, J. 2015. Freshwater diatoms as environmental indicators: evaluating the


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