Patterns in freshwater diatom taxonomic distinctness along a eutrophication gradient

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Summary

1. A variety of species richness measures have been used to assess the effects of environmental degradation on biodiversity. Such measures can be highly influenced by sample size, sampling effort, habitat type or complexity, however, and typically do not show monotonic responses to human impact. In addition to being independent of the degree of sampling effort involved in data acquisition, effective measures of biodiversity should reflect the degree of taxonomical relatedness among species within ecological assemblages and provide a basis for understanding observed diversity for a particular habitat type. Taxonomic diversity or distinctness indices emphasise the average taxonomic relatedness (i.e. degree of taxonomical closeness) between species in a community.
2. Eutrophication of freshwater ecosystems, mainly due to the increased availability of nutrients, notably phosphorus, has become a major environmental problem. Two measures of taxonomic distinctness (Average Taxonomic Distinctness and Variation in Taxonomic Distinctness) were applied to surface sediment diatoms from 45 lakes across the island of Ireland to examine whether taxonomic distinctness and nutrient enrichment were significantly related at a regional scale. The lakes span a range of concentrations of epilimnic total phosphorus (TP) and were grouped into six different types, based on depth and alkalinity levels, and three different categories according to trophic state (ultra-oligotrophic and oligotrophic; mesotrophic; and eutrophic and hyper-eutrophic).
3. The taxonomic distinctness measures revealed significant differences among lakes in the three different classes of trophic state, with nutrient-rich lakes generally more taxonomically diverse than nutrient-poor lakes. This implies that enrichment of oligotrophic lakes does not necessarily lead to a reduction in taxonomic diversity, at least as expressed by the indices used here. Furthermore, taxonomic distinctness was highly variable across the six different lake types regardless of nutrient level.
4. Results indicate that habitat availability and physical structure within the study lakes also exert a strong influence on the pattern of taxonomic diversity. Overall the results highlight problems with the use of taxonomic diversity measures for detecting impacts of freshwater eutrophication based on diatom assemblages.

Introduction

Eutrophication has had a major impact on inland waters over the last century. Increasing availability of nutrients such as phosphorus, commonly associated with eutrophication, affects the productivity and community structure of primary producers in aquatic ecosystems. Biological diversity is generally considered an indicator of the quality of freshwater systems (Tilman *et al.*, 1997; Sondergaard & Jeppesen, 2007) and is often assumed to decrease with increasing nutrient levels (Tilman, Kilham & Kilham, 1982; Tilman, Lehman & Thomson, 1997; Burkholder, 2001; Wassen *et al.*, 2005). Measures of biodiversity based on species richness, abundance and evenness have been used to assess the effects of environmental degradation on biota, such as those caused by nutrient enrichment, despite several confounding factors. These include the influence of sample size, sampling effort, habitat type or complexity, or an absence of monotonic responses to human impact (Waide *et al.*, 1999). For these reasons, alternative measures of diversity that provide a basis for quantifying biodiversity loss as a result of environmental degradation, while making low demands on the completeness of datasets, have recently been proposed (Clarke & Warwick, 1998, 2001) and trialled in a range of ecological settings (e.g. Heino *et al.*, 2005; Campbel & Novelo-Gutierrez, 2007; Ceschia, Falace & Warwick, 2007; Campbell, Arce-Perez & Gomez-Anaya, 2008). Moreover, the capability of measures of biodiversity to go beyond measures of species richness and evenness has been widely recognised (Harper & Hawksworth, 1994; Anand & Orloci, 1996; Tilman, Lehman & Thomson, 1997).

Quantification of the structure and complexity of biotic assemblages can provide valuable information on the status of ecosystems (Tilman, 1997). Measures based on the taxonomic structure of a biological assemblage differ from more conventional diversity indices by incorporating the degree to which species are evolutionarily related to one another. The premise is that an assemblage of closely related species must be regarded as less diverse than an assemblage of the same number of more distantly related species (e.g where species belong to different taxonomic classes) (Warwick & Clarke, 1998). Warwick and Clarke (1995) introduced the concept of taxonomic distinctness, as a measure of the average degree to which individuals in an assemblage are related. Clarke and Warwick (1998, 2001) showed that taxonomic distinctness measures overcome most of the problems of traditional measures of diversity, including those linked to sample size, and have a number of properties that are desirable in the context of environmental impact assessment.

The usefulness of taxonomic distinctness for marine biodiversity assessment has been reported in several studies in recent years (Warwick *et al.*, 2002; Ellingsen *et al.*, 2005; Leonard *et al.*, 2006; Moss *et al.*, 2006; Ceschia, Falace, & Warwick, 2007), all suggesting that taxonomic distinctness of degraded locations is significantly reduced compared to relatively pristine locations for different groups of organisms (e.g. benthic nematodes, coastal fishes, echinoderms) and in different regions of the world. Apart from a few very recent studies that have focused on fauna (mainly macroinvertebrates) (e.g., Campbell & Novelo-Gutierrez, 2007; Heino *et al.*, 2007; Marchant, 2007), the value of taxonomic distinctness measures as a means of expressing anthropogenic effects has not been tested in freshwater ecosystems. Moreover, only a few studies to date have explicitly examined how measures of taxonomic distinctness perform in comparison to other biodiversity measures (Heino *et al.*, 2005; Abellan *et al.*, 2006; Bhat & Magurran, 2006).

Diatoms are one of the most diverse and widely used groups of freshwater organisms in limnological monitoring and palaeoenvironmental reconstruction (Stoermer & Smol, 1999; Battarbee *et al.*, 2001). Total phosphorus (TP) often has an important influence on the composition of diatom assemblages (Bennion, 1994; Bennion, Fluin & Simpson, 2004; DeNicola *et al.*, 2004). Algal species richness peaks at intermediate nutrient conditions, and declines towards extreme conditions (Jeppesen *et al.*, 2000), which is typically interpreted in terms of competitive abilities or limited physiological tolerance to sub-optimum conditions (Tilman, Kilham & Kilham, 1982; Chase, 2003). Our study uses sediment diatom assemblages and associated environmental data from a selection of Irish lakes that cover a range of concentrations of epilimnic TP to examine the potential of taxonomic diversity measures in environmental assessment. In addition, the paper seeks to explore the differences in taxonomic distinctness between diatom assemblages along a gradient of nutrient enrichment.

Methods

Data collection

Analyses are based on a list of diatom taxa and their abundances in surface sediment samples from 45 lakes in Ireland, together with associated environmental information (Figure 1). The lakes represent the six major types of freshwater lakes in Ireland, divided according to alkalinity (< 20 mg L^{-1} $CaCO_3$, 20-100 mg L^{-1} $CaCO_3$, > 100 mg L^{-1} $CaCO_3$) and average water depth (< > 4 m): low alkalinity (shallow and deep), moderate alkalinity (shallow and deep), and high alkalinity (shallow and deep)). The 45 lakes were also classified into three categories according to their level of nutrient enrichment: (i) ultra-oligotrophic and oligotrophic, (ii) mesotrophic, and (iii) eutrophic and hyper-eutrophic according to a modified version of the OECD (1982) scheme based on annual maxima of chlorophyll concentrations (Toner *et al.*, 2005).

Standard methods were used to collect surface sediment samples and to analyse their diatom contents (Battarbee *et al.*, 2001). Diatom species were identified to species or variety level (henceforth referred to simply as species) using standard taxonomic references (Krammer & Lange-Bertalot, 1986-1991). Species identified in the surface sediments (0.5-1 cm) typically represent all or most of the species that have been present in the different lake habitats within the previous 1–3 years (Dixit *et al.*, 1999), depending on rates of sediment accumulation. The taxonomical classification of freshwater diatoms was primarily compiled from Round, Crawford and Mann (1990), with additional information from Hartley (1996), Håkansson (2002) and Jahn and Kusber (2007), and included up to six taxonomic levels for diatoms where possible: species, genus, family, order, subclass and class.

Taxonomic distinctness analysis

Based on the assumption that the presence of a species in any sample is random, Clarke and Warwick (1998) devised a randomisation test to compare the observed value of taxonomic distinctness against an expected value derived from an inventory of species occurring in the same region as the sample population. For the current research, this regional inventory comprised a list of 602 species of freshwater diatoms enumerated in surface sediment samples obtained from 72 freshwater lakes from across the island of Ireland (Irish Ecoregion) (Chen *et al.*, 2008). The null expectation is that the presence of species represents a random selection from the species pool (i.e. every species in the inventory has an equal probability to exist at all locations). Random subsampling of different numbers of species allowed the expected values to be plotted as a probability funnel (5% level), against which the observed taxonomic distinctness values from real samples were plotted, thus permitting determination of whether a sample has a lower-than-expected taxonomic diversity.

Two indices of taxonomic diversity (Average Taxonomic Distinctness; AvTD (Δ^+); and Variation in Taxonomic Distinctness; VarTD (Λ^+)) defined by Clarke and Warwick (1998, 2001) were calculated using the PRIMER 5 software package (Clarke & Gorley, 2001). AvTD takes into account the taxonomic level at which any two species are related and can be thought of as the average length of the path connecting any two randomly chosen species present in the sample, whereas VarTD is a measure of the degree to which certain taxa are over- or under-represented in a sample. A simple form of weighting was adopted for the six taxonomic levels ($\omega = 1$ for species i and j within the same genus; $\omega = 2$ for species within different genera but the same family; $\omega = 3$ for species within different families but the same order, etc.).

The combination of AvTD and VarTD in a 2D scatter plot provides a statistically robust summary of the taxonomic relatedness patterns within the diatom assemblages. Basically, the distribution of AvTD and VarTD values from real data are compared with simulated values derived from random data subsets of the regional inventory. A bivariate distribution is then fitted to the simulated values, and a probability ellipse defined that encloses 95% of probability for the different numbers of species (m). The null hypothesis, that the observed combined AvTD and VarTD pairs of values for each sample show a taxonomic structure representative of a random sample from the regional inventory, is rejected if the sample falls outside the 95% probability ellipse.

Data analysis

The commonly used Shannon Wiener diversity index (H') and Pielou's evenness index (J') (Magurran, 2004) were also applied to the surface sediment diatom assemblage data. J' is a measure of equitability, or how evenly the individuals in a sample are distributed among the different species. The two indices were used in the current research because an assemblage may be considered more diverse if it contains many species at relatively even abundance when compared with an assemblage with the same number of species but with fewer numerically dominant taxa.

The significance of differences between samples from lake types and between samples from different levels of nutrient concentrations was tested using a one-way ANOVA and Tukey's HSD test for multiple comparisons. The relationships between species richness and taxonomic diversity measures with selected environmental variables were examined using Pearson's correlation analysis and stepwise regression analyses with forward selection (α = 0.05) of independent variables. As trophic structure and dynamics were expected to be substantially affected by lake depth, and species diversity and richness have been shown to be sensitive to lake area, variables that are not directly affected by human activities were included as independent variables in partial correlation analyses to describe the linear relationship between the variables while controlling for the effects of natural variations along the trophic gradient. These included altitude, maximum and mean depth, lake area and peatland cover; and water chemistry variables such as alkalinity. Statistical analyses were performed using SPSS for Windows (version 13.0; SPSS Inc., Illinois).

Results

Descriptive statistics for the different lake types are shown in Table 1. Taxonomic diversity measures for the surface sediment diatom samples are illustrated in Figures 2 and 3.

The 45 lake dataset comprised more than 470 species of diatoms belonging to three classes, 13 orders and 24 families (Table 2). The number of families represented in each of the three trophic categories of lakes was similar but the taxonomic structure was different. In nutrient poor lakes, which have the lowest taxonomic distinctness values, most species belonged to the families Achnanthidiaceae, Fragilariaceae and Naviculaceae. These families are classified in three different orders, respectively Achnanthales, Flagilariales and Naviculales: Achnanthidiaceae and Naviculaceae belong to the same Class (Bacillariophyceae), while the Fragilariaceae belongs to the Class Fragilariophyceae. Some taxa were found mainly in lakes with low nutrient content, including *Achnanthidium minutissimum* (Kützing) Czarnecki, *Stauroforma exiguiformis* Flower Jones et Round, *Amphora pediculus* (Kutzing) Grunow, *Tabellaria flocculosa* (Roth) Kutzing and *Pseudostaurosira brevistriata* (Grunow in Van Heurck) Williams et Round. These taxa belong to four different families but only two classes. Most species in lakes with higher nutrient levels, which show higher taxonomic distinctness values, belonged to the families Fragilariaceae, Naviculaceae and Stephanodiscaceae, which are members of three different classes (Fragilariophyceae, Bacillariophyceae and Coscinodiscophyceae, respectively). Moreover, nutrient-enriched lakes are associated with less diverse diatom assemblages. Diatom communities in these lakes were mostly characterised by *Aulacoseira subarctica* (O.Muller) Haworth, *Stephanodiscus parvus* Stoermer et Hakansson, *Stephanodiscus hantzschii* Grunow, *Aulacoseira granulata* (Ehrenberg) Simonsen and *Asterionella formosa* Hassall representative of three different families and two classes which are species poor.

Diversity varied across the different lake types and trophic condition classes according to the indices used in the current research (Figures 2 and 3). Total taxonomic distinctness (not shown) was highly correlated with species diversity (correlation coefficient = 0.70, $P < 0.05$, n = 45), and therefore does not seem to provide any significant additional information about community diversity. In addition, differences between the mean values of species diversity and total evenness across the different lake types were non-significant (one way ANOVA, $P = 0.093$ and $P = 0.112$ respectively) (Figure 2). In contrast, AvTD and VarTD were significantly different across lake types (Tukey's HSD test $P < 0.001$ and $P < 0.01$ respectively). Thus, both AvTD and VarTD were significantly higher in moderate alkalinity shallow lakes than in low and high alkalinity lakes. There were also significant differences in mean values of AvTD between deep and shallow lakes ($P < 0.05$).

Species diversity and evenness did not show a significant relationship with increased nutrient enrichment (one-way ANOVA, $P > 0.1$ in both cases) (Figure 2). However, a clear relationship between trophic state and taxonomic diversity was found (Figure 3) and values of taxonomic distinctness between lakes in the three classes of trophic state were significantly different (one-way ANOVA, $P < 0.05$). Nutrient-poor lakes were associated with the lowest levels of AvTD and VarTD and nutrient-enriched lakes with the highest. Thus, AvTD was significantly higher in eutrophic and hyper-eutrophic lakes than in ultra-oligotrophic and oligotrophic ones ($P = 0.003$), whereas VarTD differences among lake trophic classes showed a P value = 0.058.

Results of the randomisation tests to identify significant departures from the theoretical mean taxonomic distinctness measures, based on AvTD and VarTD, are shown in Figures 4 and 5. Most of the sites have an AvTD higher than the theoretical mean derived from the regional inventory of diatom species. Diatoms in surface sediment samples from 21 lakes had AvTD values higher than the upper 95% confidence level, and most of these were mesotrophic or eutrophic/hyper-eutrophic (Figure 4). All eutrophic and hyper-eutrophic lakes had AvTD values higher than the theoretical mean. Similarly most VarTD values were higher than the theoretical mean although the majority fell within the 95% confidence level for different lake types and trophic conditions (Figure 5.).

Figure 6 shows the fitted 95% probability ellipses for a range of species numbers (m) chosen to cover the range of taxa found in the dataset. For the sake of clarity the data have been divided into three scatter plots: lakes with number of species (m) = 20, 30 and 40 are displayed in 6a; lakes with m = 50 are shown in 6b; and lakes with m = 60 and 70 are recorded in 6c. Observed AvTD and VarTD values for the study lakes are superimposed on the appropriate component plot (the actual number of species found is also indicated in parantheses). A higher proportion of diatom assemblages from mesotrophic, eutrophic and hyper-trophic lakes (55%) showed a taxonomic structure significantly different from that expected according to the regional inventory compared to ultra-oligotrophic and oligotrophic lakes (21%). Observed values of AvTD and VatTD for most of the low alkalinity sites were within their respective ellipses, indicating no significant differences from expected. For moderate and high alkalinity sites, the pattern was quite different, with a clear increase in AvTD in comparison with low alkalinity lakes, although levels of VarTD were close to expected. Nearly all moderate alkalinity lakes, both deep and shallow, with moderate and high nutrient statuses, had values of AvTD outside of their respective ellipses. Depth appeared to be an important factor concerning taxonomic distinctness for high alkalinity sites with most of the high alkalinity deep lakes showing greater than expected AvTD values, while nearly all shallow lakes had values of taxonomic diversity within their respective ellipses, independent of trophic class.

Pearson's correlations on transformed data revealed a positive significant correlation between measures of taxonomic diversity (AvTD and VarTD) and those variables representative of trophic state (Table 3). TP and chlorophyll were significantly positively correlated with AvTD and VarTD and negatively correlated with species diversity and evenness. Although the alkalinity gradient in this dataset was also strong, diversity measures were not significantly correlated. More importantly, land use, a key variable determining the trophic state of surface waters because of its relationship with inputs of nutrients and water clarity, was significantly correlated to the measures of diatom taxonomic diversity, but not to species diversity and evenness. Conductivity, an integrated measure of several catchment processes and geology, also showed a significant correlation with VarTD.

The correlation between taxonomic diversity measures and trophic state indicators did not change significantly when the natural environmental variation among sites was controlled for (i.e. variables were treated as covariables in partial correlation analyses). However, land use variables that were initially significantly correlated with taxonomic distinctness were not significantly related when partial correlations were implemented, while water colour became positively correlated after partialling out the effect of natural environmental variables (including altitude, maximum and mean depth).

Multiple regression analysis revealed that indicators of trophic state as well as average depth contributed significantly to the variation in taxonomic diversity ($P < 0.05$). TP concentration was not included in the models because of its potential collinearity with chlorophyll. In general, and following stepwise selection of independent variables, the final models were highly similar for both AvTD and VarTD. AvTD was best accounted for by a model including chlorophyll, average depth, extent of pasture and water colour, whereas VarTD showed a positive relationship with chlorophyll, average depth and conductivity. In summary, taxonomic distinctness of diatom assemblages increased with increasing trophic status. Among the physical environmental variables affected by human activities, only average depth contributed significantly to the variation in taxonomic diversity.

Discussion

In our Irish dataset, nutrient poor lakes had high species diversity but low taxonomic distinctness (AvTD and VarTD) relative to those with a higher trophic status. This can be attributed to the presence of greater numbers of taxonomically more closely related species, including mainly pennate diatom taxa, in nutrient-poor lakes. Communities from sites with higher levels of nutrients but with lower species richness tended to comprise distantly related species, resulting in higher indices of taxonomic diversity. Species belonging to the families Aulacoseiraceae and Stephanodiscaceae were most common among high trophic status lakes.

Values of both AvTD and VarTD for the most nutrient rich lakes were above the expected mean value and a large number fell outside the population norm. This may be explained by the fact that these lakes supported several species also found in nutrient-poor lakes, as well as some species that are unique or more characteristic of nutrient enrichment. Variation in lake parameters (alkalinity and mean depth) among the three trophic classes of lakes was not reflected in differences in species diversity. There were, however, significant changes in taxonomic distinctness characterised by higher AvTD and VarTD in moderate alkalinity lakes probably owing to the fact that these lakes support species that are also recorded in either high or low alkalinity lakes.

The number of species belonging to each of the 24 most important families of freshwater diatoms in the dataset may be helpful when interpreting the differences in taxonomic diversity. Most of the species found in the nutrient-rich lakes belonged to the families Fragilariaceae, Naviculaceae and Stephanodiscaceae. Stephanodiscaceae contains many species that are a common component of the phytoplankton in nutrient-rich waters (Stoermer, 1978; Bennion, 1994; Rippey, Anderson & Foy, 1997; Reavie *et al.*, 2000). A family with high species richness such as Fragilariaceae, although containing some species that mainly occur in oligotrophic waters, also includes a number of opportunistic or pioneer taxa with a high tolerance to nutrient enrichment (Haworth, 1976; Stabell, 1985; Marciniak, 1986; Anderson, 1994). In addition, all three families are classified in three different taxonomic classes and are represented by a reduced number of species. This leads to greater unevenness in the taxonomic structure of the assemblages. Species associated with nutrient-rich lakes therefore appear to be more distantly related, although they occur in a similar number of families. As a consequence the values of AvTD and VarTD for nutrient-rich lakes were the highest in the dataset, indicating a simultaneous increase of both species and higher level taxa.

Nutrient enrichment was found to affect the taxonomic structure of the diatom community in each trophic class. However, in contrast to many marine organisms, the impacts of eutrophication on freshwater diatoms, and indeed many other freshwater assemblages, are not characterised by a shift to fewer and more closely related taxonomic groups (Abellan *et al.*, 2006; Bhat & Magurran, 2006). Higher species richness in ultra-oligotrophic and oligotrophic lakes was not associated with higher taxonomic diversity: in other words, increased species richness was mainly attributable to an increase in the numbers of taxonomically-close species. This pattern differs from other studies, where the increase in diatom species richness was primarily attributed to species distantly related to those found in poorer species assemblages (e.g. Heino *et al.* 2005).

According toWarwick and Clarke (1998) and Clarke and Warwick (1998, 2001) disturbance tends to cause the eradication of species from families or higher taxonomic classes that have relatively few representatives in the community, while those that remain belong to taxonomic groups that are comparatively species-rich. The results presented here, however, suggest that taxonomic diversity increases with disturbance (increased nutrient availability in this case) and diatom assemblages are not characterised by the presence of a few, species–rich and closely-related taxa in response to nutrient enrichment. As a consequence, the effects of nutrient enrichment are more commonly manifested as an increase in AvTD, contrary to Warwick and Clarke (1998). This is in close agreement with the results for freshwater beetles (Abellan *et al.*, 2006) and fish assemblages (Bhat & Magurran, 2006), where highly perturbed sites did not undergo a reduction in taxonomic diversity. Moreover, VarTD values were positively correlated with AvTD ($r = 0.64$; $P < 0.001$), indicating that as AvTD increases some taxa become over-represented and others under-represented. This suggests that nutrient-enrichment is associated with increased average path length through the taxonomic tree, while those higher taxonomic levels that have an increased representation are those with fewest species.

Eutrophication is generally associated with reduced diversity of terrestrial (e.g. Tilman, Kilham & Kilham, 1982) and aquatic plant communities. Although species diversity of aquatic ecosystems are generally highly subjected to a decreasing trend with eutrophication (Cederwall & Elmgren, 1990; Worm *et al.*, 1999), the current research revealed only a weak relationship between species diversity and logTP concentrations ($r = 0.39$; $P < 0.01$), and no significant differences between trophic states, presumably because of the confounding influence of other environmental factors. For example, there may be natural environmental factors affecting biodiversity and, at the same time, there may be collinearity between nutrient enrichment and natural variation. Changes in nutrient inputs and algal grazing by animals, two common and concurrent variables in aquatic ecosystems, can have a profound impact on algal diversity (Miller, Deoliveira, & Gibea, 1992; Proulx *et al.*, 1996).

According to Clarke and Warwick (1998, 2001), measures of taxonomic diversity may be less sensitive to differences in habitat types than indices of species richness. However, distinctness measures are, in fact, not only related to anthropogenic disturbance, but can also be strongly influenced by natural environmental features (Marchant, 2007). Heino *et al.* (2005), however, showed that species richness and taxonomic distinctness of stream invertebrates, lake molluscs and lake (littoral) insects in Finland varied strongly along environmental gradients, presumably because of the important influence of differences in factors such as habitat availability. Bhat & Magurran (2006) noted that commonly observed longitudinal changes in fish species composition in rivers, due to habitat variability, affect measurements of AvTD. Our findings also indicate that measures of diversity based on taxonomic distinctness may be overshadowed by the influence of habitat variability on species composition. Taxonomic distinctness was highly variable among the different lake types regardless of nutrient levels, and a significant portion of this variation may be due to natural factors within each lake type. High unevenness in taxonomic structure at the levels of class and order is considered to be a result of habitat heterogeneity. This conclusion relies on the assumption that more distantly-related species are typically more different ecologically, and therefore that greater environmental heterogeneity should lead to increased ecological variability and, in turn, enhanced taxonomic distinctness. In the current research, taxonomic distinctness was related to factors linked to nutrient status, but was also associated with lake water depth. An increase in average lake depth can provide a larger pelagic environment for planktonic diatom species, such as those belonging to the family Coscinodiscophyceae. In addition, deeper lakes are more likely to experience stable thermal stratification than shallower lakes. Deeper stratified lakes provide higher habitat variability that may favour the growth of a number of species within the Coscinodiscophyceae family, which are out-competed in mixing layers because of high light demand. The few freshwater studies to date (e.g., Heino *et al.* 2005; Abellan *et al.* 2006; Heino *et al*. 2007; Marchant 2007) provide evidence that taxonomic distinctness also varies along natural gradients, thus calling into question the usefulness of taxonomic distinctness as a means of quantifying biological response to disturbance in freshwater ecosystems.

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References

Abellan, P., Bilton, D.T., Millan, A., Sanchez-Fernandez, D. & Ramsay, P.M. (2006) Can taxonomic distinctness assess anthropogenic impacts in inland waters? A case study from a Mediterranean river basin. Freshwater Biology, 51, 1744-1756.

Anand, M. & Orloci, L. (1996) Complexity in plant communities: The notion and quantification. Journal of Theoretical Biology, 179, 179-186.

Anderson, N.J. (1994) Comparative Planktonic Diatom Biomass Responses to Lake and Catchment Disturbance. Journal of Plankton Research, 16, 133-150.

Battarbee, R.W., Jones, V.J., Flower, R.J., Cameron, N.G., Bennion, H., Carvalho, L. & Juggins, S. (2001) Diatoms. In: Tracking Environmental Change Using Lake Sediments. (Eds J.P. Smol & H.J.B. Birks & W.M. Last), pp. 155-202. Kluwer Academic Publishers, Dordrecht.

Bennion, H. (1994) A Diatom-Phosphorus Transfer-Function for Shallow, Eutrophic Ponds in Southeast England. Hydrobiologia, 276, 391-410.

Bennion, H., Fluin, J. & Simpson, G.L. (2004) Assessing eutrophication and reference conditions for Scottis freshwater lochs using subfossil diatoms. Journal of Applied Ecology, 41, 124-138.

Bhat, A. & Magurran, A.E. (2006) Taxonomic distinctness in a linear system: a test using a tropical freshwater fish assemblage. Ecography, 29, 104-110.

Burkholder, J.M. (2001) Eutrophication and oligotrophication. In: Encyclopedia of Biodiversity. (Ed S.A. Levin), pp. 649-670. Academic Press.

Campbell, W.B. & Novelo-Gutierrez, R. (2007) Reduction in odonate phylogenetic diversity associated with dam impoundment is revealed using taxonomic distinctness. Fundamental and Applied Limnology, 168, 83-92.

Ceschia, C., Falace, A. & Warwick, R. (2007) Biodiversity evaluation of the macroalgal flora of the Gulf of Trieste (Northern Adriatic Sea) using taxonomic distinctness indices. Hydrobiologia, 580, 43-56.

Chase, J.M. (2003) Community assembly: when should history matter? Oecologia, 136, 489-498.

Chen, G., Dalton, C., Leira, M & Taylor, D. (2008) Diatom-based total phosphorus (TP) and pH transfer functions for the Irish Ecoregion. Journal of Paleolimnology DOI 10.1007/s10933-007-9148-4

Clarke, K.R. & Gorley, R.N. (2001) PRIMER v5: User Manual/Tutorial. Primer-E), Plymouth, U.K.

Clarke, K.R. & Warwick, R.M. (1998) A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology, 35, 523-531.

Clarke, K.R. & Warwick, R.M. (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecology-Progress Series, 216, 265-278.

Denicola, D.M., De Eyto, E., Wemaere, A. & Irvine, K. (2004) Using epilithic algal communities to assess trophic status in Irish lakes. Journal of Phycology, 40, 481-495.

Dixit, S.S., Smol, J.P., Charles, D.F., Hughes, R.M., Paulsen, S.G. & Collins, G.B. (1999) Assessing water quality changes in the lakes of the northeastern United States using sediment diatoms. Canadian Journal of Fisheries and Aquatic Sciences, 56, 131-152.

EHS (2000) Managing the water environment in Northern Ireland 2000, Belfast.

Ellingsen, K.E., Clarke, K.R., Somerfield, P.J. & Warwick, R.M. (2005) Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. Journal of Animal Ecology, 74, 1069-1079.

Gibson, C.E., Wu, Y., Smith, S.J. & Wolfe-Murphy, S.A. (1995) Synoptic limnology of a diverse geological region; catchment and water chemistry. Hydrobiologia, 306, 213-227.

Håkånsson, H. (2002) A compilation and evaluation of species in the general *Stephanodiscus*, *Cyclostephanos* and *Cyclotella* with a new genus in the family Stephanodiscaceae. Diatom Research, 17, 1-139.

Harper, J.L. & Hawksworth, D.L. (1994) Biodiversity - Measurement and Estimation - Preface. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 345, 5-12.

Hartley, B. (1996) An Atlas of British Diatoms, Biopress Ltd., Bristol.

Haworth, E.Y. (1976) Changes in Composition of Diatom Assemblages Found in Surface Sediments of Blelham Tarn in English Lake District During 1973. Annals of Botany, 40, 1195-1205.

Heino, J., Mykrä, H., Hämäläinen, H., Aroviita, J. & Muotka, T. (2007) Responses of taxonomic distinctness and species diversity indices to anthropogenic impacts and natural environmental gradients in stream macroinvertebrates. Freshwater Biology, 52, 1846-1861.

Heino, J., Soininen, J., Lappalainen, J. & Virtanen, R. (2005) The relationship between species richness and taxonomic distinctness in freshwater organisms. Limnology and Oceanography, 50, 978-986.

HMSO (1990) Environmental Issues in Northern Ireland, London.

Irvine, K., Allott, N., Caroni , R., Eyto, E.D., Free, G. & White, J. (2001) The Ecological Assessment of Irish Lakes: the development of a new methodology suited to the needs of the EU Directive for surface waters. Epa), Wexford.

Jahn, R. & Kusber, W.-H. (2007) AlgaTerra Information System [online]. . Botanic Garden and Botanical Museum Berlin-Dahlem, FU-Berlin.

Jennings, E., Mills, P., Jordan, P., Jensen, J.-P., Søndergaard, M., Barr, A., Glasgow, G. & Irvine, K. (2003) Eutrophication from agricultural sources Seasonal patterns & effects of phosphorous. Final Research Report (2000-LS-2.1.7-M2). EPA, Wexford.

Jeppesen, E., Jensen, J.P., Sondergaard, M., Lauridsen, T. & Landkildehus, F. (2000) Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology, 45, 201-218.

Krammer, K. & Lange-Bertalot, H. (1986-1991) Bacillariophyceae. In: Süßwasserflora von Mitteleuropa. (Eds H. Ettl & J. Gerloff & H. Heynig & D. Mollenhauer). Fischer-Verlag, Stuttgart.

Leonard, D.R.P., Clarke, K.R., Somerfield, P.J. & Warwick, R.M. (2006) The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessments. Journal of Environmental Management, 78, 52-62.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Oxford

Mann, D.G. (1999) The species concept in diatoms. Phycologia, 38, 437-495.

Marchant, R. (2007) The use of taxonomic distinctness to assess environmental disturbance of insect communities from running water. Freshwater Biology, 52, 1634-1645.

Marciniak, B. (1986) Late Quaternary Diatoms in the Sediments of Przedni-Staw Lake (Polish Tatra Mountains). Hydrobiologia, 143, 255-265.

Miller, M.C., Deoliveira, P. & Gibeau, G.G. (1992) Epilithic Diatom Community Response to Years of PO^4 Fertilization - Kuparuk River, Alaska (68 N Lat.). Hydrobiologia, 240, 103-119.

Moss, J.A., Nocker, A., Lepo, J.E. & Snyder, R.A. (2006) Stability and change in estuarine biofilm bacterial community diversity. Applied and Environmental Microbiology, 72, 5679-5688.

OECD (1982) Eutrophication of Waters, Monitoring, Assessment and Control. OECD, Paris.

OJEC (2000) Directive 2000/60/EC of the European Parliament and of the council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities, 1-327.

Proulx, M., Pick, F.R., Mazumder, A., Hamilton, P.B. & Lean, D.R.S. (1996) Experimental evidence for interactive impacts of human activities on lake algal species richness. Oikos, 76, 191-195.

Reavie, E.D., Smol, J.P., Sharpe, I.D., Westenhofer, L.A. & Roberts, A.M. (2000) Paleolimnological analyses of cultural eutrophication patterns in British Columbia lakes. Canadian Journal of Botany-Revue Canadienne De Botanique, 78, 873-888.

Rippey, B., Anderson, N.J. & Foy, R.H. (1997) Accuracy of diatom-inferred total phosphorus concentrations and the accelerated eutrophication of a lake due to reduced flushing and increased internal loading. Canadian Journal of Fisheries and Aquatic Sciences, 54, 2637-2646.

Round, F.E., Crawford, R.M. & Mann, D.G. (1990) The Diatoms: Biology and Morphology of the Genera, Cambridge University Press, Cambridge.

Sondergaard, M. & Jeppesen, E. (2007) Anthropogenic impacts on lake and stream ecosystems, and approaches to restoration. Journal of Applied Ecology, 44, 1089-1094.

Stabell, B. (1985) Diatoms in Upper Quaternary Skagerrak Sediments. Norsk Geologisk Tidsskrift, 65, 91-95.

Stoermer, E.F. & Smol, J.P. (1999) The Diatoms: Applications for the Environmental and Earth Sciences, Cambridge.

Stoermer, E.F. (1978) Phytoplankton Assemblages as Indicators of Water-Quality in Laurentian Great Lakes. Transactions of the American Microscopical Society, 97, 2-16.

Tilman, D. (1997) Distinguishing between the effects of species diversity and species composition. Oikos, 80, 185-185.

Tilman, D., Kilham, S.S. & Kilham, P. (1982) Phytoplankton Community Ecology - the Role of Limiting Nutrients. Annual Review of Ecology and Systematics, 13, 349-372.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997) Plant diversity and ecosystem productivity: Theoretical considerations. Proceedings of the National Academy of Sciences of the United States of America, 94, 1857-1861.

Tilman, D., Naeem, S., Knops, J., Reich, P., Siemann, E., Wedin, D., Ritchie, M. & Lawton, J. (1997) Biodiversity and ecosystem properties. Science, 278, 1866-1867.

Toner, P., Bowman, J., Clabby, K., Lucey, J., McGarrigle, M., Concannon, C., Clenaghan, C., Cunningham, P., Delaney, J., O'Boyle, S., MacCárthaigh, M., Craig, M., Quinn, R. (2005) Water Quality in Ireland 2001-2003. EPA, Wexford.

Waide, R.B., Willing, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between productivity and species richness. Annual Review on Ecology and Systematics, 30, 257-300.

Warwick, R.M. & 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. & Clarke, K.R. (1998) Taxonomic distinctness and environmental assessment. Journal of Applied Ecology, 35, 532-543.

Warwick, R.M., Ashman, C.M., Brown, A.R., Clarke, K.R., Dowell, B., Hart, B., Lewis, R.E., Shillabeer, N., Somerfield, P.J. & Tapp, J.F. (2002) Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. Marine Ecology-Progress Series, 234, 1-13.

Wassen, M.J., Venterink, H.O., Lapshina, E.D. & Tanneberger, F. (2005) Endangered plants persist under phosphorus limitation. Nature, 437, 547-550.

Table 1: Water chemistry and catchment characteristics for the study lakes. Lake type codes are as follows: 1, low alkalinity shallow; 2, low alkalinity deep; 3, moderate alkalinity shallow; 4, moderate alkalinity deep; 5, high alkalinity shallow; and 6, high alkalinity deep.

Lake Type	Statistic	Altitude	Lake Area	Catchment Area	Mean Depth	Alkalinity	Conductivity	pH	TP	Chlorophyll	Agriculture	Fores t	Pasture	Peat
		M	ha	ha	m	mg $CaCO_3$ L^{-1}	µS cm^{-1}		µg L^{-1}	µg L^{-1}	%	%	%	%
Type 1	*Mean*	87	48	740	2.38	10.53	114	6.8	39	7.5	1.0	4.8	22.0	71.7
	Median	71	14	427	2.75	10.40	109	6.8	30	6.4	0.0	0.0	3.5	84.0
	Minimum	10	3	44	0.70	4.00	48	6.5	7	0.6	0.0	0.0	0.0	0.0
	Maximum	180	130	2275	3.90	17.90	165	7.1	100	15.2	6.0	23.0	100.0	100.0
Type 2	*Mean*	100	128	4475	8.9	2.80	72	6.1	7	1.8	1.4	19.9	0.3	67.8
	Median	52	82	3728	7.3	2.25	78	6.0	7	1.8	0.0	18.0	0.0	68.0
	Minimum	11	7	56	4.10	-0.10	33	5.1	0	0.5	0.0	0.0	0.0	25.0
	Maximum	283	395	11308	14.50	9.60	101	7.4	12	3.8	6.0	44.0	1.0	100.0
Type 3	*Mean*	77	472	6372	2.23	54.88	226	7.9	62	31.4	14.0	0.8	82.0	1.3
	Median	69	388	131	2.25	51.00	214	7.9	64	26.4	8.0	0.5	84.5	0.5
	Minimum	49	6	77	1.40	47.50	171	7.8	35	14.7	3.0	0.0	63.0	0.0
	Maximum	120	1106	25150	3.00	70.00	304	8.0	88	58.1	37.0	2.0	96.0	4.0
Type 4	*Mean*	86	267	1846	6.12	50.55	207	7.9	63	20.3	20.0	5.6	50.5	20.8
	Median	81	42	208	6.25	57.00	210	7.9	31	11.4	8.0	1.0	48.5	9.5
	Minimum	8	3	30	4.20	20.00	86	7.1	5	1.9	0.0	0.0	10.0	0.0
	Maximum	180	1974	16072	8.90	85.10	318	8.5	344	62.7	85.0	16.0	89.0	71.0
Type 5	*Mean*	27	265	9403	2.34	146.60	340	8.3	26	8.1	9.1	6.7	47.9	12.1
	Median	20	96	7750	2.70	138.00	333	8.4	12	2.6	8.0	3.0	52.0	10.0
	Minimum	10	20	414	1.40	121.10	268	7.9	5	0.8	0.0	0.0	32.0	0.0
	Maximum	77	1438	28250	3.40	280.60	462	8.5	84	29.3	25.0	23.0	650	45.0
Type 6	*Mean*	38	67	7292	8.31	154.54	350	8.3	18	4.7	7.8	4.8	57.3	3.1
	Median	28	51	2708	7.05	160.60	348	8.3	20	4.1	8.0	5.5	56.5	3.0
	Minimum	10	14	167	4.10	116.30	297	7.9	5	0.4	0.0	0.0	32.0	0.0
	Maximum	112	153	29042	13.40	173.30	393	8.5	40	9.2	13.0	11.0	96.0	8.0

Table 2: Mean number of diatom species that belong to the same family, order and class in each trophic state class. Numbers indicate the trophic state category: 1 = ultra-oligotrophic and oligotrophic sites, 2 = mesotrophic and 3 = eutrophic and hyper-eutrophic.

			Trophic State Category		
Class	Order	Family	1	2	3
Bacillariophyceae	Achnanthales	Achnanthaceae	0.79	0.56	0.31
		Achnanthidiaceae	4.14	3.28	2.69
		Cocconeidaceae	0.57	1.17	0.92
	Bacillariales	Bacillariaceae	1.86	1.72	2.69
	Cymbellales	Cymbellaceae	3.79	2.11	1.08
		Gomphonemataceae	1.50	2.28	1.62
	Eunotiales	Eunotiaceae	2.71	1.61	1.92
		Peroniaceae	0.14	0.11	0.08
	Mastogloiales	Mastogloiaceae	0.50	0.28	0.08
	Naviculales	Amphipleuraceae	1.07	0.33	0.08
		Brachysiraceae	1.79	1.00	0.08
		Cavinulaceae	0.29	0.50	0.15
		Diploneidaceae	0.50	0.28	0.15
		Naviculaceae	4.50	3.94	5.31
		Pinnulariaceae	0.57	0.33	0.38
		Sellaphoraceae	0.29	0.17	0.54
		Stauroneidaceae	0.21	0.17	0.23
	Rhopalodiales	Rhopalodiaceae	0.43	0.50	0.15
	Surirellales	Surirellaceae	0.14	0.06	0.31
	Thalassiophysales	Catenulaceae	1.43	1.28	0.62
Coscinodiscophyceae	Aulacoseirales	Aulacoseiraceae	0.43	1.50	2.46
	Thalassiosirales	Stephanodiscaceae	2.64	4.11	4.92
Fragilariophyceae	Fragilariales	Fragilariacea	4.93	5.56	6.77
	Tabellariales	Tabellariaceae	0.71	0.61	0.38

Table 3: Correlations between species richness (H'), evenness (J'), average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+), and environmental factors for the surface sediment diatom communities. Partial correlations denote the correlation between diversity measures and environmental variables when the more conservative environmental variables (i.e. slightly affected by human activities) are controlled for.

	Pearson's correlations				Partial correlations			
	J'	H'(loge)	Δ^+	Λ^+	J'	H'(loge)	Δ^+	Λ^+
NormAgr	-0.243	-0.237	0.313*	0.420**	-0.202	-0.199	0.189	0.259
NormFor	0.060	0.091	-0.154	-0.285	0.078	0.129	-0.073	-0.314
NormPast	-0.276	-0.263	0.489**	0.474**	-0.160	-0.170	0.333	0.174
LogChl	-0.470**	-0.453**	0.673**	0.491**	-0.429*	-0.413*	0.693**	0.453**
LogColor	-0.164	-0.159	0.196	-0.156	-0.317	-0.300	0.567**	0.148
LogCond	-0.032	-0.009	0.257	0.373*	0.043	0.076	-0.170	-0.021
LogTP	-0.405**	-0.385*	0.583**	0.389*	-0.401*	-0.379*	0.581**	0.305

*$p < 0.05$, **$p < 0.01$.

FIGURE CAPTIONS

Figure 1: Location of 45 study lakes in Ireland, with those in County Clare inserted.

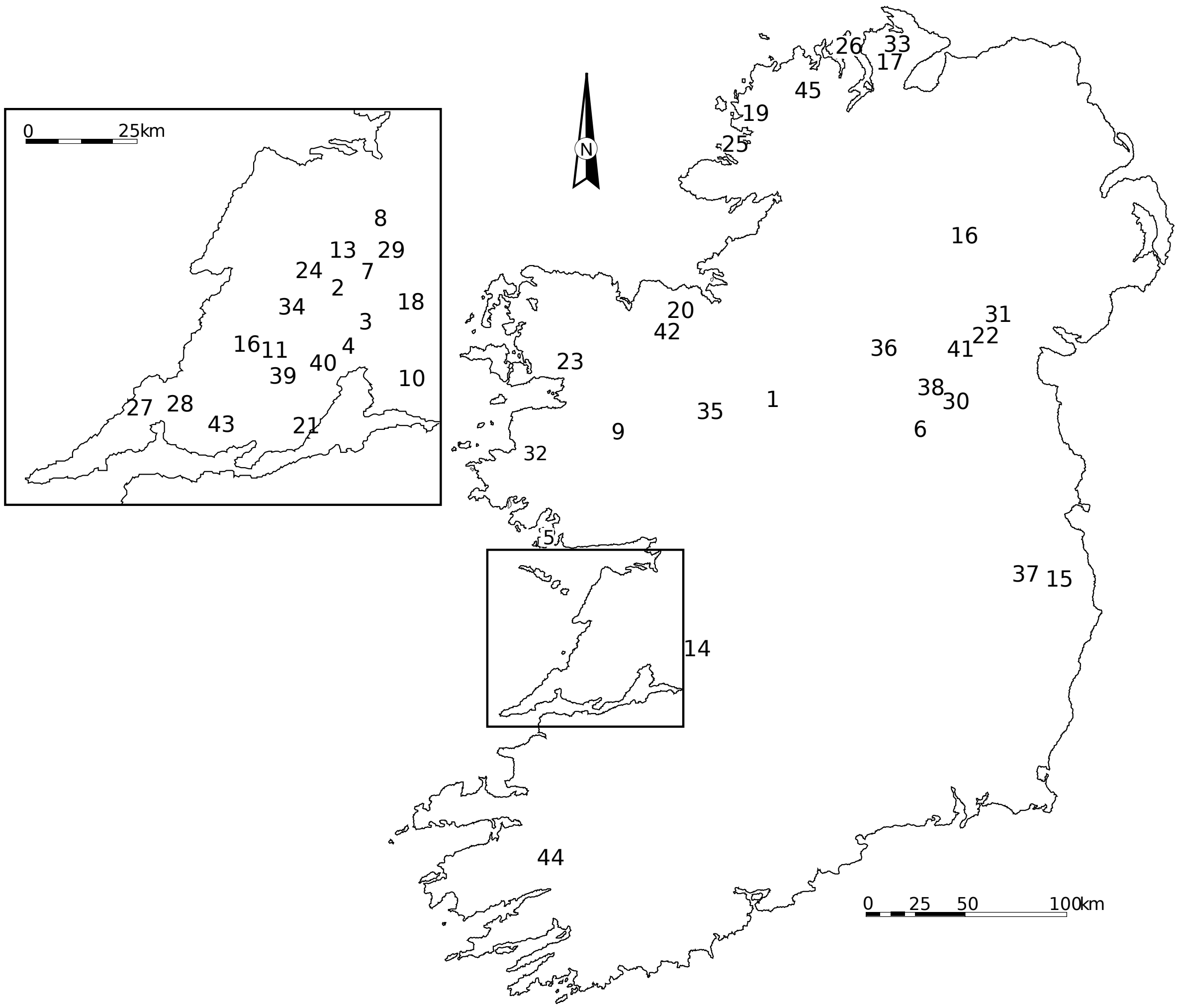
Figure 2: Mean values and 2 squared error intervals for species richness ($\log_e H'$) and evenness (J') calculated for surface sediment diatom communities for each lake type (1, low alkalinity shallow; 2, low alkalinity deep; 3, moderate alkalinity shallow; 4, moderate alkalinity deep; 5, high alkalinity shallow; and 6, high alkalinity deep) and for each trophic class (1, low nutrient content; 2, moderate nutrient content; and 3, high nutrient content). One-way ANOVA F and *P* values included

Figure 3: Mean values and 2 squared error intervals for average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) for surface sediment diatom communities for each lake type (1, low alkalinity shallow; 2, low alkalinity deep; 3, moderate alkalinity shallow; 4, moderate alkalinity deep; 5, high alkalinity shallow; and 6, high alkalinity deep) and for each trophic class (1, low nutrient content; 2, moderate nutrient content; and 3, high nutrient content). One-way ANOVA F and *P* values included

Figure 4: Variation in average taxonomic distinctness and variation in taxonomic distinctness versus number of species for diatom communities data with theoretical mean and 95% confidence funnel obtained from the regional inventory of more than 600 diatom species (based on surface samples of lake sediments from 72 freshwater lakes from across the island of Ireland). Symbols indicate the trophic level of lakes: ultra-oligotrophic and oligotrophic sites are indicated by circles, mesotrophic sites by triangles and eutrophic and hyper-eutrophic sites by squares.

Figure 5: Average taxonomic distinctness and variation in taxonomic distinctness versus number of species for diatom assemblage data with theoretical mean and 95% confidence funnel obtained from a regional species list. Symbols indicate the lake types studied: low alkalinity shallow lakes are indicated by hollow circles, low alkalinity deep by dark shaded circles, moderate alkalinity shallow by hollow triangles, moderate alkalinity deep by dark shaded triangles, high alkalinity shallow by hollow squares and high alkalinity deep by dark shaded squares.

Figure 6: Fitted 95% probability contours of the VarTD and AvTD pairs, from 1000 simulations for a range of values of the number of species (m). For the sake of clarity, these are separated into 3 plots (a-c; m = 20, 30, 40; 50; and 60, 70, respectively), to allow the real Δ^+ and Λ^+ pairs to superimposed on a contour plot for their appropriate values of m. Lake code numbers refer to their trophic state (1 to 3) followed by the ecological type they have been classified within (1 to 6) as in figures 2 and 3. The size of their species lists is indicated in parentheses. Sites outside the relevant 95% ellipse imply statistical evidence of the departure from expectation for those sites.



0 25km
8
13 29
24 7
2
34 18
3
16 11 4
39 40 10
27 28
43 21
N
26 33
17
45
19
25
16
20
42
31
22
23
36 41
38 30
1
35
9 6
32
5
37 15
14
44
0 25 50 100km

Figure 1

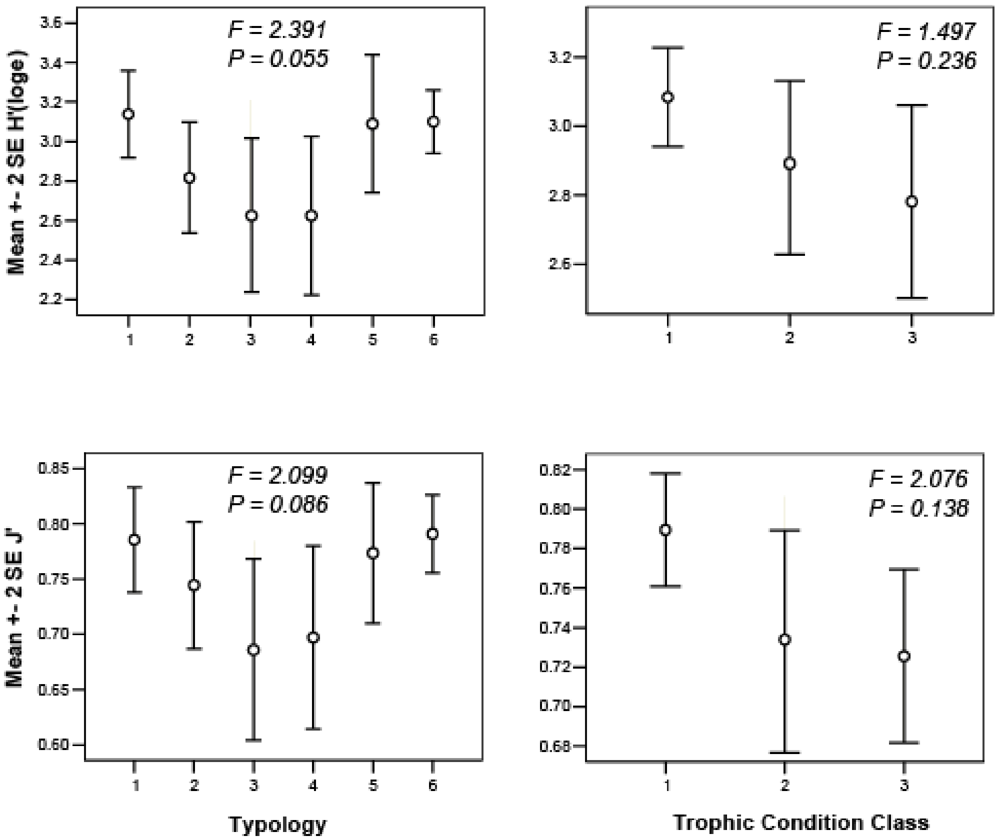

F = 2.391
P = 0.055
Mean +- 2 SE H'(loge)
F = 1.497
P = 0.236
F = 2.099
P = 0.086
Mean +- 2 SE J'
F = 2.076
P = 0.138
Typology
Trophic Condition Class

Figure 2

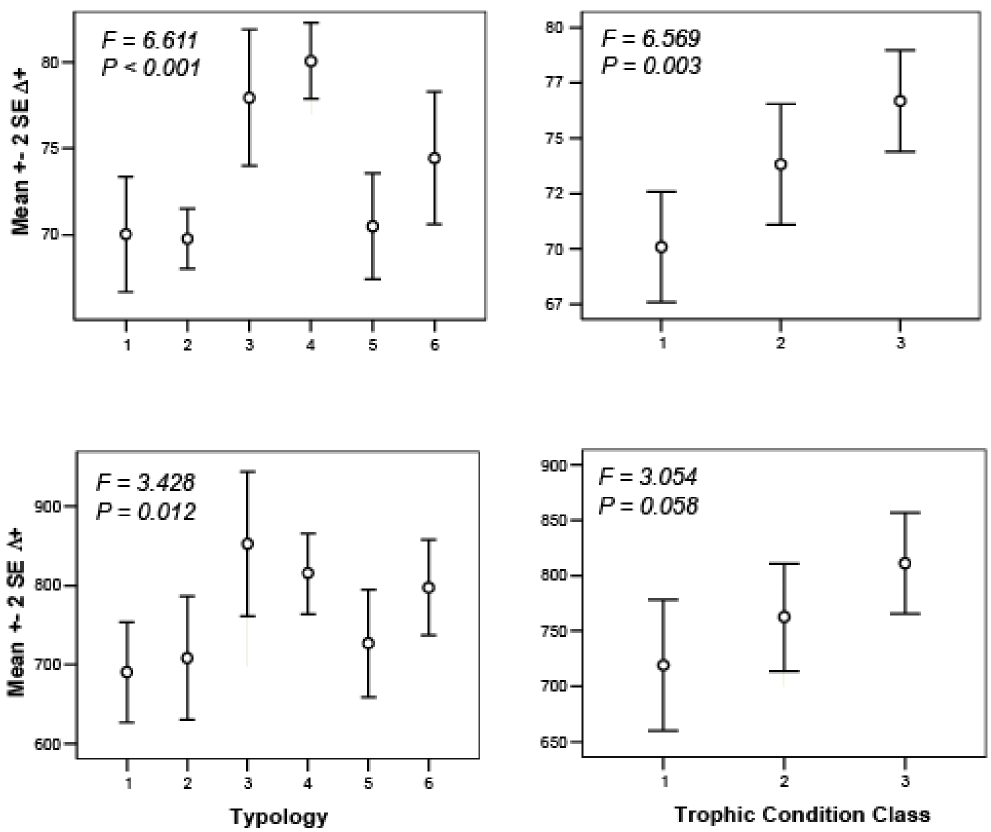

F = 6.611
P < 0.001
F = 6.569
P = 0.003
F = 3.428
P = 0.012
F = 3.054
P = 0.058
Mean +- 2 SE Δ+
Mean +- 2 SE Λ+
Typology
Trophic Condition Class

Figure 3

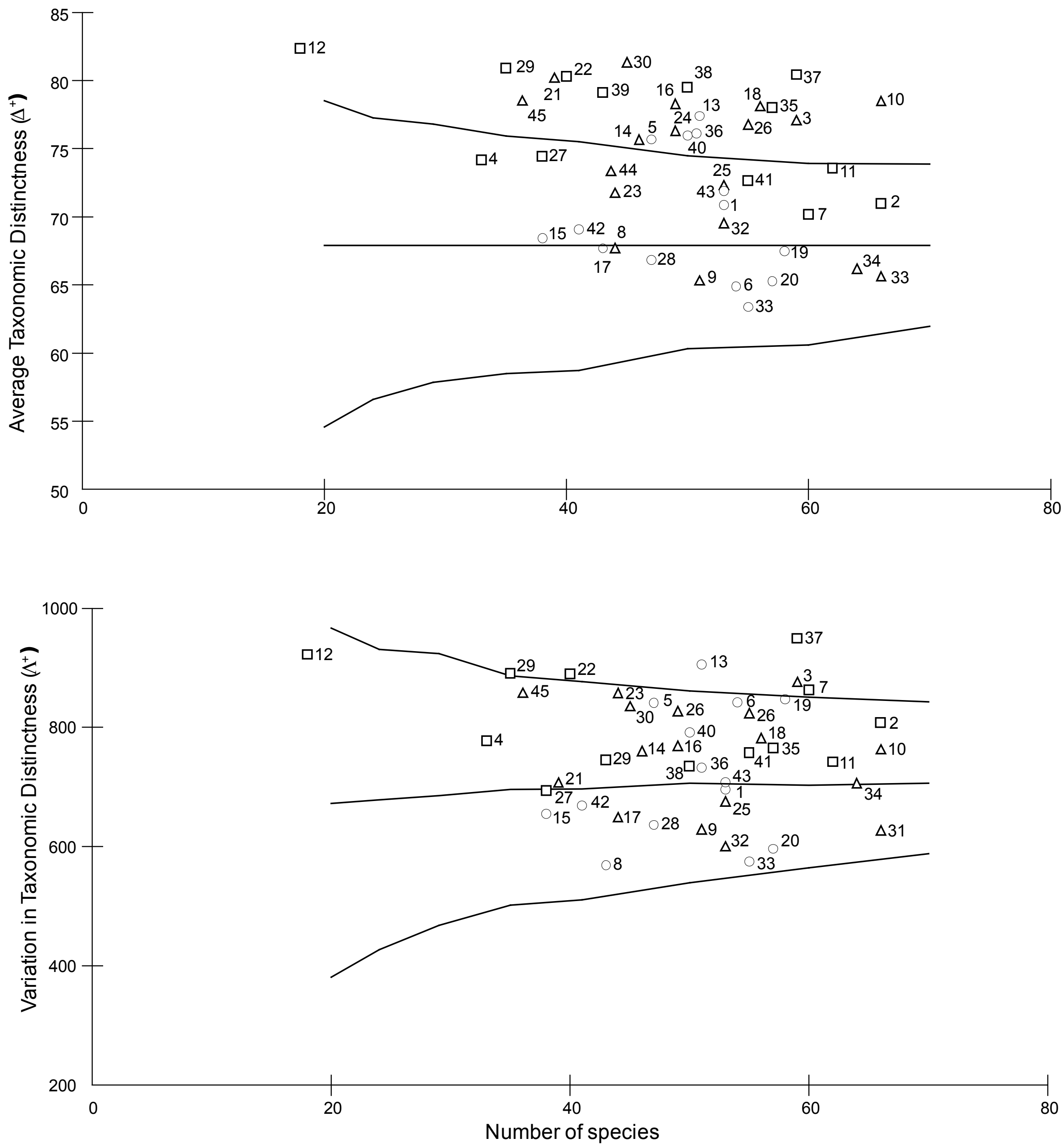

Average Taxonomic Distinctness (Δ+)
Variation in Taxonomic Distinctness (Λ+)
Number of species

Figure 4

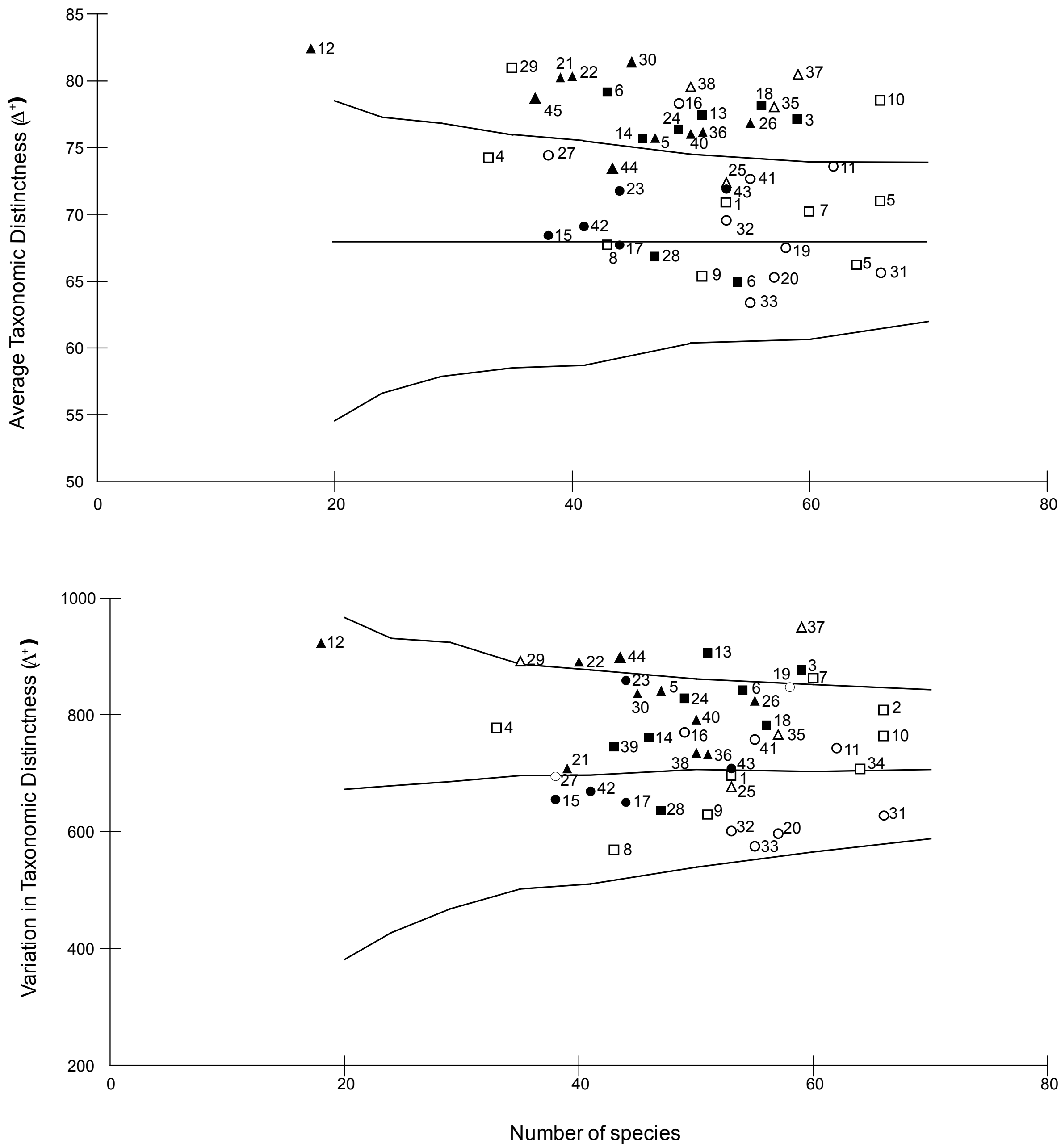
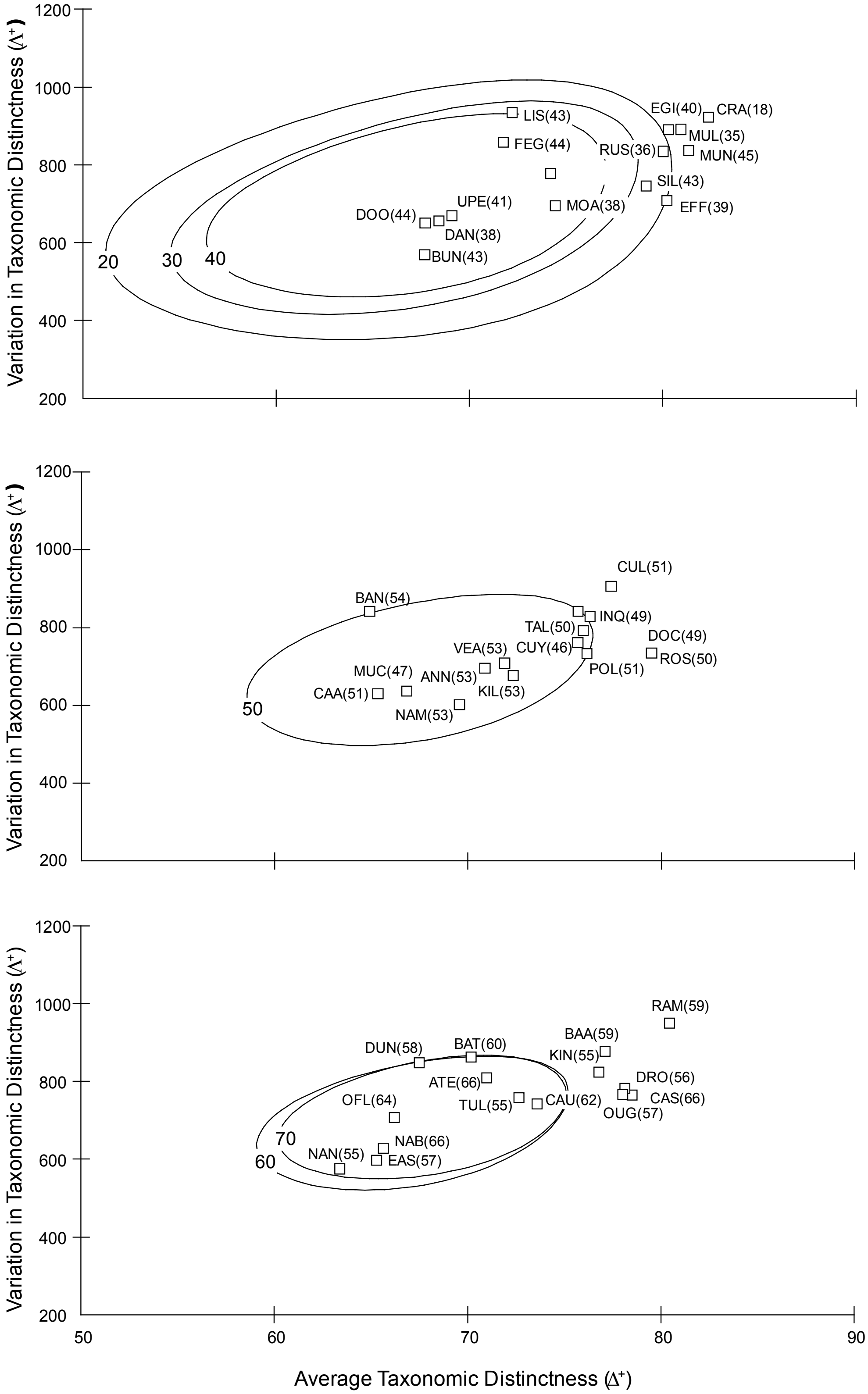

Average Taxonomic Distinctness (Δ⁺)
85
80
75
70
65
60
55
50
0
20
40
60
80
Variation in Taxonomic Distinctness (λ⁺)
1000
800
600
400
200
0
20
40
60
80
Number of species

Figure 5



Variation in Taxonomic Distinctness (Λ+)
Average Taxonomic Distinctness (Δ+)
20
30
40
LIS(43)
FEG(44)
EGI(40)
CRA(18)
MUL(35)
MUN(45)
RUS(36)
SIL(43)
EFF(39)
MOA(38)
UPE(41)
DOO(44)
DAN(38)
BUN(43)
50
BAN(54)
CUL(51)
INQ(49)
TAL(50)
DOC(49)
CUY(46)
ROS(50)
VEA(53)
POL(51)
MUC(47)
ANN(53)
KIL(53)
CAA(51)
NAM(53)
RAM(59)
BAA(59)
BAT(60)
DUN(58)
KIN(55)
ATE(66)
DRO(56)
OFL(64)
TUL(55)
CAU(62)
CAS(66)
OUG(57)
70
NAB(66)
60
NAN(55)
EAS(57)

Figure 6