Can taxonomic distinctness assess anthropogenic impacts in inland waters? A case study from a Mediterranean river basin

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SUMMARY
1. It is increasingly recognised that adequate measures of biodiversity should include information on the ‘relatedness’ of species within ecological assemblages, or the phylogenetic levels at which diversity is expressed. Taxonomic distinctness measures provide a series of indices to achieve this, which are independent of sample size. Taxonomic distinctness has been employed widely in marine systems, where it has been suggested that this index can provide a reliable measure of anthropogenic impact.
2. We tested the behaviour of three related taxonomic distinctiveness indices (Average Taxonomic Distinctness, $D^+$; Variation in Taxonomic Distinctness, $K^+$; and Total Taxonomic Distinctness, $sD^+$) in relation to putative levels of anthropogenic impact in inland waters and their potential utility in environmental monitoring, using an extensive data set for aquatic beetles from the south-east of the Iberian Peninsula.
3. Taxonomic distinctness measures were not able to identify human disturbance effects and there were no clear relationships between these new biodiversity measures and the disturbance level recorded at individual localities. Furthermore, the taxonomic distinctness measures used were apparently less sensitive to the effects of anthropogenic impact than other diversity metrics, such as species richness and rarity.
4. We conclude that taxonomic distinctness indices may not always perform as well as other metrics in the assessment of environmental quality. In addition, taxonomic distinctness measure should be interpreted with caution, as their performance and ability to detect anthropogenic disturbance may depend on the phylogenetic structure of sampled taxa within a region, and their evolutionary and ecological history.

Keywords: biodiversity, environmental assessment, Iberian Peninsula, species diversity, water beetles

Introduction

It is increasingly recognised (e.g. Harper & Hawksworth, 1994; Anand & Orloci, 1996) that adequate measures of biodiversity should go beyond measures of species richness and evenness, which capture only some aspects of the composition of ecological assemblages. Measures based on richness, abundance or evenness have traditionally been used for assessing the effects of environmental degradation on biodiversity, despite the fact that these can be highly influenced by sample size, sampling effort, habitat type or complexity, and typically do not show monotonic responses to human impact (Leonard et al.,...
In addition, the structure and the complexity of biotic assemblages are certainly important, and quantification of these aspects can provide valuable information about the status of ecosystems (Tilman et al., 1997). This is the case with measures based on the phylogenetic structure of the assemblage, which differ from more conventional diversity indices by incorporating the degree to which species are evolutionarily related to each other. Under this framework, an assemblage comprising a group of closely related species must be regarded as less diverse than an assemblage of the same number of more distantly related species, for example all belonging to different phyla.

Measures of phylogenetic structure, based on analysis of cladograms of particular groups of organisms, have been advocated widely for the design of protected area networks, in order to conserve sets of species that include as much ‘evolutionary history’ as possible (e.g. Williams, Humphries & Vane-Wright, 1991; Faith, 1992; Nee & May, 1997). However, as some authors have pointed out (Clarke & Warwick, 1998; Barker, 2002) the applicability of such phylogenetic measures to a wide range of conservation and resource management issues has not been adequately demonstrated. As a consequence, phylogenetic and related taxonomic measures have seen limited use in environmental monitoring and assessment, where the emphasis is not on choosing species to conserve, but instead on monitoring environmental degradation or the benefits of remediation.

Warwick & Clarke (1995) introduced the concept of taxonomic distinctness, as a measure of the average degree to which individuals in an assemblage are related to each other. The use of taxonomic distances means that the approach can be applied to groups where we still lack robust phylogenies, and also recognises the important role taxonomy may play in community assembly. Clarke & Warwick (1998, 2001) have showed that taxonomic distinctness measures overcome most of the problems of traditional measures of diversity, and have a number of desirable properties as measures of biodiversity in the context of environmental impact assessment. These include their relative independence with sampling effort (which makes their use attractive in spatially extensive or long time-series studies where total sampling effort in different areas or at different times is rarely standardised) and a relatively simple statistical frame-

work against which departures from expected values can be assessed, which enables a comparison to be made between an observed taxonomic distinctness measure and its expected range of variation.

The usefulness of taxonomic distinctness for marine biodiversity assessment has been reported in several studies in recent years (e.g. Piepenburg, Voss & Gutt, 1997; Hall & Greenstreet, 1998; Warwick & Clarke, 1998; Rogers, Clarke & Reynolds, 1999; Brown, Clarke & Warwick, 2002; Warwick & Light, 2002), all suggesting that taxonomic distinctness of degraded locations is significantly reduced when compared with those of relatively pristine locations for different groups of organisms (e.g. benthic nematodes, coastal fishes, echinoderms) and in different regions throughout the world.

Despite this, taxonomic distinctness has seen limited use outside marine ecology, and, in addition, no studies to date have explicitly examined how these indices perform in comparison with other approaches in the detection of anthropogenic impact. Here we attempt this for inland waters in south-east Spain, using data from aquatic Coleoptera, one of the most diverse and best understood groups of freshwater animals in the region (Ribera, Hernando & Aguilera, 1998; Ribera, 2000). Inland waters are among the most endangered ecosystems, both in Europe and worldwide (Allan & Flecker, 1993; Master, Flack & Stein, 1998; Ricciardi & Rasmussen, 1999; Saunders, Meeuwwig & Vincent, 2002), meaning that evaluation of these measures for assessing the effects of human activities on biological diversity is a crucial task. In addition, such an approach may be particularly useful in the context of the European Water Framework Directive (WFD), which establishes a framework for the protection of all inland and coastal waters and aims to achieve high quality status for all waters by 2015 (EC, 2000). The WFD highlights the importance of measures which can determine the biological effects of disturbance and distinguish different levels of ecological quality to classify surface waters.

In this paper, our aim was to determine whether taxonomic distinctness and related indices are useful in environmental monitoring of inland waters, and specifically whether they provide complementary information to existing measures of biodiversity. For this purpose, we use an extensive data set for water beetles from the south-east of the Iberian Peninsula to test whether these new taxonomic diversity indices...
reflect changes in species diversity at different habitats types. Water beetles have a number of advantages for environmental monitoring (Foster, 1991; Ribera & Foster, 1993; Bilton et al., 2006; Sánchez-Fernández et al., 2006): their taxonomy is well known and they are easily sampled; they occur across the entire spectrum of inland waters, and include species with a wide range of ecological tolerances; they tend to be the dominant macroinvertebrates present in many small inland waters; and their biology and distribution are well understood. In fact, their importance as indicators of spatial and temporal changes in aquatic systems has been demonstrated on a number of occasions (e.g. Bournaud, Richoux & Usseglio-Polaterra, 1992; Richoux, 1994; Eyre et al., 2006). In the Iberian Peninsula, water beetles are a well-known and relatively species-rich group (e.g. Ribera et al., 1998; Ribera, 2000). They are also one of the best studied groups of aquatic insects in the south-east of Iberian Peninsula (e.g. Millán, Moreno & Velasco, 2002; Sánchez-Fernández et al., 2003; Millán et al., 2006).

Methods

Study area and data set

This study was conducted in the Segura river basin, in the south-east of the Iberian Peninsula, encompassing an area of 18,815 km² (Fig. 1). The region has a Mediterranean climate, with a mean annual rainfall of around 375 mm. The geology ranges from limestone in the upland headwaters, to salt-rich tertiary marls at intermediate altitudes and in the lowlands, and this shapes the environmental conditions of waterbodies in the area, allowing a wide range of aquatic ecosystems to be present. These include headwater streams, rivers, saline and hypersaline streams, reservoirs, natural wetlands, fresh and saline lagoons and salt-pans or rock-pools (Millán et al., 1996; Gómez et al., 2005).

All families of Coleoptera in which a substantial proportion of species are linked to water in at least one developmental stage were included in the study. In order to minimise uncertainty, some species were excluded owing to insufficient knowledge of their distribution and/or taxonomy (see Abellán et al., 2005b). Records were obtained from the literature and from fieldwork and, as far as possible, all published and unpublished data presently known were included. The resulting database included over 5800 available records (species/site/date records) for 209 aquatic beetle species. Such extensive inventory data is not available for other aquatic taxa in the Segura river basin, and the water beetle records used in this analysis represent the most comprehensive freshwater biodiversity data currently available for the region.

Field data were collected between 1981 and 2004 from a total of 422 sites (Fig. 1), most of which were sampled at least twice. The sites selected represent all major water body types present within the study area, which are grouped into four major habitat categories for the purpose of this investigation, which reflect the most fundamental ecological divisions present: lotic (n = 245) and lentic (n = 54) freshwaters and lotic (n = 82) and lentic (n = 41) saline-waters.

Taxonomic distinctness measures

We compiled a composite taxonomy based primarily on Ribera et al. (1998), with additional information for Dytiscidae and Hydrophiloidea from Nilsson (2001) and Hansen (1999), respectively. We included up to eight taxonomic levels where possible: species, gen-
era, tribes, superfamilies, families, superfamilies, suborders and order. Three indices of taxonomic diversity (Average Taxonomic Distinctness, $\Delta^+$; Variation in Taxonomic Distinctness, $\Lambda^+$; and Total Taxonomic Distinctness, $s\Delta^+$) defined by Clarke & Warwick (1998, 2001) for presence/absence data were then calculated using the PRIMER 5 software package (Clarke & Gorley, 2001):

$$\Delta^+ = \frac{\sum \sum_{i<j} \omega_{ij}}{s(s-1)/2}$$  \hspace{1cm} (1)

$$\Lambda^+ = \frac{\sum \sum_{i \neq j} (\omega_{ij} - \bar{\omega})^2}{s(s-1)/2}$$  \hspace{1cm} (2)

$$s\Delta^+ = \frac{\sum \sum_{i,j} \omega_{ij}}{s - 1}$$  \hspace{1cm} (3)

where $s$ is the number of species present and $\omega_{ij}$ is the ‘distinctness weight’ given to the path length linking species $i$ and $j$ in the taxonomy. Following Warwick & Clarke (1995), the simplest form of path length weighting was adopted for the eight taxonomic levels, such that $\omega = 1$ (for species $i$ and $j$ within the same subgenus), $\omega = 2$ (for species within different subgenera but the same genus), $\omega = 3$ (for species within different genera but the same tribe), etc. Although such a constant path length between each taxonomic level is somewhat arbitrary, alternatives weighted to reflect the reduced number of representatives at each taxonomic level result in values which are highly correlated with those produced using the approach adopted here (Rogers et al., 1999). Average taxonomic distinctness, eqn 1, takes into account the taxonomic level at which any two species are related (i.e. their identity matters) and can be thought of as the average length between any two randomly chosen species present in the sample. The degree to which certain taxa are over- or under-represented in samples is another biodiversity attribute of ecological relevance and it is reflected by the variation in taxonomic distinctness, eqn 2. Finally, total taxonomic distinctness, eqn 3, was proposed by Clarke and Warwick as a useful measure of the total taxonomic breadth of an assemblage.

In addition, two more commonly used biodiversity metrics were also calculated for each site: species richness and rarity. Rarity simply equated to the number of rare species (i.e. those species occurring in no more than three $5 \times 5$ km grid cells within the study area) at each site.

**Evaluation of sensitivity to human impact**

In order to evaluate anthropogenic impacts on biodiversity, sampling localities were grouped into three categories according to their level of anthropogenic modification: (i) little or no modification, (ii) modified and (iii) highly modified. This was achieved based on the number and magnitude of the different impact types affecting the sampling site (see Abellán et al., 2005a for details). This assessment of impacts was based on a review of the literature and fieldwork. ‘Highly modified’ indicates very poor water quality as a consequence of wastewater or industrial wastes plus the existence of severe physical modifications to the habitat and the shore (dredging and stream channelisation, drainage, urbanisation and other human developments); ‘modified’ indicates some impact from agricultural activity (non-point source pollution, clearing land for crops, water extraction for irrigation, etc.) or exotic species and ‘little or no modification’ indicates good or excellent water quality, good quality of riverine habitat without important man-made structures, and only some less severe impacts such as those from low-density agrotourism or grazing.

In addition, we also made an alternative assessment based on the percentage of intensive land use present within a 1-km radius of each sampling site. For this, we used land-use classes from the CORINE Land Cover database (EC, 1993). Site categorisation based on the two approaches was very similar, although land use-based assessment failed to recognise impacts such as the influence of dams upstream or alien species, both of which could be scored by field-workers.

Clarke & Warwick (1998) devised a randomisation test to compare the observed value of taxonomic distinctness against an ‘expected’ value derived from the master list of species from all samples (the species pool). The null expectation is that the species present at any one place behave like a random selection from the species pool (i.e. every species in the pool has an equal probability to exist at all locations). Random subsamples of different numbers of species allow the expected values to be plotted as a probability funnel (5% level), against which the observed taxonomic distinctness values from real samples may be plotted. Such an analysis allows one to determine whether a sample has ‘lower-than-expected’ taxonomic representation.
We conducted this test for both average taxonomic distinctness and variation in taxonomic distinctness using PRIMER 5 software package (Clarke & Gorley, 2001). According to Clarke & Warwick (1998), values of taxonomic distinctness from unperturbed sites should fall within the confidence limits of the distribution, and impacted locations fall outside (below) them. This would mean that a common reference condition could be established for a particular group of organisms from the range of habitats in which they occur, and anthropogenic impacts on biodiversity could be assessed against this standard. The biodiversity of any designated location needs to be evaluated against a reference condition. Because each habitat type has a distinctive coleopteran fauna, as some families are represented only in some habitats, separate reference conditions would need to be established for each habitat. Accordingly, separate species lists were used for analyses in the four different habitat categories.

The significance of differences between samples from different habitat types, and between samples from different levels of human modification within each habitat category, was tested using one-way ANOVA and Tukey's HSD test for multiple comparisons of mean values. Statistical analyses were performed using STATISTICA for Windows (release 4.5; StatSoft, Tulsa, Oklahoma, U.S.A.).

Results

Natural variability

The different measures of water beetle biodiversity (species richness, rarity and taxonomic distinctness) showed different patterns across the four habitats types (Fig. 2), with the exception of the total taxonomic distinctness (not shown in Fig. 2) and species richness, which were highly correlated (Spearman'

![Fig. 2](image-url)
correlation coefficient = 0.98). Total taxonomic distinctness is therefore very similar to species richness, and fails to provide significant additional information about an assemblage.

There were no significant differences between the mean values of taxonomic distinctness (based on both $\Delta^+$ and $\Lambda^+$) across the different habitats (one-way ANOVA, $P = 0.485$ and $0.277$, respectively; Fig. 2). Rarity did not show significant differences ($P = 0.195$). In contrast, species richness was significantly different across the different habitats ($P < 0.001$). Thus, species richness was significantly higher in lotic freshwaters than in lentic habitats (both fresh and saline; Tukey’s HSD test, $P < 0.001$ in both cases), and in lotic saline-waters than in lentic environments ($P < 0.05$ in both cases).

Figs 3 & 4 show departures from the theoretical mean taxonomic distinctness based on $\Delta^+$ and $\Lambda^+$. In both cases, there was no relationship between the total number of species in individual samples and their taxonomic distinctness. Although most $\Delta^+$ sample values fell within the 95% confidence funnel for the different habitats (with the exception of lotic freshwaters), most of them also had lower values of $\Delta^+$ than the theoretical mean determined by random sampling from the entire water beetle fauna of each habitat. In lotic freshwaters, many values fell below the 95% confidence funnel. In the case of variation in taxonomic distinctness, most sample values fell within the 95% confidence limit, although in this case most of them also had higher values than the theoretical mean.

The number of species belonging to each of the 11 families of water beetles in the data set is shown in the Table 1. It may be helpful when interpreting the habitat differences in taxonomic distinctness to identify which beetle taxa have contributed most to the observed patterns. In the running-waters habitats, including saline but especially in running freshwaters, there were greater number of families than in lentic waters, and furthermore the number of species within each family was higher. In lentic freshwaters, which had the highest mean value of $\Delta^+$ and the lowest value of $\Lambda^+$, a small number of families occurred, and most species belonged to the

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**Fig. 3** Average Taxonomic Distinctness versus number of species for water beetle data. Symbols indicate the modification level of sites: rhombuses, low modification; stars, modified; circles, highly modified. Separate plots are given for the four habitat types studied: (a) lotic freshwaters, (b) lotic saline-waters, (c) lentic freshwaters and (d) lentic saline-waters. Expected mean (dashed line) and 95% probability limits (continuous lines) are derived from the full species lists for these habitats.

Dytiscidae and Hydrophilidae, which are classified in different suborders. On the other hand, in the lentic saline-waters, which had the lowest values of $\Delta^+$, most species belonged to the families Dytiscidae, Hydrophilidae and Hydraenidae.

### Table 1

<table>
<thead>
<tr>
<th>Family</th>
<th>Lotic freshwaters</th>
<th>Lotic saline-waters</th>
<th>Lentic freshwaters</th>
<th>Lentic saline-waters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>LM</td>
<td>M</td>
<td>HM</td>
</tr>
<tr>
<td>Gyrinidae</td>
<td>0.5</td>
<td>0.7</td>
<td>0.5</td>
<td>0.2</td>
</tr>
<tr>
<td>Haliplidae</td>
<td>0.8</td>
<td>1.1</td>
<td>0.8</td>
<td>0.4</td>
</tr>
<tr>
<td>Noteridae</td>
<td>0.1</td>
<td>0</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Hygrobiidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dytiscidae</td>
<td>3.7</td>
<td>5.2</td>
<td>3.4</td>
<td>2.1</td>
</tr>
<tr>
<td>Hydropsidae</td>
<td>0.2</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hydropsidae</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Heliophoridae</td>
<td>0.2</td>
<td>0.3</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>Hydrochidae</td>
<td>0.1</td>
<td>0.3</td>
<td>0</td>
<td>0.1</td>
</tr>
<tr>
<td>Hydrophilidae</td>
<td>2.2</td>
<td>3</td>
<td>2</td>
<td>1.4</td>
</tr>
<tr>
<td>Hydraenidae</td>
<td>1.6</td>
<td>3.1</td>
<td>1.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Elmidae</td>
<td>1.6</td>
<td>3.4</td>
<td>0.7</td>
<td>0.2</td>
</tr>
<tr>
<td>Dryopidae</td>
<td>0.8</td>
<td>1.2</td>
<td>0.8</td>
<td>0.5</td>
</tr>
</tbody>
</table>

LM, low modification; M, modified; HM, highly modified.

### Sensitivity to anthropogenic changes

In general, there was no clear relationship between the taxonomic distinctness measures and the disturbance level. There were no significant differences in values...
of average taxonomic distinctness across different level of putative human perturbation for all samples (one-way ANOVA, \( P = 0.480 \)) and within the four habitat types. However, we found significant differences in variation in taxonomic distinctness \( (P < 0.001) \) for all samples. Nevertheless, by habitat type these differences were only significant in lotic freshwaters, where values for sites with limited modification were significantly higher than the other two groups (Tukey’s HSD test, \( P < 0.001 \) in both cases; Fig. 5).

With regard to the other biodiversity measures, species richness and rarity showed a clear trend of reduction with increasing levels of perceived human impact (Fig. 5) and there were significant differences in values of both measures across different level of human perturbation for all samples (one-way ANOVA, \( P < 0.001 \) in both cases). By habitat type, species richness was significantly different along the gradient of human impact in lotic freshwaters (Tukey’s HSD test, \( P < 0.001 \) in all cases; Fig. 5) and significantly lower in highly modified sites than in sites with limited modification \( (P < 0.01) \) in lentic freshwaters. Similarly, rarity showed significant differences between sites with high and low levels of modification from lotic freshwaters, lentic freshwaters and lentic saline-waters \( (P < 0.01 \) in both lotic and lentic freshwaters, and \( P < 0.001 \) in lentic saline-waters).

The randomisation test for both average taxonomic distinctness and variation in taxonomic distinctness was not able to discriminate clearly between the three levels of human perturbation in any habitat (Figs 3 & 4). In general, ‘modified’ and ‘highly modified’ sites fell within the probability funnel, and therefore samples from impacted localities did not have a lower-than-expected values. On the contrary, some ‘little or no modification’ sites fall below the confidence limits, especially in lotic freshwaters in which many well-conserved localities had lower values than those which would be expectation from random selection. Furthermore, in lotic freshwaters, average taxonomic distinctness and variation in taxonomic distinctness show an inverse pattern. Most of the sites had \( \Delta^+ \) values below the theoretical mean, and the majority of sites falling below the 95% confidence funnel were the least modified ones. Many of these ‘high quality’ sites had high values of \( \Lambda^+ \) in this habitat, and most of the sites falling above the 95%
limits were ones with low perceived levels of human impact.

Table 1 shows the number of species belonging to each of the 11 families of water beetle along the anthropogenic impact gradient in each of the four different habitat categories. Such information is potentially helpful in interpreting the differences in taxonomic distinctness in relation to modification level. In running freshwaters, there was a general reduction in the mean number of species representing each family with increasing environmental impact, especially in the Hydraenidae and Elmidae. In saline running waters, the effects of human perturbation on taxonomic structure were a reduction in the number of species belonging to some families such as Dytiscidae, Hydraenidae and Hydrophilidae, whereas other families actually increased their representation (Gyrinidae, Haliplidae and Noteridae). There was also a reduction in the number of species belonging to each family in lentic freshwaters, especially in the Dytiscidae. Finally, in lentic saline-waters the most important effect was a reduction in the number of species belonging to the Hydraenidae.

Discussion

Under the framework proposed by Clarke & Warwick (1998, 2001), variability in taxonomic distinctness because of natural environmental factors generally falls within a predictable range, based on the expectation from random selection from a regional species pool (see also Leonard et al., 2006). This could be seen as an advantage of taxonomic distinctness measures over more traditional biodiversity indices based on species richness, which are strongly affected by natural environmental variability. Furthermore, as anthropogenic influences may modify this pattern, such that values fall below the predicted range, taxonomic distinctness measures should be useful to discriminate between natural and impacted sites. However, our results generally fail to support these predictions.

First, many of the less modified sites, especially in running freshwaters, fell outside the predicted range based on random expectations, i.e. the species in these samples were not as distantly related to each other as those from random samples of the local species pool. The main reason for this is that a few families are especially species rich in some unperturbed environments, some of which contain radiations of recent endemics, which may themselves be of conservation concern (Ribera, 2000). For example, in small headwaters streams, the families Hydraenidae and Elmidae have a greater number of species than expected at random. In the case of the family Hydraenidae, most species belong to the genus *Hydraena*, many of which are Iberian, or indeed local, endemics. A similar situation is found in some pristine saline habitats, in which the family Hydraenidae is represented by a high number of species whereas the remaining families are poorly represented. This is especially true in extreme environments such as salt-pans or rock pools, among the lentic systems, and hypersaline streams, among the lotic waters, which are naturally species poor, with most of species occurring in them belong to the single genus *Ochthebius*, which also contains a number of endemics.

In addition to the influence of anthropogenic changes there are ecological and evolutionary factors which may be behind the non-random distribution of species among habitats (or samples). In some communities, as in this study, this may relate to phylogeny or taxonomy. From an evolutionary perspective, this clumped phylogenetic distribution of taxa (‘phylogenetic attraction’) indicates that habitat-use is a conserved trait within the pool of species in a community, and that genotypic attraction dominates over repulsion (Webb et al., 2002). Indeed, this is related to the fact that different clades have different potentials for diversification (Sanderson & Donoghue, 1996; Dodd, Silvertown & Chase, 1999; Gardezi & da Silva, 1999) and some families such as Hydraenidae have been able to adapt to, and then diversify in, some environments better than other families of water beetles.

The second, and certainly important, characteristic attributed to the taxonomic distinctness, which was not supported by our results, is its capacity to detect anthropogenic changes. Clarke & Warwick (2001) hypothesise that, under anthropogenic disturbance, the species that disappear first tend to be those representative of relatively species-poor higher taxa, meaning that the remaining species are from a smaller number of groups, each of which tends to be relatively more species rich. In other words, perturbed communities tend to have reduced taxonomic distinctness, being composed on average of more closely related species than unperturbed communities, which tend to
have more taxonomically distant species resulting in greater taxonomic distinctness.

However, in contrast to some marine systems, water beetles, and indeed many freshwater assemblages more generally, are not characterised by the presence of a few, species-rich and closely related families (or genera) in response to perturbation. In Fig. 6, cases 1 and 2 represent two alternative changes in an assemblage due to anthropogenic modification. In case 1, according to the hypothesis proposed by Warwick & Clarke (1998), the species that disappear are those representative of higher taxa which are species poor. This effect is manifested both as a decrease in average taxonomic distinctness and a decrease in variation of taxonomic distinctness (i.e. the variability of pairwise relatedness of species in the taxonomic tree). In case 2, the species that disappear are those representative of lower taxa which are species rich. In this case, this effect is manifested both as an increase in average taxonomic distinctness and a decrease in variation of taxonomic distinctness.

With the water beetle data reported here the number of species belonging to each family tends to decrease with disturbance, as in case 2, especially in the more species-rich families such as Hydraenidae. These families contain numerous restricted ranges (ecologically specialised species), which are the most sensitive to the anthropogenic changes, as a consequence. Other species-rich families such as Dytiscidae and Hydrophilidae, although containing some species that only occur in well-conserved inland waters, also contain a number of relatively opportunistic and widespread species, with a high dispersal ability and tolerance to pollution or other human disturbances. Therefore, the remaining species (or the new ones colonising) in a perturbed site are from a smaller number of families, each of which is represented by a reduced number of species. As a consequence, the effects of human perturbation are more commonly manifested as an increase or lack of change in average taxonomic distinctness, and a decrease in the variation of taxonomic distinctness (Fig. 6, case 2). For example, in the case of the most highly modified systems, such as irrigation pools or very polluted streams, it is usual to find only two or three widespread mobile species – e.g. Laccophilus hyalinus (De Geer, 1774) and Helochares lividus (Forster, 1771) – belonging to two different families in two different suborders (Dytiscidae and Hydrophilidae). In such a case, the value of average taxonomic distinctness would be the highest in the data set. Such a situation is not unique to aquatic beetle communities, and may explain in general terms why taxonomic distinctiveness indices do not always respond in a predictable manner to anthropogenic impact. This is in agreement with the results reported by Bhat & Marrugan (2006) for freshwater fish assemblages. These authors also found that highly perturbed sites did not display a reduction in taxonomic distinctness relative to random expectations.

In this study, total taxonomic distinctness did not provide additional information over species richness, which makes it relatively redundant as an index. In fact, Warwick & Clarke (1998) did not recommend the general use of this measure, which tends to track species richness rather closely. They suggest that it is only useful for tightly controlled sampling programmes, in which sampling effort is identical for the samples being compared, or sampling is sufficiently exhaustive for the asymptote of the species–area curve to have been reached. This is backed up by our findings, and indeed the situations in which $s\lambda'$ will add to species richness are limited, particularly in environmental monitoring, where such uniform sampling programmes are the exception rather than the rule.

In the Segura Basin at least, taxonomic distinctness measures (both $\lambda'$ and $\lambda''$) were less sensitive...
than other diversity measures, such as species richness and rarity, to anthropogenic changes in the different habitats studied. Thus, in spite of the fact that richness and rarity show different patterns across the four habitats (which suggests that the information provided by them are complementary), both show a clear tendency to decrease under perturbation. Similarly, Salas et al. (2006) found that taxonomic distinctness measures of marine benthic communities were less sensitive than other diversity measures to the effects of eutrophication in coastal lagoons. In addition, Somerfield, Olsgard & Carr (1997) found no consistent pattern between decreasing taxonomic diversity of marine macrofaunal assemblages and increasing environmental impact, and Hall & Greenstreet (1998), studying fish communities, found that taxonomic distinctness measures showed identical trends to conventional diversity indices.

Taxonomic distinctness values were highly variable within each habitat type regardless of the level of human perturbation (Fig. 5). Much of the variation found may result from the effects of natural environmental gradients within each habitat, and this high variability may overshadow the response of these indices to human disturbances (see Bhat & Marrugan, 2006 for similar results). Assuming this limitation, our findings indicate that taxonomic distinctness measures are not independent of natural variability, as has been assumed in the past (Warwick & Clarke, 1998; Leonard et al., 2006). These authors suggested that the variability in taxonomic distinctness among very different habitats should allow one to distinguish, through the randomisation test (which creates a 95% probability funnel from the total species list), the unperturbed sites from the impacted locations, which should show biodiversity values below the expected range. In our study, even in lotic freshwaters, which show a relatively low variability for the values of taxonomic distinctness (i.e. it is a homogeneous group of sites) the randomisation test did not allow us to distinguish between unperturbed and perturbed sites (see Figs 3–5).

Certainly, taxonomic distinctness measures have important characteristics (such as the incorporation of a master list of taxa, which reflects what could be considered to represent reference conditions, and a statistical framework from which to measure the distance in relation to those reference conditions) that make their use in environmental assessment attractive; for example in the classification of ecological status following the WFD. However, our results do not support Warwick & Clarke’s (1995) statement regarding the monotonic behaviour of these indices in response to environmental degradation. In conclusion, our analyses demonstrate that taxonomic diversity measures, as well other measures based on the ‘relatedness’ of species such as phylogenetic diversity, are not always useful tools for such approaches, and highlights that their widespread, and particularly sole, use as biodiversity indicators should be treated with caution.

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References


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