The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels

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ABSTRACT: Taxonomic distinctness is a univariate (bio)diversity index which, in its simplest form, calculates the average 'distance' between all pairs of species in a community sample, where this distance is defined as the path length through a standard Linnean or phylogenetic tree connecting these species. It has some appealing properties: it attempts to capture phylogenetic diversity rather than simple richness of species and is more closely linked to functional diversity; it is robust to variation in sampling effort and there exists a statistical framework for assessing its departure from 'expectation'; it appears to decline monotonically in response to environmental degradation whilst being relatively insensitive to major habitat differences; and, in its simplest form, it utilises only simple species lists (presence/absence data). Many of its practical characteristics remain to be explored, however, and this paper concentrates on the assumptions made about the weighting of step lengths between successive taxonomic levels (species to genera, genera to families etc.), which when accumulated give the overall path lengths. Using data on free-living marine nematodes from 16 localities/habitat types in the UK, it is shown that the relative values of taxonomic distinctness for the 16 sets are robust to variation in the definition of step length. For example, there is a near perfect linear relationship between values calculated using a constant increment at each level and a natural alternative in which the step lengths are proportional to the number of species per genus, genera per family, family per suborder etc. These weightings are then manipulated in more extreme ways, to capture the structure of phylogenetic diversity in more detail, and a contrast is drawn between the biodiversity of island (the Isles of Scilly) and mainland (UK) locations and habitats. This paper concludes with a discussion of some of the strengths and weaknesses of taxonomic distinctness as a practical tool for assessing biodiversity.

KEY WORDS: Biodiversity · Taxonomic distinctness · Nematodes · Island biogeography · Isles of Scilly · Mainland Britain

INTRODUCTION

The need to detect and monitor changes in biodiversity in space and time is widely recognised, and yet there has been little consideration of which attributes of biodiversity might be quantifiable and ecologically relevant. Measures based on the number of species present have been used almost exclusively, and yet biodiversity must be considered as 'the sum of the taxonomic or numerical diversity, and the ecological,

genetical, historical and phylogenetic diversity' (Van der Spoel 1994). Taxonomic distinctness measures incorporate more of this information than species richness measures (Warwick & Clarke 1995), and, although they are now beginning to be used more widely in the marine field (e.g. Hall & Greenstreet 1998, Rogers et al. in press), are still in need of methodological refinement and wider testing. In this paper we explore the robustness of one form of the taxonomic distinctness measure to modest changes in the weightings of step lengths between hierarchical taxonomic levels, which have hitherto been arbitrarily regarded as constant across all levels. We also examine the

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effects of manipulating these weightings more artificially, and how this might be used to interpret differences in the phylogenetic structure of biodiversity in different situations; specifically we have attempted to compare an island versus a mainland fauna.

METHODS

Taxonomic distinctness measures. For biological community data (species-by-sample abundance matrices), Warwick & Clarke (1995) defined 2 biodiversity indices Δ and Δ^*, capturing the structure not only of the distribution of abundances amongst species but also the taxonomic relatedness of the species in each sample. In the special case, as in the present study, where the data consist only of presence/absence information, Δ and Δ^* converge to the same statistic (Δ^+), which is defined as the average taxonomic path length between any 2 randomly chosen species, traced through a Linnean or phylogenetic classification of the full set of species involved (Clarke & Warwick 1998). Importantly for practical comparisons, these taxonomic distinctness indices are not dependent, on average, on the degree of sampling effort involved in the data collection; this is in sharp contrast with those diversity measures which are strongly influenced by the number of observed species. This implies that Δ^+ can be compared across studies with differing and uncontrolled degrees of sampling effort (subject to assumptions concerning comparable taxonomic accuracy). This is of particular significance for historic species lists from different localities or regions, as here, which at first sight do not seem amenable to valid diversity comparison of any sort. Furthermore, a randomisation test is possible (Clarke & Warwick 1998), to detect a difference in the taxonomic distinctness, for any observed set of species, from the 'expected' Δ^+ value derived from a master species list for the relevant group of organisms. The exact randomisation procedure requires heavy computation, but can be approximated by deriving an appropriate variance formula. This leads to a 'confidence funnel', against which distinctness values for any specific area, habitat type, pollution condition etc. can be checked, and formally addresses the question of whether a locality has a 'lower than expected' average taxonomic spread.

The taxonomic distinctness of nematodes from environmentally degraded locations tends to be reduced in comparison with that of more pristine locations, often significantly so (Warwick & Clarke 1998). Some habitat types may have naturally lower values of taxonomic distinctness than others, but unless the habitats are degraded in some way the Δ^+ values do not fall below the lower boundary of the 'funnel'. (The latter is the lower 95% confidence limit from the simulated distribution under a null hypothesis that the assemblages have the same structure as a random selection from the regional species pool.) This ameliorates the problems encountered with species richness measures of biodiversity, which not only are very sensitive to sampling effort but are strongly affected by habitat type and complexity, thus making comparisons difficult between data sets from different habitats or where habitat type is uncontrolled. The use of taxonomic distinctness also addresses the question of the hierarchical level at which diversity is expressed.

Weighting of steps in the taxonomic hierarchy. For the species list for each locality and/or habitat, an average taxonomic distinctness index is computed, namely

$$\Delta^+ = [\Sigma\Sigma_{i < j} \omega_{ij}]/[m(m-1)/2]$$

where m is the number of species in the particular study and ω_{ij} is the weight (path length) given to the taxonomic relationship between species i and j. Δ^+ can be thought of as the average path length between any 2 randomly chosen species from the study. It is first necessary to define the weights $\{v\}$ assigned to each section of that path, the step linking one taxonomic level with the next coarsest division. For marine nematodes, Warwick & Clarke (1995, 1998) and Clarke & Warwick (1998) used constant step lengths $v = 1$ between each taxonomic level (species, genera, families, suborders, orders, subclasses and class), giving path-length weights $\omega = 1$ for pairs of species in the same genus, $\omega = 2$ for species in the same family (but not the same genera), etc. up to $\omega = 5$ for species in the same subclass (but not the same order) and $\omega = 6$ for species in separate subclasses.

It could be thought unsatisfactory to define a constant increment, $v = 1$, between each level in the hierarchy: a taxonomic grouping which is barely used, subdividing the species into nearly as many categories as the division below it, should not attract as large a step weighting (v) as one which markedly reduces the number of categories. In this spirit, it is possible instead to define the weight given to a step as proportional to the percentage by which taxon richness decreases at that step. For the path linking 2 species, the differing step lengths involved (v) need to be accumulated, and the result standardised so that the final path-length weight (ω) always takes a value in some specified range. The simplest such standardisation, adopted throughout this paper, sets the path length ω to 100 for 2 species connected at the highest (taxonomically coarsest) possible level. Thus, the 'default' weights of 1 to 6, used by the previous papers, become $\omega = 16.7$, 33.3, 50, 66.7, 83.3 and 100, respectively, and the weighting based on taxon richness at each level (see

Table 1) is $\omega^{(0)}$ = 15.9, 37.3, 60.2, 72.2, 86.1 and 100 respectively. This scaling of the richness weighting achieves the desired objective: the insertion of a redundant subdivision cannot now alter the value of Δ^+. It has the disadvantage that Δ^+ is now a function of the particular richness hierarchy observed, making comparisons external to the data set difficult. Here, though, this will not be a problem because the analyses will be based on a single, relatively comprehensive listing of a UK faunal group (the free-living marine nematodes). This can be used to provide a common set of step-length weightings for analyses of particular regional or habitat studies.

Comparative data. As an example, we have analysed data (species lists) of marine nematodes, arguably the most diverse and abundant group of marine animals (Platt & Warwick 1980, Lawton 1998), from a variety of locations around the UK. The primary objective is to test the robustness of Δ^+ to different natural weightings of the step lengths in the taxonomic hierarchy. A secondary objective of the paper is to manipulate these weights in more experimental ways, in order to compare the hierarchical taxonomic structure of island and mainland faunas, and in the discussion that follows we have emphasised comparisons between the Isles of Scilly (an archipelago some 45 km distant from the SW tip of Cornwall, UK) and mainland Britain.

The Isles of Scilly: A listing of marine nematode species from the Isles of Scilly is given by Warwick & Coles (1977), and some additional species are recorded by Gee & Warwick (1994a,b). There have been 4 major studies: (1) Collections made by Professor L. A. Harvey from a wide range of different intertidal seaweed species, localities and seasons between 1969 and 1972, identified by Warwick (1977). (2) Collections from a variety of sublittoral habitats (hydroids, polyzoans, sponges and sediments ranging from coarse gravel and broken shell to mud) made by the University of London Sub-Aqua Club, identified by Warwick &

Coles (1977). (3) Collections made by R. M. Warwick in August 1971 from a variety of sand beaches of different sediment grade and tidal height, plus *Laminaria* holdfasts at low water on rocky shores and decomposing wrack beds on sand beaches (records in Warwick & Coles 1977). (4) Collections from 5 species of intertidal algae at 8 localities by Gee & Warwick (1994a,b).

For the purposes of this study we have considered all the species recorded to be a reasonably representative regional list, and also treated separately the faunas of 3 habitats: intertidal sands, intertidal algae and 'other habitats' (sublittoral secondary substrata and sediments, including *Laminaria* holdfasts).

The UK mainland: Here we have used published data from a range of (mainly sedimentary) habitats from widespread localities, some of which are subjected to various types of pollution impact:

(1) Sublittoral offshore sediments. (a) The relatively pristine mud and sandy mud at 3 stations off the Northumberland coast (Warwick & Buchanan 1970), (b) the Tyne sewage sludge dumping ground, a dispersive site where environmental impact on both meiobenthos and macrobenthos, in comparison with appropriate control sites in that region, is relatively slight (Somerfield et al. 1993), and (c) the heavily industrialised and sewage-polluted Liverpool Bay (Somerfield et al. 1995).

(2) Intertidal sand beaches. (a) The pristine sandflats and beaches of the Exe estuary (Warwick 1971), and the beaches subjected to industrial and sewage pollution in (b) the Clyde at Irvine Bay (Jayasree 1976) and (c) at Ettrick, Scalpsie, Irvine and Ayr Bays (Lambshead 1986) and (d) in the Forth (Jayasree 1976). Ettrick and Scalpsie Bays are non-polluted according to Lambshead (1986), and we have also considered separately the 9 samples taken at the 3 stations (Stns 4, 5 and 6) in Irvine and Ayr Bays that Lambshead regarded as polluted.

(3) Estuarine intertidal mudflats with reduced salinity. (a) The relatively pristine Exe (Warwick 1971), (b) the

Table 1. The 6 level nematode classification k, with the number of entries in each category (taxon richness, s_k) for the combined UK nematode list of 395 species used in this paper. Remaining columns give the different weighting schemes used to compute Δ^+. For a specific k, $\omega_k^{(1)}$ is the weighted path length between species belonging to differing taxon group k but the same group $k+1$, where: ω_k is the 'default' weighting for constant step length; $\omega_k^{(0)}$ sets step length proportional to percentage decrease in richness from taxon k to taxon $k+1$; $\omega_k^{(1)}$ has step lengths 1, 2,..., 6, increasing with k; $\omega_k^{(2)}$ has step lengths 6, 5,..., 1, decreasing with k; and $\omega_k^{(-t)}$ has constant step lengths but with the final (coarsest level) t steps set to zero (t = 1, 2)

k	Taxon	s_k	ω_k	$\omega_k^{(0)}$	$\omega_k^{(1)}$	$\omega_k^{(2)}$	$\omega_k^{(-1)}$	$\omega_k^{(-2)}$
1	Species	395	16.7	15.9	4.8	28.6	20	25
2	Genus	170	33.3	37.3	14.3	52.4	40	50
3	Family	39	50.0	60.2	28.6	71.4	60	75
4	Suborder	7	66.7	72.2	47.6	85.7	80	100
5	Order	4	83.3	86.1	71.4	95.2	100	100
6	Subclass	2	100	100	100	100	100	100

subsequent plots are shown in Fig. 1. The taxonomic structure of these regional data are compared in what follows with an overall UK list of free-living marine nematodes (395 species), compiled from Platt & Warwick (1983, 1988), Warwick et al. (1998).

Statistical methods. For any specified weighting, comparative values of Δ^+ for all the UK studies (16 different sets or combinations) can be plotted against the corresponding numbers of species (m) in each set. Deviation of taxonomic distinctness for any particular study, from that for the full set of $s = 395$ UK species, can be assessed by referring to the confidence limits generated either by simulation or from theoretical variance estimation (Clarke & Warwick 1998). The simulation simply generates a large number of random subsets of species from the UK list, each of size m, computes the corresponding taxonomic distinctness values Δ_m^+, and determines an interval in which 95% of these values lie. Over a range of m values this gives rise to a 'confidence funnel' for Δ^+, for which, naturally, the smaller the value of m the larger is the variability expected in Δ_m^-. Importantly, though, the mean (expectation) of these subset values, $E(\Delta_m^+)$, exactly equals Δ^+ for the full set of 395 species, whatever the sample size m. This is the lack of dependence of Δ_m^+ on sampling effort, referred to previously. An exact expression can also be derived for the variance of Δ_m^+ (Clarke & Warwick 1998), allowing quick construction of an approximate confidence funnel (mean ± 2 SD) without the necessity for extensive and time-consuming simulations.

In spite of the standardisation to a maximum value of 100 for Δ^+, of course it will be true that sets of weights $\{\omega\}$ placing differing emphases on finer or coarser levels of the taxonomic hierarchy will give differing average values for Δ^+. What matters is whether the choice of weighting affects the *relative* values of Δ^+ for the different locations/habitats. It would clearly be unsatisfactory for comparisons between studies to be sensitive to subtle weighting choices which are essentially arbitrary (for example, between a constant step length and a variable step length based on percentage reduction in taxon richness).

Scatter plots are given of Δ^+ for the various studies, computed under the 'default' weighting (constant step length) on the x-axis and for a range of alternative weightings on the y-axes. In addition to the weighting based on taxon richness, $\{\omega^{(0)}\}$, Table 1 gives weights $\{\omega^{(1)}\}$, corresponding to increasing step lengths $v = 1$, 2,…, 6 for species to genus, genus to family, …, subclass to class, respectively, and $\{\omega^{(2)}\}$ derived from decreasing step lengths $v = 6$, 5,…, 1. When accumulated and standardised, as for ω and $\omega^{(0)}$, these weights clearly give distinctness estimates either dominated $(\omega^{(1)})$ by path lengths which pass through the coarsest taxonomic level, or redress the balance $(\omega^{(2)})$ in favour

Fig. 1. UK map showing the approximate locations of the studies giving rise to the 16 habitat/location species lists: S = all Scillies, SA = Scillies algae, SS = Scillies sand, SO = Scillies other (see 'Methods'), FA = Fal mud, TA = Tamar mud, E = all Exe, EM = Exe mud, ES = Exe sand, L = Liverpool Bay, TY = Tyne dumpground, N = Northumberland offshore, FO = Forth sand, C1 = Clyde sand (Lambshead study), CP = Clyde sand 'polluted' sites (Lambshead), C2 = Clyde sand (Jayasree study)

Tamar (Austen & Warwick 1989) with a history of metalliferous mining in the catchment, extensive naval dockyards and the large conurbation of Plymouth, and (c) the Fal estuary where the levels of heavy metals in the mud are the highest in the country as a result of overspills from tin mines (Somerfield et al. 1994a,b).

We have also treated the Exe estuary data together as a combined regional species list for a range of different habitat types (mudflats in different salinity regimes and at different tidal levels, sand beaches with varying degrees of exposure and grain sizes, coastal subsoil water from coarse sediments at high water of spring tides). The Liverpool Bay data also arguably come into this mixed-habitat category, since a wide range of sediment types was studied ranging from fine silts to coarse gravels and stones. These data for a range of habitats provide a more comprehensive estimate of the local species pool than the single habitat data listed above.

In total this gives a series of 16 faunal lists for the various regional/habitat categories; their approximate locations and the code used to identify each list in the

of finer taxonomic levels. These are included not because they are advocated for practical use but simply to provide extreme cases, to bracket the effects on Δ^+ of different weightings.

An extension is to manipulate the step lengths {v} to examine the effects on Δ^+ of altogether ignoring the coarsest level, and then successively finer levels, of the taxonomic hierarchy. This should be of particular interest for the island data, a possible hypothesis being of a drop in the value of Δ^+, in relation to mainland sites, on compression of the highest-level structure, i.e. that biodiversity is expressed only at the coarsest taxonomic levels. The weights $\omega^{(-1)}$ in Table 1 correspond to step lengths of $v = 1, 1, 1, 1, 1, 0$, i.e. the usual steady increase in path lengths through most of the tree but with the subclasses treated as if they constituted a single subclass. Similarly, $\omega^{(-2)}$ further compresses the hierarchy, with step lengths of $v = 1, 1, 1, 1, 0, 0$, i.e. all species treated as in the same order.

RESULTS

Effects of varying weightings

Values of Δ^+ for all the studies, using constant step lengths between all taxonomic levels, are shown in Fig. 2. It is only at environmentally degraded sites that Δ^+ falls significantly below expectation: polluted sands in the Clyde estuary, the sublittoral fauna of Liverpool Bay and the mudflats of the Fal estuary being notable in this respect.

Using constant step lengths between taxonomic levels as a standard, the effects of varying this weighting for all the nematode studies described in this paper are given in Figs. 3 & 4. In Fig. 3a, against an x-axis of Δ^+ calculated from constant step lengths, the y-axis plots values of Δ^+ based on the percentage reductions in taxon richness at each hierarchical level (weights $\omega^{(0)}$ in Table 1). There is a very good linear relationship between these values, reassuringly suggesting that the relative values of Δ^+ are robust to modest, but realistic, changes in the balance of the weighting. The situation is similar even for the extreme case in which the weighting increases steadily as one moves up the taxonomic hierarchy {$\omega^{(1)}$} (Fig. 3b). At the other extreme, when the weighting strongly decreases on moving up the taxonomic hierarchy {$\omega^{(2)}$}, the linear relationship is maintained for all points except the 4 Scilly values, which fall clearly below the line (Fig. 3c).

Fig. 4 shows the effect of compressing the taxonomic hierarchy to successively lower levels. No additional increase in weighting is given to paths above the subclass level in Fig. 4a (weights $\omega^{(-1)}$ in Table 1); all the
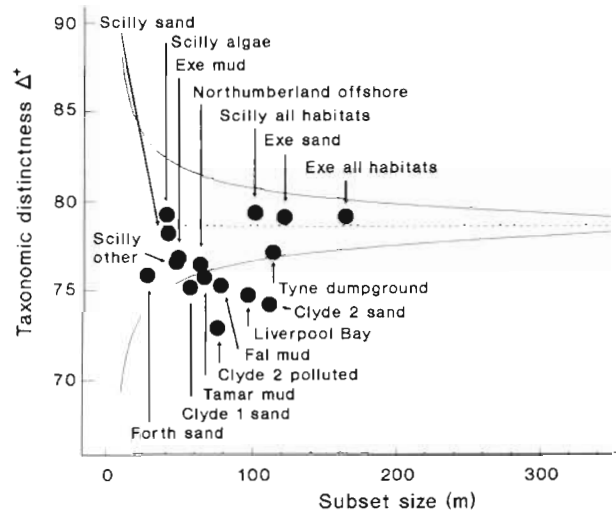

Fig. 2. Average taxonomic distinctness (Δ^+) for constant step weighting, for the 16 nematode species lists from the different habitat/location combinations (see Fig. 1), plotted against the numbers of species (m) in each list. Also shown are the taxonomic distinctness for the full list of 395 UK nematode species (----) and the 95% confidence limits for Δ^+ (——), for random selections of subsets of m species from the full list. (The latter is calculated from the variance approximation given by Clarke & Warwick 1998)

mainland sites maintain a good linear relationship with the values for the default weighting, but the 4 Scilly points fall well below the line. In Fig. 4b, additional compression of the hierarchy (to the order level) is seen not to produce further major changes in the relative values of Δ^+ across sites, i.e. a linear relationship is re-established between Δ^+ computed with weights $\omega^{(-1)}$ and $\omega^{(-2)}$.

DISCUSSION

Weight manipulations

Experiments varying the taxonomic weightings indicate that, for comparative purposes, taxonomic distinctness is very robust, at least with respect to those weightings that preserve the distinction between the levels (their ranking). More extreme manipulations, in which some step lengths are set to zero, have been used to reveal differences in the taxonomic structure of assemblages between locations. In this case, the taxonomic distinctness of nematodes from the Isles of Scilly is on average no different from that of mainland sites, but manipulation of the weightings of the step lengths between taxonomic levels has shown clearly that there is a greater spread of diversity at the very highest taxonomic level (of subclasses). Since there are only 2
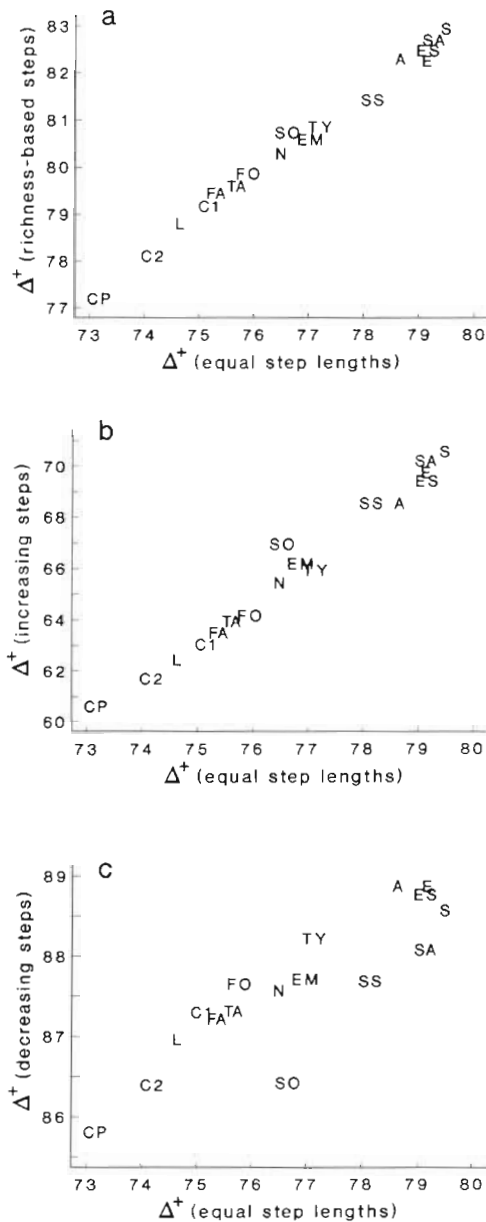
Fig. 3. Comparisons of taxonomic distinctness (Δ⁺) for the UK nematode studies, under the different weighting schemes of Table 1. All scatter plots have x-axis of Δ⁺ calculated for constant step lengths ('default' weights ω); the y-axes are Δ⁺ for weights (a) $\omega^{(0)}$, based on taxon richness at each level of the hierarchy; (b) $\omega^{(1)}$, increasing step lengths towards the coarser taxonomic levels; and (c) $\omega^{(2)}$, decreasing step lengths at the coarser levels. See Fig. 1 for codes for the 16 habitat/ location combinations; the 17th point gives the Δ⁺ values for the entire UK nematode list (code A)

Fig. 4. Comparisons of taxonomic distinctness (Δ⁺) for the 17 UK nematode lists, as in Fig. 3 but using the following weights from Table 1: (a) Δ⁺ for $\omega^{(-1)}$, compressing the taxonomic hierarchy at the subclass level, against Δ⁺ for default weights; (b) Δ⁺ for $\omega^{(-2)}$, compressing the taxonomic hierarchy to the order level, against Δ⁺ for $\omega^{(-1)}$, subclass compression

subclasses involved (Enoplia and Chromadoria), all that this implies is a more even distribution of the species between them on the Scillies compared with the mainland. In a comprehensive review of the marine
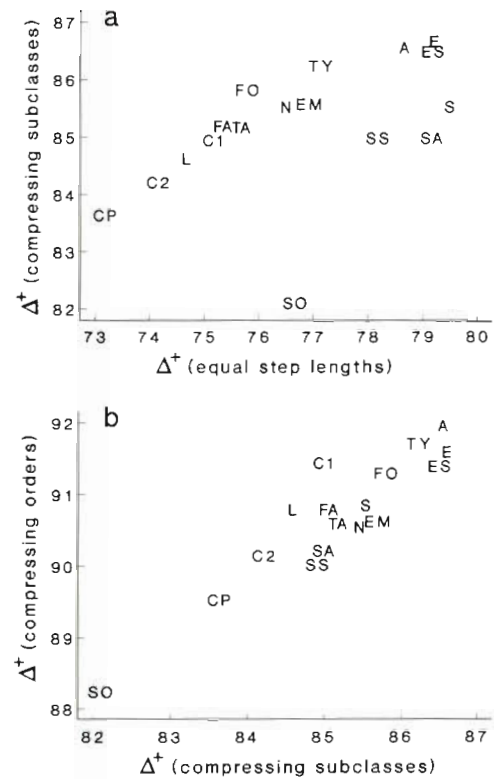
flora and fauna of the Isles of Scilly, Harvey (1969) noted 'the markedly poorer representation of most of the major phyla around the islands' in comparison with faunal lists compiled for the nearest recorded region, the Plymouth Marine Fauna (Marine Biological Association 1957). He was mainly referring to macrobenthic taxa, and cited evidence to suggest that species with long larval development times in the plankton are likely to be depleted in, or to disappear from, Scilly waters due to the prevailing West to East currents, no replenishment being possible from the West. Harvey's observation that all the major taxa are represented, but with rather few species in each, suggests that a feature of these islands is that diversity is expressed at a higher taxonomic level than at mainland locations. The present study partially bears this out, in that for marine nematodes diversity at the highest taxonomic level is higher than at mainland locations. However, this is balanced out by a lower representation of taxa at intermediate levels, so that overall the taxonomic distinctness is no higher than on the mainland.

Utility of the index

Sensitivity and robustness

This form of taxonomic distinctness index has so far proved informative in some benthic meiofaunal, macrofaunal and groundfish studies (e.g. Warwick & Clarke 1995, 1998, Hall & Greenstreet 1998, Rogers et al. in press). Clarke & Warwick (1998) demonstrated a key sampling property—the lack of dependence of the mean value of Δ^+ on sampling effort—and constructed variance formulae and a hypothesis testing framework. Warwick & Clarke (1998) discussed its relevance as a biodiversity measure—its link to functionality, its apparent monotonic response to environmental degradation and relative insensitivity to habitat differences. On the strength of one macrofaunal case study, Warwick & Clarke (1995) initially suggested that it may also have a greater sensitivity to disturbance events than is seen with species-level richness or evenness indices. This has not been confirmed in subsequent studies (e.g. Somerfield et al. 1997): there are now a number of examples where taxonomic distinctness appears no more sensitive than traditional diversity indices. This fact should not be surprising. There is much empirical evidence (e.g. Warwick & Clarke 1991) that the best way of detecting subtle community shifts arising from environmental impacts is not through univariate indices at all, but by non-parametric multivariate display and testing methods (MDS, ANOSIM etc., Clarke & Warwick 1994). The difficulty with such similarity-based approaches is that they can be sensitive to any number of modest differences in habitat type, geographic location, etc. The traditional univariate diversity measures, though independent of particular species identities, have their own sensitivities. For example, species richness can be highly (and undesirably) influenced by degree of sampling effort. The general point here is that robustness and sensitivity are often antipathetic. What is properly claimed for the taxonomic distinctness index Δ^+ is not sensitivity but a high level of robustness. It can be meaningfully compared between 2 studies with few (or no) species in common, using data in non-quantitative form (presence/absence), and obtained from very different sample sizes. Its natural use is therefore for diffuse, historic data sets, arising from unstandardised and/or unknown degrees of sampling effort. The surprise here, if any, should be that simple species lists of this type are amenable to any valid form of diversity comparison. Conversely, the use of Δ^+ on its own is unlikely to exploit the richness of community data obtained from tightly controlled, well-designed field or laboratory studies, returning fully quantitative species abundances.

Taxonomic artefacts

Another natural question which arises from the construction of taxonomic distinctness using Linnean classifications is the extent to which the index is subject to taxonomic artefacts. It is widely felt that the Linnean hierarchy can be inconsistent in the way it defines taxonomic units across different phyla. This concern can be addressed on a number of levels. Of course, the concept of mutual distinctness or relatedness of a set of species is not constrained to a Linnean classification. The natural metric is probably one of genetic distance (e.g. Nei 1996) or that from a soundly based phylogeny combining molecular tools with more traditional morphology. The Linnean classification clearly gives a discrete approximation to a more continuous distinctness measure, and this is why it is important to establish that the precise weightings given to the step lengths between taxonomic levels are not critical to the relative values that the index takes across the various studies. Nonetheless, it is a legitimate concern that a cross-phyletic distinctness analysis could represent a simple shift in the balance of 2 major phyla as a decrease in biodiversity, not because the phylum whose presence is increasing is genuinely less (phylogenetically) diverse but because its taxonomic sub-units have been arbitrarily set at a lower level. For this reason, we have concentrated in this paper on a single, reasonably taxonomically coherent group, the marine nematodes. A number of research questions inevitably follow, and these are currently being addressed: (1) the extent to which patterns in one group of well-studied organisms are indicative of a wider biodiversity trend (the issue of surrogacy); (2) the potential scale of cross-phyletic differences in the construction of taxonomies (note that this could be succinctly quantified by application of the taxonomic distinctness index to major groups within a comprehensive species inventory); (3) the degree to which spatio-temporal distinctness patterns for a particular group are sensitive to the interpolation of intermediate taxonomic levels (e.g. subgenera, superfamilies etc., as described in the groundfish data of Rogers et al. in press, which uses a 13-level taxonomic classification compiled by J. D. Reynolds).

Regional species list

The final question that arises naturally from the analysis of this paper concerns the use of a regional species list and its (bio)geographic range, since there is clearly scope for incompleteness of the former and arbitrariness of the latter. In fact, the existence of such a wide-scale inventory is not a central requirement. It is not used in constructing and contrasting the values

of Δ^+ for individual samples, and only features in 2 ways in the figures of this paper. In Fig. 2, location of the points does not require a regional species list; the latter is used only to display the mean value (dashed line) and confidence limits (continuous line) that would be expected for samples drawn at random from such a nematode inventory for the UK. In Fig. 3a, the regional species list is employed to calculate step lengths in a revised form of Δ^+—weighting by taxon richness at the different hierarchical levels (number of species per genus, genera per family, etc.). The existence of an inventory makes this procedure more appealing, since if the taxon richness weighting was determined only by the samples to hand, the index would need to be adjusted as each new sample (containing further species) was added. But the message of this paper, borne out also by the groundfish study of Rogers et al. (in press), is that the additional complication of adjusting the weights in Δ^+ for differences in taxon richness is unnecessary. Constant step lengths appear to be adequate. The inventory is therefore *only* used for setting a regional context, the theoretical mean and 'funnel' of Fig. 2. Various lists could sensibly be employed: global, local geographic (as here, reflecting the UK-wide spread of the sites, Fig. 1), biogeographic provinces, or simply the combined species list of all the studies being analysed. The addition of a small number of newly discovered species to the regional inventory is unlikely to have a detectable effect on the overall mean and confidence funnel for Δ^+. If these are located in the taxonomic tree at random with respect to the existing taxa (rather than all belonging to some new high-order group, or being a complex of sibling species), by definition they will have no effect on the theoretical mean Δ^+. This, of course, is one of the advantages of using an index of *average* rather than *total* taxonomic distinctness. It also makes clear what the limitations are to the validity of Δ^+ comparisons. Whilst, in our experience, many historic marine community studies consist of the species-level identifications which are largely necessary for meaningful computation of Δ^+, there are always some taxa that cannot be identified to this level (e.g. nemertines in soft-sediment macrobenthic samples). There is no difficulty here, since Δ^+ is always used in a relative manner, *provided* these taxa are treated in the same way in all samples (e.g. omitted). The ability to impose taxonomic consistency, by suitable omissions or regroupings, is clearly an important caveat on the use of taxonomic distinctness for historic data sets.

LITERATURE CITED

Austen MC, Warwick RM (1989) Comparison of univariate and multivariate aspects of estuarine meiobenthic community structure. Estuar Coast Shelf Sci 29:23–42

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth

Clarke KR, Warwick RM (1998) A taxonomic distinctness index and its statistical properties. J Appl Ecol 35:523–531

Gee JM, Warwick RM (1994a) Metazoan community structure in relation to the fractal dimensions of marine macroalgae. Mar Ecol Prog Ser 103:141–150

Gee JM, Warwick RM (1994b) Body-size distribution in a marine metazoan community and the fractal dimensions of macroalgae. J Exp Mar Biol Ecol 178:247–259

Hall SJ, Greenstreet SP (1998) Taxonomic distinctness and diversity measures: responses in marine fish communities. Mar Ecol Prog Ser 166:227–229

Harvey LA (1969) The marine fauna and flora of the Isles of Scilly. The islands and their ecology. J Nat Hist 3:3–18

Jayasree K (1976) Systematics and ecology of free-living marine nematodes from polluted intertidal sand in Scotland. PhD thesis, University of Aberdeen

Lambshead PJD (1986) Sub-catastrophic sewage and industrial waste contamination as revealed by marine nematode faunal analysis. Mar Ecol Prog Ser 29:247–260

Lawton J (1998) Small is beautiful, and very strange. Oikos 81:3–5

Marine Biological Association (1957) Plymouth marine fauna, 3rd edn. Marine Biological Association, Plymouth

Nei M (1996) Phylogenetic analysis in molecular evolutionary genetics. Annu Rev Genet 30:371–403

Platt HM, Warwick RM (1980) The significance of free-living nematodes to the littoral ecosystem. In: Irvine DEG, Farnham WF (eds) The shore environment. Vol 2: Ecosystems. Academic Press, Cambridge, p 729–759

Platt HM, Warwick RM (1983) Freeliving marine nematodes. Part I: British enoplids. Synopses of the British fauna no. 28. Cambridge University Press, Cambridge

Platt HM, Warwick RM (1988) Freeliving marine nematodes. Part II: British Chromadorida. Synopses of the British fauna no. 38. Brill, Leiden

Rogers SI, Clarke KR, Reynolds JD (in press) The taxonomic distinctness of coastal bottom-dwelling fish communities of the Northeast Atlantic. J Anim Ecol

Somerfield PJ, Gee JM, Widdicombe S (1993) The use of meiobenthos in marine pollution monitoring programmes. Plymouth Marine Laboratory Miscellaneous Publication LIB-33A+LIB-33B, Plymouth

Somerfield PJ, Gee JM, Warwick RM (1994a) Soft sediment meiofaunal community structure in relation to a long-term heavy metal gradient in the Fal estuary system. Mar Ecol Prog Ser 105:79–88

Somerfield PJ, Gee JM, Warwick RM (1994b) Benthic community structure in relation to an instantaneous discharge of waste water from a tin mine. Mar Pollut Bull 28:363–369

Somerfield PJ, Rees HL, Warwick RM (1995) Interrelationships in community structure between shallow-water marine meiofauna and macrofauna in relation to dredgings disposal. Mar Ecol Prog Ser 127:103–112

Somerfield PJ, Olsgard F, Carr MR (1997) A further examination of two new taxonomic distinctness measures. Mar Ecol Prog Ser 154:303–306

Van der Spoel S (1994) A biosystematic basis for pelagic biodiversity. Bijdr Dierkd 64:3–31

Warwick RM (1971) Nematode associations in the Exe estuary. J Mar Biol Assoc UK 51:439–454

Warwick RM (1977) The structure and seasonal fluctuations of phytal marine nematode associations on the Isles of Scilly. In: Keegan BF, O'Ceidigh P, Boaden PJS (eds) Biology of benthic organisms. Pergamon, Oxford, p 577–585

Warwick RM, Buchanan JB (1970) The meiofauna off the coast of Northumberland. I: The structure of the nematode population. J Mar Biol Assoc UK 50:129–146

Warwick RM, Clarke KR (1991) A comparison of some methods for analyzing changes in benthic community structure. J Mar Biol Assoc UK 71:225–244

Warwick RM, Clarke KR (1995) New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Mar Ecol Prog Ser 129:301–305

Warwick RM, Clarke KR (1998) Taxonomic distinctness and environmental assessment. J Appl Ecol 35:532–543

Warwick RM, Coles JW (1977) The marine flora and fauna of the Isles of Scilly. Free-living Nematoda. J Nat Hist 11: 393–407

Warwick RM, Platt HM, Somerfield PJ (1998) Freeliving marine nematodes. Part III: British Monhysterida. Synopses of the British fauna no. 53. Field Studies Council, Shrewsbury