

Taxonomic distinctness and environmental assessment

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Summary

1. The objectives of this paper are to test the performance of the taxonomic distinctness index, Δ^+ , in a number of environmental impact scenarios, to examine its relationship with functional diversity and to examine the influence of habitat type and diversity on the index.
2. The index was applied to data on free-living marine nematodes from the coasts of Britain and Chile.
3. The taxonomic distinctness of nematodes from environmentally degraded locations was generally reduced in comparison with that of more pristine locations, often significantly so.
4. Some habitat types may have naturally lower values of taxonomic distinctness than others. However, unless the habitats are degraded in some way the Δ^+ values do not generally fall below the lower 95% confidence limit of the simulated distribution under a null hypothesis that the assemblages behave as if they are a random selection from the regional species pool. This ameliorates the problem encountered with species richness measures of biodiversity, which are much more strongly affected by habitat type and complexity, thus making comparisons difficult between data sets from different habitats or where habitat type is uncontrolled.
5. Taxonomic distinctness in marine nematodes is shown to be related to trophic diversity: a reduction in trophic diversity will lead to a reduction in taxonomic distinctness, although not necessarily to a reduction in species richness. Trophic composition itself is clearly affected by pollution, but is also strongly responsive to the major influence of habitat type.
6. These features of the taxonomic distinctness index, coupled with its lack of dependence on sampling effort or differences in taxonomic rigour between workers and a statistical framework for the assessment of the significance of departure from expectation, suggest that it may prove to be a biologically and ecologically relevant measure of biodiversity.
7. This paper demonstrates that the taxonomic distinctness index has a number of theoretical and logistical advantages over measures of species richness for the purposes of environmental assessment.

Key-words: biodiversity, Britain, Chile, environmental degradation, marine nematodes.

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Introduction

Clarke & Warwick (1998) have shown that the pairwise averaged taxonomic distinctness index Δ^+ (hereafter referred to simply as taxonomic distinctness) has a number of desirable properties as a measure of biodi-

versity in the context of environmental impact assessment, notably its lack of dependence on sampling effort and a statistical framework for the assessment of the significance of departure from expectation. The purpose of this paper is threefold:

1. To test the performance of the distinctness index in a number of environmental impact scenarios.
2. To examine its relationship with functional diver-

sity. An index of biodiversity would be more ecologically relevant if it is related to changes in functional diversity, and measures of species richness are not necessarily so related.

3. To examine the influence of habitat type and diversity on the index. Indices that are not dependent on habitat type (again unlike species richness measures) would be particularly valuable for comparing presence/absence data (species lists) from different areas where the types or range of habitats differ.

Materials and methods

THE TEST DATA

We chose to use data on marine free-living nematode assemblages as our examples for three reasons:

1. A comprehensive phylogenetic classification exists, based on cladistic principles (Lorenzen 1981, 1994), which is not the case for most other groups of marine invertebrates.

2. The functional role, in terms of feeding type, for each species can be deduced from the physiognomic characters of its buccal cavity (Fig. 1). The four feeding groups proposed by Wieser (1953a) are (1A) species with no buccal cavity, or a narrow tubular one, regarded as 'selective deposit feeders' that ingest bacterial-sized particles; (1B) species with a large buccal cavity, but unarmed with teeth, 'non-selective deposit feeders'; (2A) species with a buccal cavity armed with small or moderately sized teeth, 'epigrowth' or diatom feeders; (2B) species with large teeth or jaws, the 'predator/omnivore' group. This classification has been elaborated on subsequently (see the recent review by Moens & Vincx 1997) but largely remains valid in the absence of direct confirmatory observations on feeding behaviour.

3. Free-living nematodes are the most abundant and diverse metazoans in the sea and play important functional roles in the ecosystem (Platt & Warwick 1980).

We evaluated subsets of data from the coastlines of two regions where relatively comprehensive inventories of species are available, to enable use of the statistical significance testing procedure for departure from random expectation (Clarke & Warwick 1998). These were the British Isles, records for which have been compiled in Platt & Warwick (1983, 1988) and Warwick, Platt & Somerfield (1998), and Chile, where a range of habitats was surveyed along the coastline by Wieser (1953b, 1954, 1956, 1959). The total species list for Britain is 395, and for Chile 252. These were classified into genera, families, suborders, orders and subclasses according to Lorenzen (1981, 1994).

To examine environmental impacts on taxonomic distinctness, only the data from the British Isles were used. For three different habitats (sublittoral sediments, intertidal sands and estuarine mudflats) we examined data from studies covering a range of levels and types of pollution:

1. Sublittoral offshore sediments. (a) The relatively pristine mud and sandy mud at three 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, Gee & Widdicombe 1993); and (c) the heavily industrialized and sewage-polluted Liverpool Bay (Somerfield, Rees & Warwick 1995).

2. Intertidal sand beaches. (a) The pristine sandflats and beaches of the Isles of Scilly (Warwick & Coles 1977) and (b) the mouth of the Exe Estuary (Warwick 1971); and the beaches subjected to industrial and sewage pollution (c) in the Clyde at Irvine Bay (Jayasree 1976), (d) at Ettrick, Irvine and Ayr Bays (Lamshead 1986), and (e) in the Forth (Jayasree 1976). Ettrick Bay is non-polluted according to Lamshead (1986) but, since we were considering taxonomic distinctness in a regional rather than a site-by-site context, we included all the species he recorded from 16 samples in the three Bays. However, we also calculated Δ^+ separately for the nine samples taken at the three stations (4, 5 and 6) he regarded as polluted.

3. Estuarine intertidal mudflats with reduced salinity. (a) The relatively pristine Exe (Warwick 1971); (b) the 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, Gee & Warwick 1994a,b).

We also compared combined species lists for a range of different habitat types from two well-defined regions of Britain: the Isles of Scilly (beach sands with different levels of exposure, intertidal algae, kelp holdfasts, sublittoral secondary and coarse substrata) and the Exe estuary (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 regional species pool than the single habitat data listed above.

The data used for this comparative study were by no means standardized or controlled in terms of the number of locations sampled, the number of replicate samples taken at each location, the core size, etc., so that relative diversity measures based on the number of species would be unsuitable as a basis for comparisons.

Both the Chilean and British data have been used to examine the influence of habitat type on taxonomic distinctness. Wieser (1959) has listed the species found

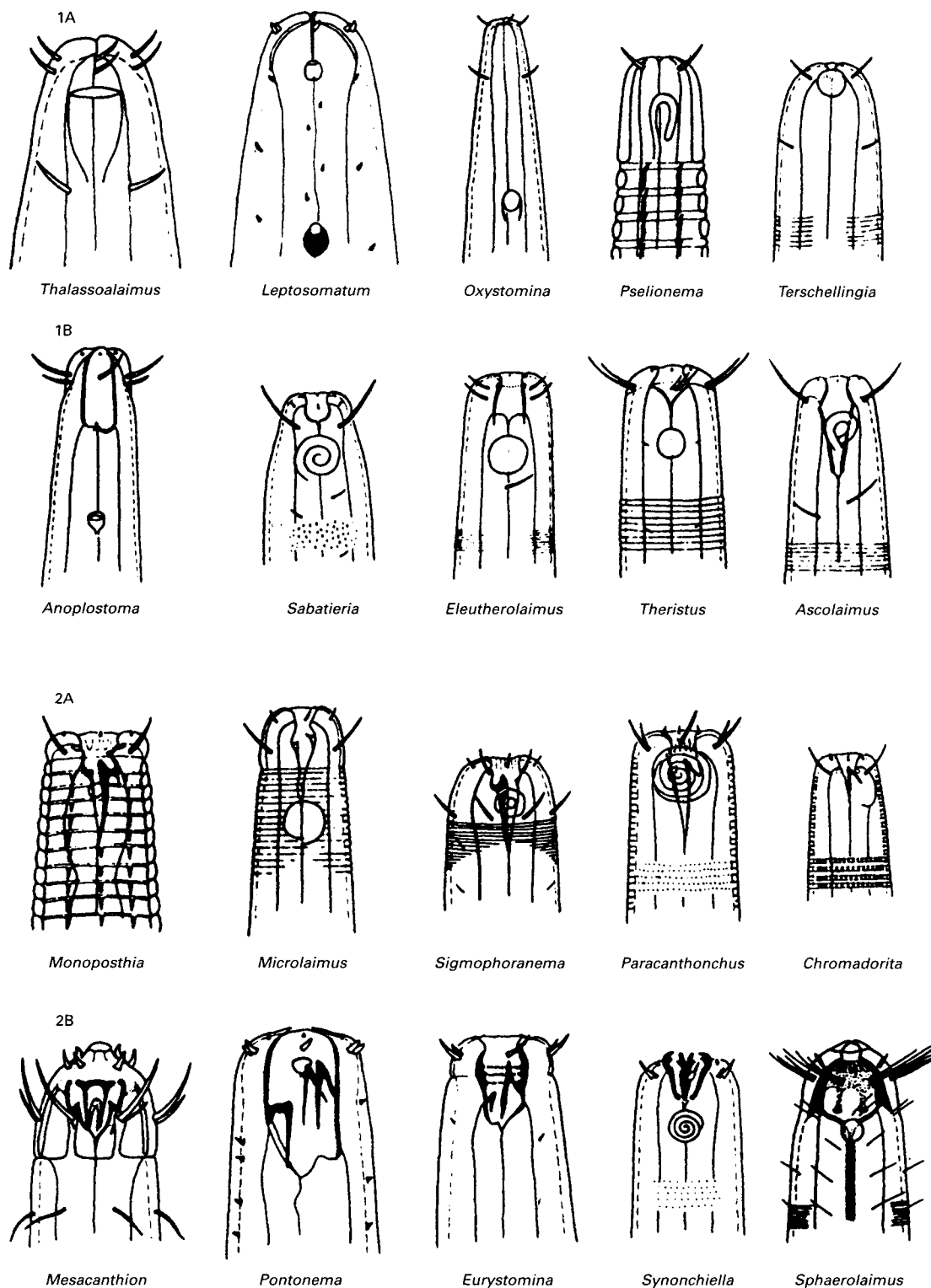


Fig. 1. Diagrammatic representation of the heads of marine nematodes, belonging to common British genera, representative of the four feeding groups. (1A) No buccal cavity, or a narrow tubular one, 'selective deposit feeders' ingesting bacterial-sized particles. (1B) Large unarmed buccal cavity, 'non-selective deposit feeders'. (2A) Buccal cavity armed with small or moderately sized teeth, 'epigrowth' or diatom feeders. (2B) Species with large teeth or jaws, the 'predator/omnivore' group.

in eight habitat types along the Chilean coast, seven of which have sufficient species and replication of sampling locations to make comparisons viable. These are: littoral exposed algae, littoral sheltered algae, littoral exposed sand, littoral sheltered sand, sublittoral secondary substrata (sponges, anthozoans, mytilids, echinoids, algae), sublittoral coarse bottom (stones, gravel, coarse sand) and sublittoral soft bottom (mud, fine sand). All these habitats were unpolluted. For Britain we examined a smaller range of unpolluted habitats: littoral sand (Scilly and Exe combined), estuarine mudflats (Exe and Tamar combined), intertidal algae (from Scilly only) and offshore soft sediments (Northumberland coast only), the data for each habitat being based on samples from multiple sites and sampling times.

For both the British and Chilean total species complements, taxonomic distinctness was calculated for the four feeding groups separately.

ANALYTICAL METHODS

Taxonomic distinctness is calculated as:

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

where the summation is taken over all species i, j , the number of species is s , and ω_{ij} is the taxonomic path length between species i and j (Clarke & Warwick 1998). Because of the way the taxonomic distinctness index is formulated it takes on a rather restricted range of values. Nevertheless, differences in these values can achieve significance. The significance of departure from random expectation was determined by comparison of the measured value of Δ^+ with the values of 1000 random selections of the same number of species from the total species pool (Clarke & Warwick 1998). For the case studies of environmental impact, the individual histograms (Δ^+ against frequency for the random selections) have been presented for comparison with the measured values, and also the values for all studies have been combined into a single figure by plotting them as points on a confidence funnel (confidence intervals for Δ^+ for a range of values for the number of species). For the studies of feeding and habitat types, only the latter form of presentation has been adopted, for economy of space.

Results

RELATIONSHIP BETWEEN TAXONOMIC DISTINCTNESS AND POLLUTION

Sublittoral sediments

Both the unpolluted Northumberland site and Tyne sewage sludge dumping ground samples have Δ^+ values at the lower end of the simulated distribution under the null hypothesis, but in neither case is there a significant departure at the 5% level. However,

Liverpool Bay, which is heavily polluted, has a Δ^+ value that is lower than any of the 1000 simulated values, indicating a significant departure at $P < 0.1\%$ (Fig. 2).

Intertidal sand beaches

The pristine sandy intertidal sites in the Isles of Scilly and the Exe have values close to the mode of the simulated distribution. Polluted sites in the Clyde studied by Lamshead (1986) have a Δ^+ value of 4.46, which is lower than any of the 1000 simulations and so leads to a significant departure ($P < 0.1\%$). When the three stations he regarded as polluted (4, 5 and 6) are considered alone, the Δ^+ value drops to 4.39, the lowest value found in any of the studies described in this paper. Those sites in the Clyde studied by Jayasree (1976) also show a significant departure ($P = 3\%$). Her sites in the Forth are at the lower end of the distribution, but they are marginally non-significant (Fig. 3).

Estuarine intertidal mudflats with reduced salinity

Compared with the previous two habitats, the results for the reduced salinity estuarine mudflats are less clear-cut because all values of Δ^+ are low in comparison to the simulated values. However, the rank order of distinctness is as expected. In the relatively clean Exe estuary Δ^+ is not significantly reduced, while the Tamar, which we have reason to regard as moderately polluted on the evidence of present and past human activities as noted above, has a lower Δ^+ than the Exe, significantly below the lower 95% confidence limit from the simulated values ($P = 2\%$). The Fal, as anticipated, has the lowest Δ^+ , and is also significantly below the simulated lower confidence limit ($P = 0.7\%$) (Fig. 4).

With respect to broader-scale regional species lists where the data for several habitats were amalgamated, the Isles of Scilly and the Exe estuary have Δ^+ values well within the 95% confidence limits of the simulated values, in fact they are both on the high side of this distribution (Fig. 5). As noted above, the Δ^+ for the polluted Liverpool Bay is lower than all 1000 simulated values.

All the above data are presented as points on the 95% confidence funnel in Fig. 6. Five points fall below the 95% confidence limits: the Clyde sand in two separate and independent studies, Liverpool Bay sublittoral sediments, and estuarine mudflats in the Fal and the Tamar. Four points fall within the 95% confidence limits, but towards the lower edge of the funnel: sand beaches in the Forth, sublittoral soft sediments off Northumberland and in the vicinity of the Tyne dumpground, and mudflats in the Exe estuary. Four points occur close to the mean value of Δ^+ (4.72): intertidal sand in the Isles of Scilly and the Exe,

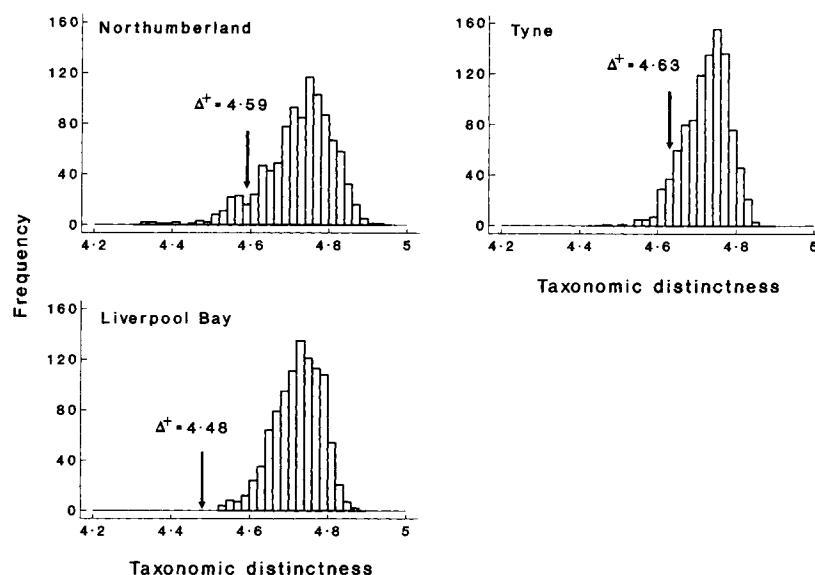


Fig. 2. Comparison of the measured value of Δ^+ for offshore nematode assemblages in Britain with a histogram of the values of 1000 random selections of the same number of species from the total British species list. Numbers of species are: Northumberland, 63; Tyne, 114; Liverpool Bay, 97.

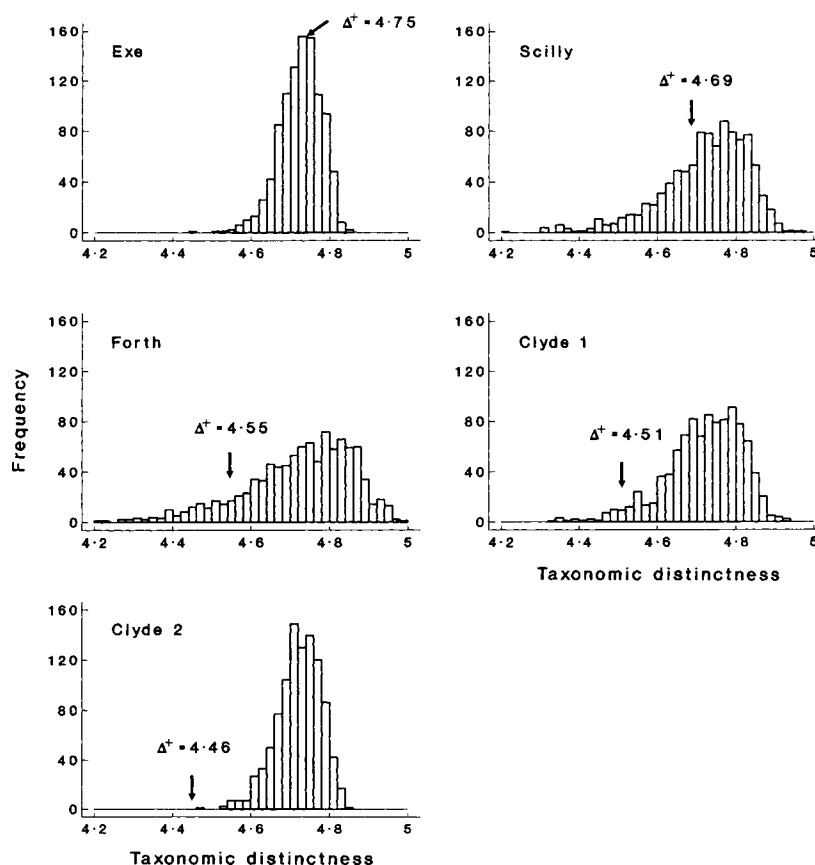


Fig. 3. Comparison of the measured value of Δ^+ for intertidal sands of the British coast with a histogram of the values of 1000 random selections of the same number of species from the total British species list. Clyde 1 = Irvine Bay (Jayasree 1976); Clyde 2 = Ettrick, Irvine and Ayr Bays (Lamshead 1986). Numbers of species are: Exe, 122; Scilly, 42; Forth, 27; Clyde 1, 53; Clyde 2, 111.

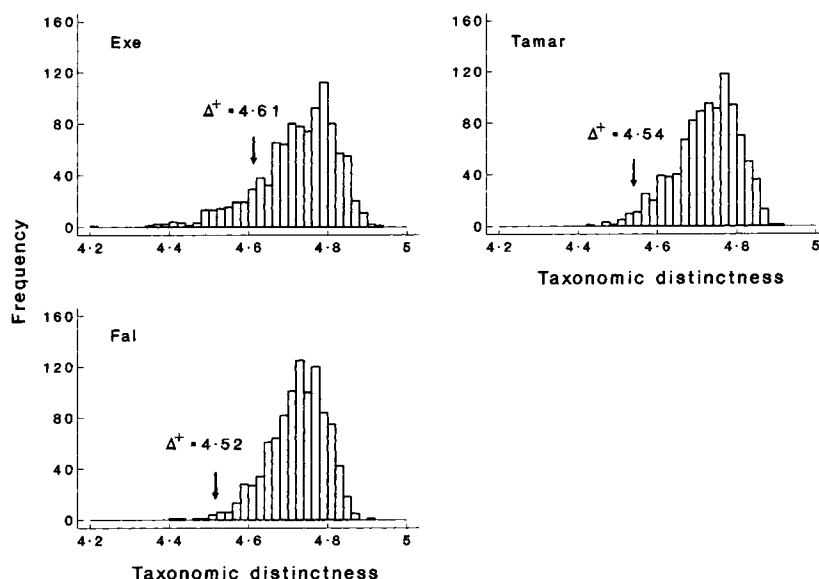


Fig. 4. Comparison of the measured value of Δ^+ for British estuarine mudflats with a histogram of the values of 1000 random selections of the same number of species from the total British species list. Numbers of species are: Exe, 48; Tamar, 66; Fal, 78.

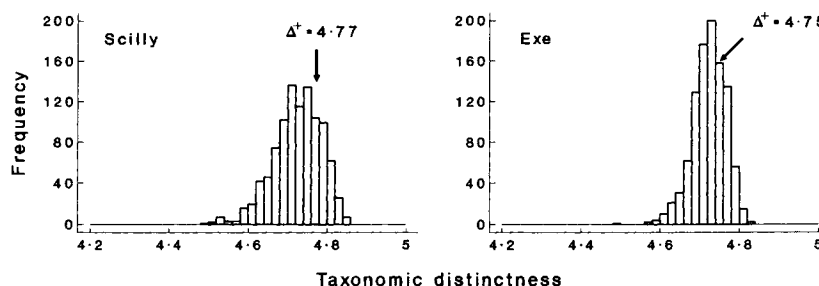


Fig. 5. Comparison of the measured value of Δ^+ for the combined data from various habitats in two British localities with a histogram of the values of 1000 random selections of the same number of species from the total British species list. Numbers of species are: Scilly, 102; Exe, 164.

and the combined data for all habitats in both the Isles of Scilly and the Exe.

THE INFLUENCE OF HABITAT TYPE

The taxonomic distinctness of nematodes in four of the seven Chilean habitats falls close to the mean value. These four habitats are: littoral exposed sand, sublittoral coarse bottom, sublittoral secondary substrata and littoral sheltered algae (Fig. 7a). One habitat (littoral sheltered sand) falls within the lower part of the confidence funnel, while two (exposed littoral algae and sublittoral soft bottom) are on the borderline of the lower 95% confidence limit of the simulated distribution.

Of the four habitat types considered for the British coast, the nematodes of intertidal sand (Scilly and Exe

data combined) and algae (eight sites on Scilly, five algal species at each) have Δ^+ values close to the mean value for all British nematodes (Fig. 7b). As noted above, the offshore soft sediments (three stations off the Northumberland coast) have a Δ^+ on the low side but within the 95% confidence interval of the simulated distribution. Estuarine mudflats (Exe and Tamar estuaries combined) have a Δ^+ on the borderline of the lower 95% confidence limit of the simulated distribution.

TAXONOMIC DISTINCTNESS FOR INDIVIDUAL FEEDING GROUPS

For the Chilean data, the taxonomic distinctness for individual trophic groups within the full inventory is markedly lower than values for equivalently sized

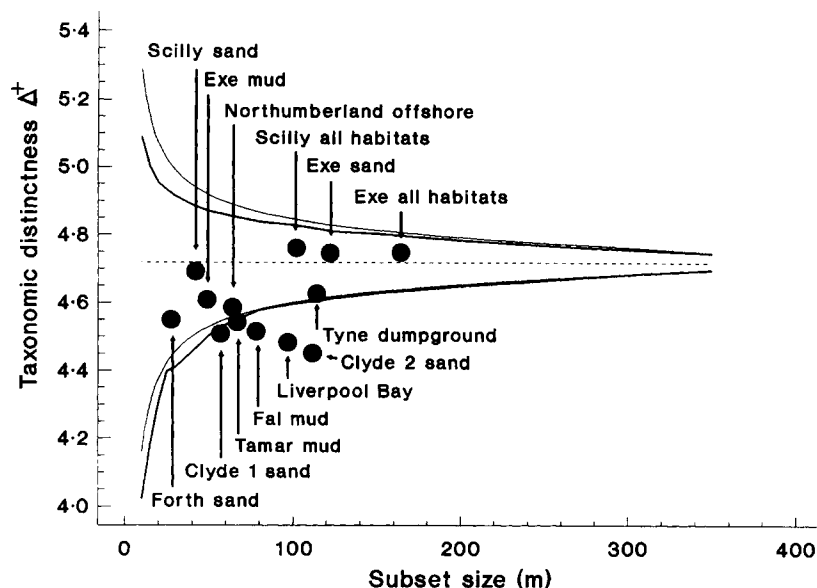


Fig. 6. Measured values of Δ^+ from the examples in Figs 2–5, plotted against the number of species (m) as points on the simulated 95% confidence funnel (thick lines, based on random selections from the total British species list) and theoretical 95% confidence funnel (thin lines, based on mean and variance formulae).

subsets of the total nematode fauna (Fig. 8a). Note that the randomization test is not really a valid formulation here, although the differences are clear-cut in any case. Group 1A (no buccal cavity, bacterial feeders) has the highest Δ^+ and group 1B (unarmed buccal cavity, non-selective deposit feeders) the lowest, with 2A (small teeth, diatom feeders) and 2B (large teeth or jaws, carnivores/omnivores) intermediate. A similar pattern is evident for the British data, but the value for the 1A feeding group is much closer to the mean value for all species (Fig. 8b).

THE RELATIONSHIP BETWEEN TROPHIC COMPOSITION AND TAXONOMIC DISTINCTNESS

The trophic structure of the UK nematode assemblages is compared in Fig. 9a, which is a two-dimensional non-metric multidimensional scaling ordination (MDS) (Kruskal & Wish 1978) based on the proportions of species in the four trophic groups in each study, and the Bray–Curtis measure of similarity (Bray & Curtis 1957) between every pair of studies. This can be thought of as a map in which the distance apart of the samples is a measure of their dissimilarity in trophic composition: note that the scaling and orientation are arbitrary. The long axis of this ordination represents a gradation from habitats that are free of fine particulate material (clean intertidal sands and algae) on the left to fine sedimentary habitats (estuarine mudflats) on the right. Habitat type thus has a major effect on trophic composition. The vertical axis of this ordination reflects the pollution status at

each location, with the non-polluted locations at the top and the polluted locations at the bottom of the configuration. Pollution effects are therefore also reflected in changes in trophic structure. In Fig. 9b circles that are scaled in size to represent the relative values of taxonomic distinctness (Δ^+) in the 12 studies are superimposed on this same ordination. From this figure it is clear that habitat type in itself does not have a major effect on taxonomic distinctness: the Δ^+ values are similar along the top of the ordination, which spans unpolluted locations with a wide range of habitat types. The major differences in taxonomic distinctness are between the non-polluted sites at the top of the ordination (high values) and the polluted ones at the bottom of the ordination (low values). In Fig. 9c,d circles that are scaled in size to represent the relative proportions of species in trophic group 1A (bacterial feeders) and 2B (predators/omnivores), respectively, are superimposed on the configuration. This shows that the polluted sites are characterized by a high proportion of 1A species and a low proportion of 2B. Similar plots for trophic groups 1B (non-selective deposit feeders) and 2A (diatom feeders) have a more even distribution across the configuration (data not shown), suggesting that they are not strongly influenced by either habitat type or pollution stress.

Discussion

The data suggest that the taxonomic distinctness of nematodes from environmentally degraded locations is reduced in comparison with that of more pristine

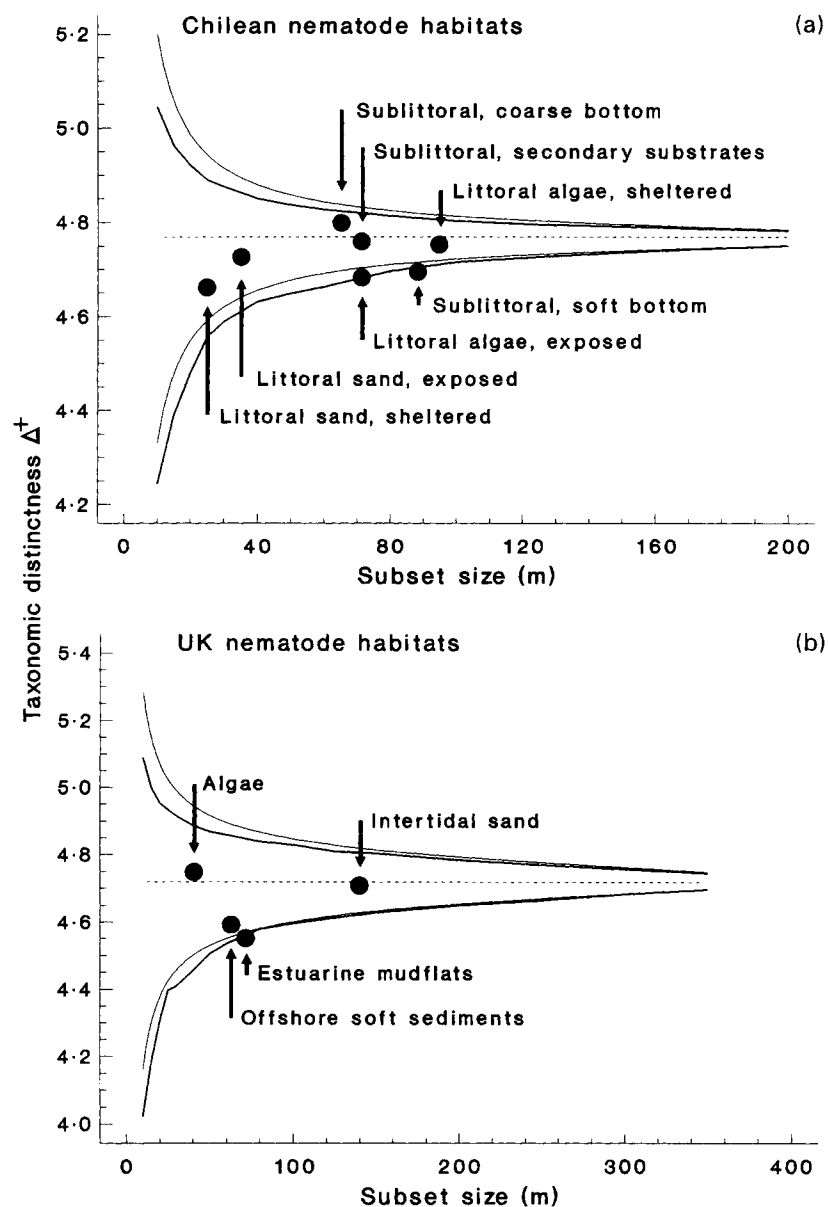


Fig. 7. (a) Measured values of Δ^+ from seven different habitat types on the Chilean coast, plotted against the number of species (m) as points on the simulated 95% confidence funnel (thick lines, based on random selections from the total British species list) and theoretical 95% confidence funnel (thin lines, based on mean and variance formulae). (b) as (a) but for four different habitat types in Britain.

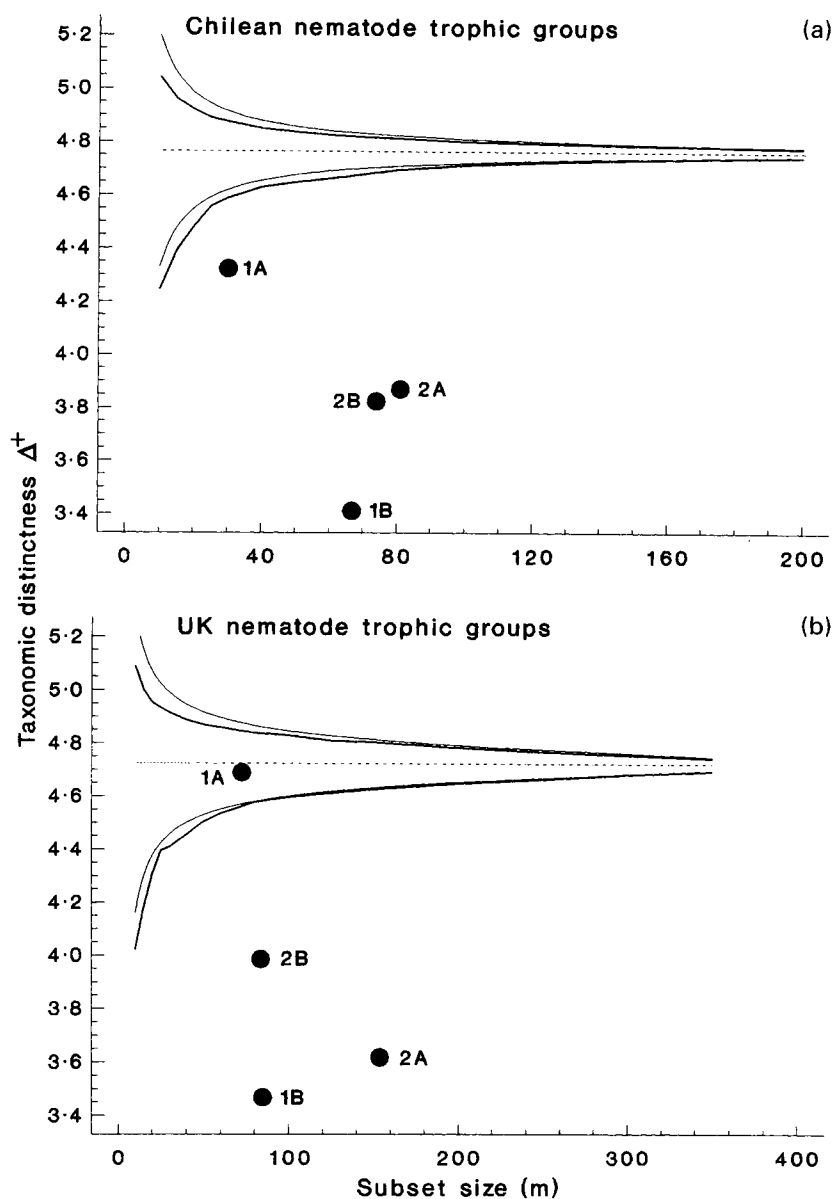


Fig. 8. (a) Values of Δ^+ for all nematode species recorded in Wieser's survey of the Chilean coast, divided into the four separate feeding groups and plotted against the number of species (m) as points on the simulated 95% confidence funnel (thick lines, based on random selections from the total Chilean species list) and theoretical 95% confidence funnel (thin lines, based on mean and variance formulae). (b) as (a) but for the British species list.

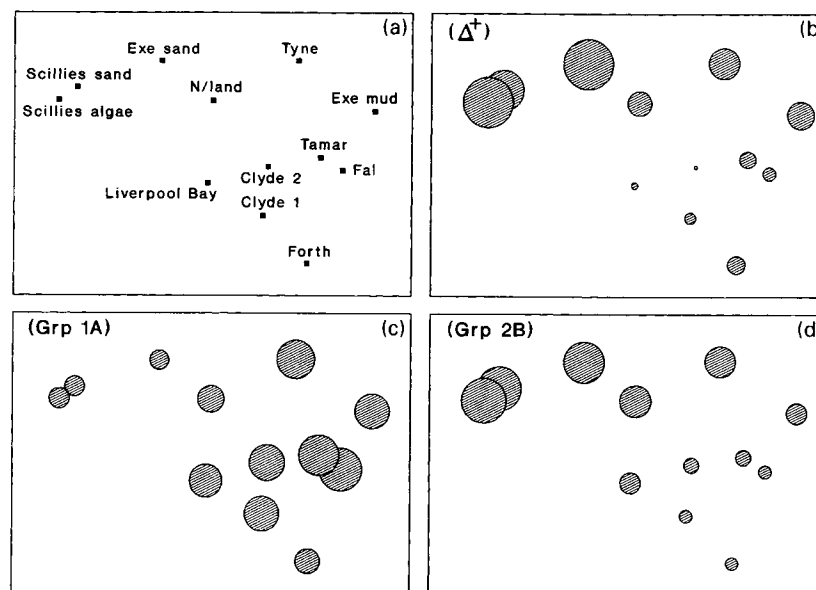


Fig. 9. (a) Two-dimensional MDS plot based on the proportions of nematode species in the four feeding groups, for the UK studies described in the text. (b) Circles that are scaled in size to represent the relative values of taxonomic distinctness (Δ^+) superimposed on this same ordination. (c and d) Circles that are scaled in size to represent the relative proportions of species in trophic group 1A (bacterial feeders) and 2B (predators/omnivores), respectively, superimposed on the same ordination.

locations, often significantly so. The exception to this seems to be in reduced salinity estuarine mud flats for which, at least in the three examples for which data were available, Δ^+ always seems to be low. Even in locations assumed to be relatively clean, it may be on the borderline of being significantly lower than the simulated distribution under the null hypothesis. We postulate that the measure of taxonomic distinctness reflects the effects of both ecological and evolutionary mechanisms which determine taxonomic composition, and that only a restricted number of taxa have evolved species capable of tolerating the physiologically stressful conditions that prevail in estuarine mudflats, with their reduced and strongly fluctuating salinity.

Clarke & Warwick (1998) have already stressed the advantage of the taxonomic distinctness index over traditional species richness indices as a measure of biodiversity, through its lack of dependence on sampling effort. Thus it is possible to compare biodiversity between localities or times for which the species inventories are in various states of completeness, assuming that the taxonomic rigour applied to the species identifications is uniform across taxa. On this basis the lack of standardization of taxonomic rigour between different workers should make no difference to the value of the distinctness index, which again is not a feature of species richness measures. Bias could arise through, for example, an expert in the taxonomy of a particular group of organisms recognizing many sib-

ling species in that group, but not doing the same for any other taxon. However, there is no reason to expect such a bias to be found only among workers at predominantly polluted sites, and it is reassuring both that an interpretable pattern of change in Δ^+ with putative pollution status does emerge (e.g. from Fig. 6) and that, in the one locality where different workers were sampling with different protocols (the two Clyde studies) the values of Δ^+ come out as significantly reduced and rather similar to each other, in spite of a very different number of recorded species.

The marine nematode data suggest two additional advantages:

1. 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 seem to fall below the lower 95% confidence limit for the simulated distribution under the null hypothesis. This ameliorates the problem encountered with species richness measures of biodiversity, which are much more strongly affected by habitat type and complexity, thus making comparisons difficult between data sets for which the habitat types studied might be different.
2. Taxonomic distinctness in marine nematodes is clearly related to trophic diversity, since individual trophic groups have Δ^+ values substantially below those for equivalently sized subsets of species that span all the trophic groups. Thus a reduction in trophic diversity will lead to a reduction in taxonomic

distinctness, although not necessarily to a reduction in species richness. Trophic composition is clearly affected by pollution (Fig. 9a), but unlike taxonomic distinctness is strongly influenced by habitat type. This relation to functionality, and hence ecological relevance, is another potential advantage of the taxonomic distinctness measure over species richness measures of biodiversity, for environmental impact assessment.

Testing the significance of departures in taxonomic distinctness from expectation requires a relatively comprehensive list of the species representative of the regional species pool, but this does not need to approach completeness (the lists of nematodes from Britain and Chile are certainly far from complete). The requirement is for a list that is representative of the range of habitats present in the region and that is substantially longer than the list for the location under test. The regional list will almost inevitably include data from the individual locations being compared, but this in no way invalidates the procedure.

In conclusion, we suggest that taxonomic distinctness may prove to be a biologically and ecologically relevant measure of biodiversity, with a number of theoretical and logistical advantages over species richness measures for the purposes of environmental impact assessment. However, the work described here is obviously restricted in its coverage, and much more work needs to be done to broaden the range of taxa studied, the range of habitats and of geographical regions, before any generality can be attached to our findings.

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