

Average functional distinctness as a measure of the composition of assemblages

Paul J. Somerfield, K. Robert Clarke, Richard M. Warwick, and Nick K. Dulvy

Somerfield, P. J., Clarke, K. R., Warwick, R. M., and Dulvy, N. K. 2009. Average functional distinctness as a measure of the composition of assemblages. – ICES Journal of Marine Science, 65.

Indices are used to quantify change in the environment by reducing aspects of environmental complexity to numbers. Biodiversity indices are typically calculated using the numbers of species and their relative abundances. A recent advance has been the development of additional measures of diversity, such as phylogenetic diversity, based on relationships between organisms. The emerging paradigms of the importance of biodiversity to ecosystem services and the ecosystem approach to fishery management could be well served by the development of indicators of ecosystem functioning. We discuss how relatedness measures may be adapted to quantify aspects of community structure of relevance to ecosystem functioning, by combining information on species' occurrence, life history, and ecological traits. We present an index that reflects average functional distinctness within assemblages. We illustrate the approach using North Sea fish. Results reveal that average functional distinctness is not independent of taxonomic distinctness. This is expected, but the weakness of the relationship suggests that both indices may prove useful, because they are not constrained to convey the same information about samples. Both indices are shown to be weakly related to species richness, which was not expected. This is a consequence of differences in the frequencies of occurrence among species.

Keywords: biodiversity, functional distinctness, marine, monitoring, relatedness, taxonomic distinctness.

Received 23 November 2007; accepted 21 May 2008.

P. J. Somerfield, K. R. Clarke, and R. M. Warwick: Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK. N. K. Dulvy: Department of Biological Science, Simon Fraser University, Burnaby, BC, Canada V5A 1S4. Correspondence to P. J. Somerfield: tel: +44 1752 633100; fax: +44 1752 633101; e-mail: pjs@pml.ac.uk.

Introduction

Human activities are changing the environment on scales ranging from local to global, leading to sometimes drastic alterations in the structure and composition of ecological communities and prompting research into the possible consequences of such changes for the functioning of ecosystems and derived ecosystem services (Loreau *et al.*, 2001; Hooper *et al.*, 2005). However, no clear relationship between species diversity and ecosystem functioning has been demonstrated, although it would be useful in predicting the consequences of changes in species richness and composition, or biodiversity in general, on ecosystem properties. This is despite more than a decade of high-profile research into the relationships between diversity (generally species diversity) and environmental processes (such as nutrient cycling or biomass accumulation). Functional diversity, i.e. the diversity and range of functional traits possessed by the biota of an ecosystem (Wright *et al.*, 2006), is likely to be the component of biodiversity most relevant to the functioning of ecosystems (Hooper *et al.*, 2002, 2005; Heemsbergen *et al.*, 2004), but there is no simple, standardized measure (Petchev and Gaston, 2002, 2006), and quantifying functional diversity can be difficult (Hooper *et al.*, 2005).

Indices reflect our desire to quantify change in the environment by reducing aspects of environmental complexity to numbers with which we may detect and measure change. As such, an index may be adopted as an indicator for management purposes if it meets

necessary criteria (Rice, 2003; Leonard *et al.*, 2006). Indicators of marine biodiversity change may take many forms and vary in their ecological relevance and validity (Féral *et al.*, 2003). Indices of biodiversity of selected taxa, whether of intrinsic scientific interest, for environmental-impact assessment, or used as a proxy for overall biodiversity, are generally expressed in terms of the number of taxa present (species richness), the distribution of relative abundances of taxa within samples (dominance or evenness), or measures that aim to combine and balance both dimensions (e.g. Shannon–Wiener diversity). Indices of α -diversity (sample or local diversity) may be formulated in terms of species richness and/or evenness. For large scales, only the species-richness component is relevant: γ -diversity (regional diversity) is no more than the number of species in a region (Rosenzweig, 1995).

Measures based on species richness and most dominance or evenness measures present a number of problems as biodiversity and environmental assessments (Leonard *et al.*, 2006). Critically, they are sample-size or sampling-effort dependent. This is particularly problematic when comparing data collected by sampling methods that are difficult to standardize in terms of effort or sample size. There is no statistical framework for testing whether species richness is higher or lower than expected for a given location or region. Testing for significant differences depends on the selection of appropriate sites to act as controls or reference conditions, but problems may arise unless habitat type and complexity are strictly comparable, which is rarely the case.

Recognizing that useful measures of biodiversity can be derived from the “relatedness” of species (Harper and Hawksworth, 1994), Warwick and Clarke (2001) described a range of measures based on the taxonomic spread of species within samples, rather than the number of species. Using simulations based on the null expectation that the species present at any one place or time behave like a random selection from the species pool (or in other words, every species in the pool has an equal probability to exist at all locations or times), Clarke and Warwick (1998) demonstrated that pairwise average taxonomic distinctness (Δ^+) overcame most of the problems of species-richness measures and had a number of desirable properties as an indicator of biodiversity, notably a lack of dependence on sampling effort. They devised a randomization test to compare the observed value of Δ^+ against an “expected” value derived from a “master list” of species (the species pool). Random subsamples (n is typically 1000) of a set number of species, drawn from the species pool, are used to calculate the null distribution of Δ^+ values for that number of species. If the procedure is repeated for different numbers of species, the expected values can be used to plot a 95% probability funnel. The question of whether a sample has a “smaller than expected” or “greater than expected” taxonomic spread for the number of species present is addressed by examining whether the observed value lies below or above the 95% funnel (Clarke and Warwick, 1998). If the values of taxonomic distinctness from a variety of unperturbed habitats fall within the confidence limits of this distribution and impacted locations fall outside of it, 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 (Leonard *et al.*, 2006). The approach has been applied successfully to a range of taxa, including nematodes (Clarke and Warwick, 1998) and fish (Rogers *et al.*, 1999; Leonard *et al.*, 2006).

Although there are good reasons for monitoring biodiversity, underpinned by national commitments and agreements, what about monitoring, maintaining, and managing how ecosystems work (“function”)? There is no clear relationship between species richness and functional diversity. For example, a reduction in trophic diversity will not necessarily lead to a reduction in species richness. It can be argued that indices that take into account taxonomic or phylogenetic relationships between organisms may be more likely to reflect the functional composition of assemblages, although this has not, to our knowledge, been tested. We describe how the idea of taxonomic relatedness among species may be extended to incorporate functional relatedness among species, and we consider how this may be used to derive functional indices. We go on to compare and contrast the formulation and behaviour of such an index with one based on taxonomic relationships. We exemplify our approach with groundfish assemblages in the North Sea, a group of organisms for which functional-trait information is available or can be derived, for which occurrence data are available, and in which functional changes can be considered indicative of changes in environmental condition of relevance to management.

Material and methods

Occurrence data

The English groundfish survey is conducted annually in autumn and aims to estimate the abundance, size, and species composition of fish at locations throughout the North Sea (Maxwell and

Jennings, 2005). We used data from 1991 to 1995. Samples were collected with a Grand Ouverture Verticale (GOV) trawl fitted with a codend liner of 20 mm stretched mesh, hauled for 30 min (Maxwell and Jennings, 2005). All fish caught were identified and measured. Species were excluded if <150 individuals have been caught in the history of the survey and the North Sea is outside the main part of their range, whereas samples were excluded if they contained fewer than five species. This left us with 70 species and their occurrences in 87 samples in 1991, 74 in 1992, 71 in 1993, 73 in 1994, and 72 in 1995, 377 in total.

Taxonomic information

Nomenclatural changes through the years, including synonyms, were corrected. A taxonomic hierarchy was constructed based on Eschmeyer (1990) and Howson and Picton (1997) with five levels: species, genera, families, orders, and classes.

Trait information and coding

There is no standard or agreed method for collating functional information. Information on life history and ecological traits for each species (Table 1) was compiled using a range of sources, starting with Fishbase (1999), then searches of primary literature, regional guidebooks, and species catalogues. Any trait for which information was available, or could be inferred, for all 70 species was included.

Some traits are continuous, such as average trophic level or egg size, whereas others are categorical—a species is either anadromous or it is not. We converted all traits to a series of binary possibilities by scoring the trait as 1 if a species falls within a trait category and 0 if it does not. Although apparently straightforward, such an approach masks a number of possibilities. Species were considered to possess the assigned trait category throughout their life cycle. Thus, a species could score 1 for a range of weights or lengths, for example. The number of categories into which a continuous scale is divided provides an implicit weighting for that trait in the next step in the analysis. With this in mind, we limited continuous variables to four categories (Table 1). A binary pair of traits that are mutually exclusive (e.g. brooder or broadcast spawner) could be represented by a single column (either brooder or broadcast spawner), but this would downweight this aspect of each species’ ecology compared with other groups of traits. Therefore, both columns were kept in the matrix.

Trait similarities between species

Having developed and coded the trait matrix, the next step is to choose a resemblance measure to reflect how similar each species is to every other species in the functional traits it possesses. There is a range of possibilities here, depending on how one considers the multivariate structure within the matrix (Clarke *et al.*, 2006). We chose to use the simple matching coefficient:

$$S_{ij} = 100 \frac{a + d}{a + b + c + d},$$

where a is the number of traits common to species i and j ; b the number possessed by i and not j ; c the number possessed by j and not i ; and d the number possessed by neither.

This similarity measure is scaled to vary between 0 (no traits in common) and 100 (all traits identical) and can be expressed as a percentage. Unlike more widely used similarity measures, such as Bray–Curtis (which for these presence–absence data is simply

Table 1. Trait groups for which data were collated for all 70 fish species, categories into which trait groups were divided, and functional scores for a subset of fish species: 1, species has trait (category); 0, species does not have trait (category).

Trait groups	Category	Subset of species*							
		Eg	Ga	Gm	Gg	Gc	Hd	Hp	Hh
Length (mm)	L > 800	0	0	1	1	0	0	0	1
	L > 400	1	0	1	1	1	1	0	1
	L > 200	1	0	1	1	1	1	1	1
	L > 100	1	1	1	1	1	1	1	1
Weight (g)	W > 10 000	0	0	1	1	0	0	0	1
	W > 1 000	0	0	1	1	0	1	0	1
	W > 100	1	0	1	1	1	1	1	1
	W > 10	1	1	1	1	1	1	1	1
Habitat	Pelagic	0	1	0	0	0	0	0	0
	Demersal	1	0	1	1	1	1	1	1
Body shape	Flat	0	0	0	0	1	0	1	1
	Round	1	1	1	1	0	1	0	0
	Elongate	0	0	0	0	0	0	0	0
	Laterally flat	0	0	0	0	0	0	0	0
Motility	Mobile	1	0	0	0	1	1	0	0
	Sedentary	0	1	1	1	0	0	1	1
Trophic level	>5	0	0	1	0	0	0	0	0
	>4.5	1	0	1	0	0	0	0	1
	>4	1	0	1	1	1	0	1	1
	>3.5	1	1	1	1	1	1	1	1
Life history	Anadromous	0	0	0	0	0	0	0	0
	Marine/estuarine	1	0	0	0	0	0	0	0
	Fully marine	0	1	1	1	1	1	1	1
Spawning	Broadcast	1	1	1	0	1	1	1	1
	Brooder	0	0	0	1	0	0	0	0
Egg location	Demersal eggs	0	0	0	0	0	0	0	0
	Pelagic eggs	1	1	1	0	0	1	1	1
E (mm)	>10	0	0	0	1	0	0	0	0
	1–10	1	0	1	0	1	0	1	1
	<1	0	1	0	0	0	1	0	0

Note pseudo-log scales for division of continuous traits (length = L, weight = W, average egg size = E).

*Eg: *Eutrigla gurnardus*; Ga: *Gadiculus argenteus*; Gm: *Gadus morhua*; Gg: *Galeorhinus galeus*; Gc: *Glyptocephalus cynoglossus*; Hd: *Helicolenus dactylopterus*; Hp: *Hippoglossoides platessoides*; Hh: *Hippoglossus hippoglossus*.

the Sørensen coefficient), the simple matching coefficient is influenced by joint absences (0, 0), but this makes sense in the present context because species may be considered similar if neither possesses a certain trait.

Calculating a functional-diversity index

The next step is to calculate an index to reflect the similarity among species, in terms of functional traits, within each sample. Taxonomic distinctness (Δ^+) was described by Clarke and Warwick (1998) as the average path or branch length between species occurring in a sample, through a taxonomic hierarchy or phylogenetic tree. Many relatedness measures have the idea of a taxonomic tree explicit in their definition. For example, Faith's (1992, 1994) phylogenetic diversity (PD) is the total branch

length in the tree. Thus, one approach would be to submit the trait-resemblance matrix to a clustering algorithm, such as hierarchical agglomerative clustering, to produce a dendrogram (Petchev and Gaston, 2002). The trouble with this approach is that a dendrogram is merely a constrained representation of the full multivariate information contained in the trait-resemblance matrix, and the structure of the dendrogram is sensitive to the linkage method used. Although it makes sense to think of trees when considering taxonomic information, with a hierarchical, fixed set of levels, there is nothing fixed about the levels of functional similarity between species, which are likely to be much more continuous. The key here is to abandon the hierarchy altogether and use the resemblance information directly. Therefore, we define average functional distinctness (X^+ , from χαρακτηριστικό, meaning a trait) simply as the average resemblance among species in a sample. Incidentally, the same logic may be applied to Δ^+ . Once branch lengths are defined between taxonomic levels, a matrix of resemblances (Euclidean distances) between species becomes implicit, and the index is the average resemblance between species. Although a tree may help in the interpretation, it is not required for the calculation of the index, unlike for measures requiring a tree by their definition.

Implementation

Routines were implemented in Primer version 6 (Clarke and Warwick, 2001; Clarke and Gorley, 2006). Calculation of relatedness measures and associated simulations using resemblance matrices and calculation of resemblance matrices from an aggregation file were carried out in a developmental version of the software (Primer 6 and PERMANOVA+ β 18).

Results

The continuous nature of differences between species in trait space is illustrated by multidimensional scaling (MDS; Figure 1a), based on trait resemblances between species, and contrasts markedly with the strong clustering structure displayed in a similar analysis based on a resemblance matrix derived from the equivalent taxonomic hierarchy (Figure 1b). The implication is that X^+ has the potential to behave differently from Δ^+ . For example, the large distances in the plot derived from the taxonomic hierarchy that reflect differences between classes are not reflected to the same extent in differences between species in terms of their functional traits. The two measures are positively related (slope = 0.2). Although the linear relationship is weak ($R^2 = 0.11$), it is significant ($p < 0.01$) owing to the large number of degrees of freedom ($\nu = 375$).

A funnel plot for X^+ based on all species having an equal probability of occurring in samples, on which the sample values from all 377 samples are overlain (Figure 2a), demonstrates that most samples (71%) fall below the lower 95% probability limit. Therefore, we reject the null hypothesis that the functional composition of fish assemblages in the North Sea behaves as though species are assembled at random from the regional species pool.

To consider the hypothesis in more detail, why should all species have the same probability of occurring in all samples? Some species are common and tend to occur everywhere, whereas others are relatively rare and do not. Among the samples examined, five species occur in >80% of samples, whereas 20 occur in <2%. An alternative null hypothesis is that the functional composition of assemblages in samples behaves as though species are assembled at random from the master list,

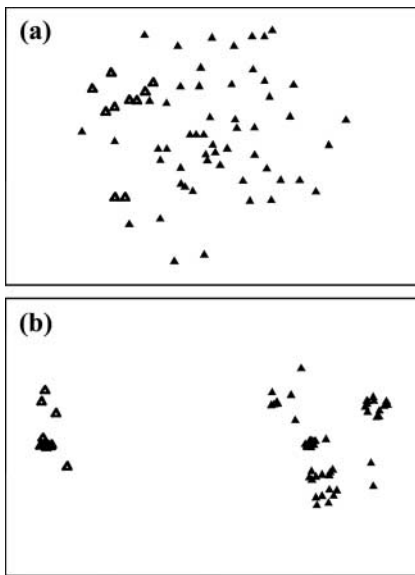


Figure 1. Ordination of fish species (filled triangle, Osteichthyes; open triangle, Chondrichthyes) by non-metric MDS (no interpretable axes): (a) based on the simple matching coefficient calculated between pairs of species using trait scores (stress = 0.18); and (b) based on distances through a taxonomic classification (stress = 0 as the algorithm has no difficulty reproducing a two-dimensional structure in two dimensions; note the relatively strong clustering).

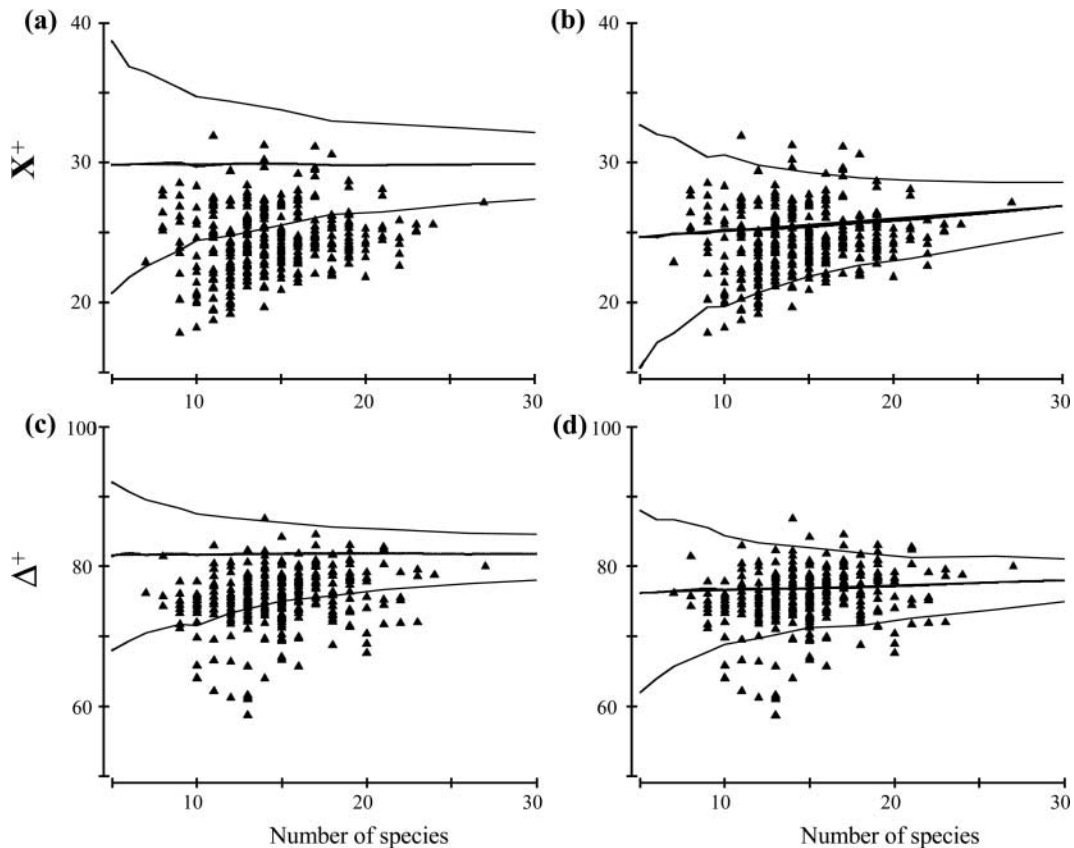


Figure 2. (a, b) Average functional distinctness (X^+) and (c, d) average taxonomic distinctness (Δ^+) against numbers of species of fish in all 377 samples (closed triangle) in relation to the “expected” value (and its upper and lower 95% probability limits) of these indices as derived from 1000 subsamples from the list of 70 fish species for a range of species subset sizes: (a, c) as derived by random subsampling of the full list; and (b, d) as derived from the full list using subsampling constrained by the frequency of occurrence of species across all samples.

but the probability of species occurring depends on their frequency of occurrence across all samples. To address this hypothesis, the simulation of random draws from the master list was constrained to match the probabilities of occurrence of each species as defined by their frequency of occurrence in the complete dataset. Thus, certain species were picked more often in the random subsets because they are observed more often in real samples.

The probability funnel for X^+ , derived using frequency-based random draws (Figure 2b), demonstrates that the corresponding null expectation is a sensible one because most samples (87%) fall within the funnel. The simulated mean now increases with the number of species in the random subsets, although the increase is small on the scale of the probability limits. Thus, a positive relationship between X^+ and the number of species in samples (S) is to be expected. For these samples, $X^+ = 0.158 S + 22$. Although significant ($p < 0.01$; $\nu = 375$), the relationship is weak ($r^2 = 0.047$).

The same issue applies to Δ^+ (calculated from the taxonomic resemblances underlying Figure 1b), because 29% of sample values fall below expectation under a hypothesis of random assembly with equal probabilities (Figure 2c), whereas 87% lie within a funnel derived from frequency-based random draws (Figure 2d). Again, there is a weak but significant ($r^2 = 0.041$; $p < 0.01$) increase in values with increasing numbers of species in samples ($\Delta^+ = 0.237 S + 72$).

Discussion

It should come as no surprise that a measure calculated from trait-based resemblances among species (X^+) behaves in a fashion similar to an identically formulated measure (Δ^+) calculated using taxonomic relationships among species. Because information about the possession of particular traits underpins the classical taxonomy of species, closely related species tend to share traits. What is, perhaps, surprising is that the relationship between the two is not stronger. The fact that it is not leads us to believe that the functional-diversity measure provides additional information with which to examine changes in assemblages.

It is arguable, but we believe that ideally a functional index should not depend on species richness, constrained to increase or decrease with changes in species numbers simply because the two measures are structurally related. If they are, then change in the former is simply a proxy for change in the latter. If, on the other hand, a functional index that has been demonstrated to be structurally independent turns out to be positively (or negatively) correlated with species richness in observations taken from the real world, then these correlations may allow a useful interpretation. Clarke and Warwick (1998) demonstrated that Δ^+ is independent of sampling effort (i.e. of number of species observed), using random draws from a large and real species pool. They used this finding in constructing a test of their hypothesis that, in non-impacted conditions, Δ^+ behaves as though species are drawn at random from a regional species pool, motivated by the observation that impacted marine benthic assemblages tend to be dominated by groups of closely related species (Warwick and Clarke, 1995). For both the simulations and the test, they used equal probabilities of selection for all species. It may well be that, for some analyses, equal probabilities of occurrence represent a sensible hypothesis (Hubbell, 2001), in which case it is valid to assume that the index is independent of sampling effort. Tests of this hypothesis, using species lists of nematodes from a variety of studies, successfully discriminated degraded locations from undegraded ones (Clarke and Warwick, 1998). Subsequent studies have reported similar results for organisms as diverse as fish (Rogers *et al.*, 1999; Leonard *et al.*, 2006), epibenthos (Callaway *et al.*, 2007), macrobenthos (Somerfield *et al.*, 2006), macroalgae (Ceschia *et al.*, 2007), freshwater insect communities (Campbell and Novelo-Gutierrez, 2007; Marchant, 2007), and vascular plants (da Silva and Batalha, 2007). For North Sea fish, an unquestioning adoption of a testing structure based on a particular conceptual model (decreasing distinctness indicates stress) and a particular statistical model (all species have equal probabilities of occurrence) could be taken as providing evidence that many of the areas sampled are being impacted by some sort of stress. However, such a conclusion should not be drawn until it is demonstrated that, under non-impacted conditions, the taxonomic or functional composition of fish assemblages in the North Sea does behave as though species are assembled at random. A problem is that, arguably, all fish assemblages in the area may already be impacted.

Instead, we chose to reject the initial hypothesis and to formulate an alternative one, modifying the probabilities of selection of species in random draws in proportion to their relative frequencies of occurrence across samples. We demonstrate that the two different measures of the structure (X^+ and Δ^+), constructed in a similar fashion though from different underlying information, are not completely independent of sampling effort because of a weak tendency of both to increase with increasing species richness.

Furthermore, we demonstrate that the null expectation of equal probabilities of occurrence for all species underlying Clarke and Warwick's (1998) test is not appropriate for these fish assemblages. The distribution of sample values is consistent with the alternative hypothesis. Assessment of the extent to which these findings are applicable to other datasets is a subject for further research, but it may be that features of the dataset investigated, such as the wide range of frequencies of occurrence among species (from >98% of samples to single samples), the large number of samples available (377), or possibly aspects of the underlying ecology and distribution of the species involved, have influenced the results. Alternatively, the tendency of the average distinctness between species to increase as the number of species in a sample increases may represent a general feature, in which case it ought to be taken into consideration in all analyses.

The use of null models in ecology has a long (Lomolino *et al.*, 2004) and often divisive (Weiher and Keddy, 1999) history, and it is not our intention to review it here. According to Tokeshi (1986), however, a null model should include every feature of the observed data except the one it intends to test. If frequencies of occurrence of species vary widely, this feature is probably one that should be included. However, having done so, there are still departures from expectation that may be amenable to interpretation.

We recognize that, in addition to average taxonomic distinctness Δ^+ (Clarke and Warwick, 2001), there are other taxonomic relatedness measures incorporating information about relationships between individuals within samples (e.g. taxonomic diversity Δ and taxonomic distinctness Δ^*), about the number of species in samples (total taxonomic distinctness $S\Delta^+$), or about other aspects of the relationships between species (variation in taxonomic distinctness Λ^+). Functional resemblance-based versions of all indices in this family may be calculated, and their behaviour needs to be explored in real-life situations. Similarly, additional relatedness measures have been calculated using functional information whose behaviour needs to be explored and described. We do not intend to review these in detail here but will mention just two. Rao's (1982) Quadratic Entropy is closely related to Δ^+ . Botta-Dukát (2005) described a version derived using functional information, and Leps *et al.* (2006) made recommendations for its derivation and application. Petchey and Gaston (2002) described a measure they called FD, which is Faith's (1992) PD calculated from distances through a dendrogram derived using a slightly different set of choices from those described above. PD (and by implication FD) is highly dependent on the number of species in samples (Warwick and Clarke, 2001). We are not aware of any studies that have examined the effect of differences in the frequency of occurrence on the behaviour of these measures.

Apart from reviewing the range of measures available, their structural similarities and differences, and how these will influence their behaviour for purely mathematical reasons, much work needs to be done on methods of collating functional information and calculating resemblances (and hence measures) in a standardized manner. Although scientists working in different places and on different datasets may agree on a basic taxonomy to use, and hence may consider the values of indices derived using that taxonomy to be comparable, we are a long way from being able to apply similar thinking to functional measures. For example, we included both length and weight among the traits used to calculate similarities between species. As these traits are undoubtedly highly correlated, it may be argued that to do so gives too much weight to differences in size between species. A counterargument,

however, could be that, because the asymptotic length of species is a key functional trait underpinning many aspects of the life histories of North Sea fish (Gislason *et al.*, 2008), giving size additional weight may be appropriate.

In addition to the potentially huge difficulties associated with getting any useable trait information for most groups of organisms, there is no agreement about the best way to use the information once gathered. Functional traits may be defined as those that influence ecosystem properties or species' responses to environmental conditions (Hooper *et al.*, 2005). One school of thought promotes the view that one should examine only those traits "relevant" to the property or response under consideration (Petchey and Gaston, 2006). This strikes us as a circular argument. Selecting *a priori* to include only traits thought to be likely to respond also misses the opportunity to see how traits may be responding, whose relationship with the property or response under consideration may not be clear. Our approach has been to include all traits, and there is a body of multivariate theory and methods that may be brought to bear to decide which traits, or combinations of traits, are determining species' responses under different conditions. Traits determining responses to environmental drivers may differ from those that influence ecosystem properties, and different studies have tended to focus on one group or the other (Petchey and Gaston, 2006). Understanding links between the two is an important challenge and is critical to understanding the dynamics of ecosystem functioning in a changing world (Hooper *et al.*, 2005). Focusing the definition of functional types on specific ecosystem properties or processes presents the difficulty that those traits are not necessarily relevant to other properties or processes.

The indices that have been found so far to be most useful to large-scale management are not based on counts or amounts of things, but on averages within ecosystem components, calculated in such a way as to convert categorical information into a continuous scale. The Marine Trophic Index (Pauly *et al.*, 1998; Pauly and Watson, 2005), selected by the Convention for Biological Diversity in 2004 for immediate testing for monitoring progress towards the 2010 target of halting the rate of biodiversity loss and the only "headline biodiversity indicator" agreed for marine biodiversity in Europe, reflects the average trophic level of fish caught (or landed) in a region. The AZTI Marine Biotic Index (Borja *et al.*, 2000, 2003), widely incorporated into plans for the implementation of the EU Water Framework Directive, is a weighted average (within assemblages) of species scores according to their sensitivity to anthropogenic stress. These two indices share a number of properties: they require *a priori* knowledge of the biology of the species involved, and they are based on evidence about how ecosystem components (assemblages) change in response to anthropogenic stresses. As such, they may be considered to represent measures of the functional composition of assemblages. Their similarity in philosophy (based on averages, using species-specific information) and successful application gives us faith that a properly researched and constituted index of functional relatedness between species has the potential to provide information of use to the future management of the seas.

Ed Ricketts, writing in early 1948 (shortly before his death), foresaw such an approach. Based on his observation that the assemblages of species present in different places were not the same whereas representatives of specific functional types tended to be present within each assemblage, he concluded that "Of course the 'answer' is that an integration of all this would give a

true picture of ecology. But all of these things could be tied in together by a true ecology in which the important thing is neither the region, nor the association, nor the animal itself, nor its various stages or needs, nor even the ecological niche, but in which the unit is the relationship. And that could be an exact and a satisfyingly quantitative science in which the vectors representing these relationships – their direction, extension and strength or intensity – would be considered and evaluated" (Ricketts, 2006). This is an idea whose time has come.

Acknowledgements

This work was funded by the UK government's Defra (Project No. ME3109) and builds on previous work with Cefas Lowestoft (Project No. MF0731) led by S. Jennings. KRC and RMW acknowledge their positions as honorary fellows of the Plymouth Marine Laboratory, and KRC of the Marine Biological Association of the UK. We thank R. Gorley for programming routines specifically for this work. We thank S. Greenstreet, A. Rijnsdorp, and N. Daan for their constructive comments on the manuscript.

References

- Borja, A., Franco, J., and Perez, V. 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin*, 40: 1100–1114.
- Borja, A., Muxika, I., and Franco, J. 2003. The application of a marine biotic index to different impact sources affecting soft-bottom benthic communities along European coasts. *Marine Pollution Bulletin*, 46: 835–845.
- Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16: 533–540.
- Callaway, R., Engelhard, G. H., Dann, J., Cotter, J., and Rumohr, H. 2007. A century of North Sea epibenthos and trawling: comparison between 1902–1912, 1982–1985 and 2000. *Marine Ecology Progress Series*, 246: 27–43.
- Campbell, W. B., and Novelo-Gutierrez, R. 2007. Reduction in odonate phylogenetic diversity associated with dam impoundment is revealed using taxonomic distinctness. *Fundamental and Applied Limnology*, 168: 83–92.
- Ceschia, C., Falace, A., and Warwick, R. 2007. Biodiversity evaluation of the macroalgal flora of the Gulf of Trieste (northern Adriatic Sea) using taxonomic distinctness indices. *Hydrobiologia*, 580: 43–56.
- Clarke, K. R., and Gorley, R. N. 2006. *Primer v6: User Manual/Tutorial*. Primer-E Ltd, Plymouth, UK.
- Clarke, K. R., Somerfield, P. J., and Chapman, M. G. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis measure for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, 330: 55–80.
- Clarke, K. R., and Warwick, R. M. 1998. A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, 35: 523–531.
- Clarke, K. R., and Warwick, R. M. 2001. *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*, 2nd edn. Primer-E Ltd, Plymouth, UK.
- da Silva, I. A., and Batalha, M. A. 2006. Taxonomic distinctness and diversity of a hyperseasonal savannah in central Brazil. *Diversity and Distributions*, 12: 725–730.
- Eschmeyer, W. N. 1990. *Catalogue of the Genera of Recent Fishes*. California Academy of Sciences, San Francisco. 697 pp.
- Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61: 1–10.

- Faith, D. P. 1994. Phylogenetic pattern and the quantification of organismal biodiversity. *Philosophical Transactions of the Royal Society of London, Series B*, 345: 45–58.
- Féral, J.-P., Fourt, M., Perez, T., Warwick, R. M., Emblow, C., Hummel, H., Van Avesaath, P., *et al.* 2003. European Marine Biodiversity Indicators. Netherlands Institute of Ecology, Centre for Estuarine and Marine Ecology, Yerseke, The Netherlands. 130 pp.
- Fishbase. 1999. Fishbase 99: a Global Information System on Fishes. CD-ROM, ICLARM, Manila.
- Gislason, H., Pope, J. G., Rice, J. C., and Daan, N. 2008. Co-existence in North Sea fish communities: implications for growth and natural mortality. *ICES Journal of Marine Science*, 65: 514–530.
- Harper, J. L., and Hawksworth, D. L. 1994. Biodiversity: measurement and estimation. *Philosophical Transactions of the Royal Society of London, Series B*, 345: 5–12.
- Heemsbergen, D. A., Berg, M. P., Loreau, M., van Hal, J. R., Faber, J. H., and Verhoef, H. A. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science*, 306: 1019–1020.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75: 3–35.
- Hooper, D. U., Solan, M., Symstad, A., Diaz, S., Gessner, M. A., Buchmann, N., Degrange, V., *et al.* 2002. Species diversity, functional diversity, and ecosystem functioning. *In Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*, pp. 195–208. Ed. by M. Loreau, S. Naeem, and P. Inchausti. Oxford University Press, Oxford.
- Howson, C. M., and Picton, B. E. (Eds). 1997. The species directory of the marine fauna and flora of the British Isles and surrounding seas. Ulster Museum and Marine Conservation Society, Belfast and Ross-on-Wye. 508 pp.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton. 375 pp.
- Leonard, D. R. P., Clarke, K. R., Somerfield, P. J., and Warwick, R. M. 2006. The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessments. *Journal of Environmental Management*, 78: 52–62.
- Leps, J., de Bello, F., Lavorel, S., and Berman, S. 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia*, 78: 481–501.
- Lomolino, M. V., Sax, D. F., and Brown, J. H. (Eds). 2004. *Foundations of Biogeography: Classic Papers with Commentaries*. University of Chicago Press in association with the International Biogeographic Society and the National Center for Ecological Analysis and Synthesis, Chicago. 1291 pp.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., *et al.* 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294: 804–808.
- Marchant, R. 2007. The use of taxonomic distinctness to assess environmental disturbance of insect communities from running water. *Freshwater Biology*, 52: 1634–1645.
- Maxwell, D. L., and Jennings, S. 2005. Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. *Journal of Applied Ecology*, 42: 25–37.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. *Science*, 279: 860–863.
- Pauly, D., and Watson, R. 2005. Background and interpretation of the “Marine Trophic Index” as a measure of biodiversity. *Philosophical Transactions of the Royal Society of London, Series B*, 360: 415–423.
- Petchey, O. L., and Gaston, K. J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5: 402–411.
- Petchey, O. L., and Gaston, K. J. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters*, 9: 741–758.
- Rao, C. R. 1982. Diversity and dissimilarity coefficients—a unified approach. *Theoretical Population Biology*, 21: 24–43.
- Rice, J. 2003. Environmental health indicators. *Ocean and Coastal Management*, 46: 235–259.
- Ricketts, E. F. 2006. *Breaking Through: Essays, Journals and Travelogues of Edward F. Ricketts*. Ed. by K. A. Rodger. University of California Press Ltd, London. 261 pp.
- Rogers, S. I., Clarke, K. R., and Reynolds, J. D. 1999. The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic. *Journal of Animal Ecology*, 68: 769–782.
- Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge. 436 pp.
- Somerfield, P. J., Cochrane, S. J., Dahle, S., and Pearson, T. H. 2006. Free-living nematodes and macrobenthos in a high-latitude glacial fjord. *Journal of Experimental Marine Biology and Ecology*, 330: 284–296.
- Tokeshi, M. 1986. Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. *Journal of Animal Ecology*, 55: 491–506.
- Warwick, R. M., and Clarke, K. R. 1995. New “biodiversity” measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series*, 129: 301–305.
- Warwick, R. M., and Clarke, K. R. 2001. Practical measures of marine biodiversity based on relatedness of species. *Oceanography and Marine Biology: an Annual Review*, 39: 207–231.
- Weiher, E., and Keddy, P. (Eds). 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge. 418 pp.
- Wright, J. P., Naeem, S., Hector, A., Lehman, C., Reich, P. B., Schmid, B., and Tilman, D. 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters*, 9: 111–120.