

Measuring β -diversity using a taxonomic similarity index, and its relation to spatial scale

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ABSTRACT: We present a new similarity index, taxonomic similarity (Δ_S), which can be used to measure β -diversity. Δ_S utilises species presence/absence data, and incorporates both higher taxon richness and evenness concepts. It is derived from the average taxonomic distance (relatedness) of any 2 species from different sites. Therefore Δ_S is analogous to taxonomic distinctness recently developed for biodiversity assessment at α - and γ - (landscape or seascape) scales. Δ_S is a new index, although its derivation uses a concept similar to the 'optimal taxonomic mapping statistic' developed independently for quantifying structural redundancy in marine macrobenthos. Using echinoderm data, we show that Δ_S exhibits smoother behaviour and is less influenced by species richness, and hence sampling effort, than the widely used Jaccard coefficient of species similarity. We also believe Δ_S to be a more intuitive and comprehensive measure of similarity than Jaccard and other conventional indices based solely on species held in common. Taxonomic similarity between sites is computed for echinoderms examined over 3 different spatial scales: local/small-scale (<10 km), intermediate-scale (10 to 100s km) and province/oceanic-scale (100s to 1000s km). Taxonomic similarity between sites increases progressively with spatial scale, with significantly lower values and higher β -diversity at small spatial scales. The same pattern is evident for species similarity, using the Jaccard coefficient. Possible explanations for this pattern centre on: (1) the large-scale oceanic area examined (Indo-West Pacific), representing a metapopulation of echinoderms for the 2 other, smaller areas examined within (Pula Wé, Sumatra and Lakshadweeps); (2) greater biophysical instability and unpredictability at small spatial scales. Compared with larger spatial scales, these may be characterised by greater likelihood and influence of species migrations and extinctions on a site's total species composition. Hence, species composition may be highly changeable at small scales, leading to high β -diversity. These findings are based on 1 set of comparative data for 1 faunal group. Any wider conclusions drawn would be premature, although corals may also show greater β -diversity at small spatial scales. The extent to which patterns observed are evident for other marine species groups is not well known.

KEY WORDS: Biodiversity · β -diversity · Taxonomic similarity · Echinoderms · Indo-West Pacific

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INTRODUCTION

The utility of biodiversity measures which incorporate higher taxon richness and evenness is becoming increasingly recognised (review in Clarke & Warwick 1999). Recently developed measures satisfying both requirements include taxonomic diversity (Δ) computed

from species abundance data, and taxonomic distinctness (Δ^*) determined from species (presence/absence) records, or 'quantitative' data such as biomass, prevalence or % cover, rather than counts of individuals (Warwick & Clarke 1995, Price et al. 1999). Taxonomic diversity/distinctness, being an average measure (of the relatedness between any 2 individuals/species in a community sample), is relatively insensitive to disparities in sampling effort (Clarke & Warwick 1998a) and taxonomic rigour (Warwick & Clarke 1998). Apart from

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Simpson's diversity index (Lande 1996), most conventional measures of diversity (e.g. Shannon-Wiener, Pielou, Margalev) are based heavily on sample size. Additionally, taxonomic diversity/distinctness may have useful application in environmental monitoring and assessment (Warwick & Clarke 1995, 1998), although this has not been confirmed in all subsequent studies (review in Clarke & Warwick 1999).

Taxonomic diversity/distinctness measures biodiversity at α - (within-habitat) and γ - (within-region) scales, the latter also termed 'landscape' or 'seascape' diversity (Gray 1997) and including large ocean provinces (Price et al. 1999). Another aspect of biodiversity is β -diversity, an area much neglected in the marine environment (Gray 2000). This is an estimate of spatial turnover of species along a gradient (e.g. from site to site). Methods for assessing β -diversity have involved measuring changes in species composition along a gradient (Whittaker 1960, 1975, Wilson & Shmida 1984, Gray 2000), with recent modifications for transects of unequal size (Harrison et al. 1992), and also changes in values of a species similarity index (Gray 2000).

In this paper we define a similarity index, taxonomic similarity (Δ_S), using a similar idea to that of Δ (and Δ^*), through consideration of taxonomic relatedness. This is a new index, although its derivation uses a similar concept to the 'optimal taxonomic mapping statistic' developed independently by Clarke & Warwick (1998b) for quantifying structural redundancy in marine macrobenthos. We use our index, Δ_S , which utilises species presence/absence data, as a measure of β -diversity. We argue that Δ_S may have advantages over conventional similarity indices, which utilise only data at the species level, since higher taxonomic levels (genera, families, orders etc.) in Δ_S are taken into account in comparisons between sites/areas. We also examine some theoretical and empirical properties of Δ_S and present analyses of several echinoderm datasets sampled over different spatial scales. For comparison, the behaviour of Δ_S is assessed against the Jaccard coefficient, perhaps the most commonly used species similarity measure.

METHODS

Definition of taxonomic similarity. Δ_S is a similarity index derived from taxonomic distance (TD) which is computed from species presence/absence data. TD is the average minimum path length between any 2 species in different sites/areas. We use path length in the same way as Warwick & Clarke (1995), i.e. the relative taxonomic distance between any 2 species. If the species are classified into genera, families, orders, etc., the

taxonomic path lengths are 0 (same species), 1 (different species but same genus), 2 (different genus but same family), 3 (different family but same order), etc. However, path length here refers to species in different sites/areas, rather than in only one site/area. Δ_S is computed in 2 steps as follows:

(1) Given 2 sites, A and B, we define the TD between Sites A and B as follows:

$$TD = \frac{\sum_i w_{iB} + \sum_j w_{jA}}{n_A + n_B}$$

where w_{iB} is the minimum path length between Species i at Site A and all species at Site B; w_{jA} is the minimum path length between Species j at Site B and all species at Site A; and n_A and n_B are the number of species at Sites A and B respectively. Note that $\sum_i w_{iB}$ and $\sum_j w_{jA}$ are not necessarily equal (see Fig. 1). TD is similar to the statistic, M , 'optimal taxonomic mapping statistic' (Clarke & Warwick 1998b), which uses an unweighted, rather than weighted, average path length.

(2) Δ_S is defined as:

$$\Delta_S = 1 - \frac{TD}{L-1}$$

where L is the number of taxonomic levels used to classify the species (e.g. if the species have been classified into genus, family, order, class and phylum, $L = 6$). $L-1$ can also be thought of as the maximum path length between a pair as species. Note that 1 minus the quotient of TD and $L-1$ makes Δ_S satisfy the property of a similarity measure having values between 0 and 1. An example of how Δ_S is computed for 2 sites, A and B, is shown diagrammatically in Fig. 1. In this example, these sites contain 6 and 7 species respectively, classified into genera, families and orders and here all assumed to belong to the same class. We have used constant incremental path lengths (0, 1, 2, etc.) in this example and throughout this study, following the robustness of relative values of taxonomic distinctness to variation in the definition of path length (Clarke & Warwick 1999).

Determination of β -diversity from taxonomic similarity. As with conventional similarity indices (e.g. Sheppard 1985) a species similarity matrix is compiled of Δ_S values for all pair-wise comparisons of species between 'sites'. Sites are here taken as the spatial units used for comparisons, irrespective of their area (Fig. 2). β -diversity is computed as the average (median) taxonomic similarity coefficient value in the similarity matrix. Since similarity matrix values are not independent of each other, it is not possible to perform statistical tests on the data to compare β -diversity between spatial scales and depths (see below).

	Site A	Site B	genus (1)	family (2)	order (3)
Species 1	1	0			
Species 2	1	0			
Species 3	0	1			
Species 4	1	0			
Species 5	1	0			
Species 6	0	1			
Species 7	1	1			
Species 8	0	1			
Species 9	1	0			
Species 10	0	1			
Species 11	0	1			
Species 12	0	1			
Total in site	6	7			

$$\begin{aligned}
 TD &= \frac{\sum_i W_{iB} + \sum_j W_{jA}}{n_A + n_B} \\
 &= \frac{(1+1+2+2+0+1) + (1+2+0+1+1+3+3)}{6+7} = \frac{18}{13} \\
 \Delta_S &= 1 - \frac{TD}{L-1} = 1 - \frac{1.615}{4-1} = 0.54
 \end{aligned}$$

Fig. 1. Illustration of how taxonomic similarity (Δ_S) is computed for 2 different sites, A and B. Firstly, the minimum path length is determined between each species in Site A and all those at Site B, and then between each species in Site B and all those in Site A. Values for species at Site A are: **1** for Species 1, since it is absent from Site B but the genus is present at Site B (represented by Species 3), and similarly **1** for Species 2; **2** for Species 4, since the species and genus are absent from Site B but the family is present at Site B (represented by Species 3), etc. Conversely, the minimum path length for species at Site B is: **1** for Species 3, since it is absent from Site A but the genus is present at Site A (represented by Species 1 and 2), and **2** for Species 6, since the species and genus are absent from Site A but the family is present at Site A (represented by Species 7 and 9), etc. The path lengths (shown in bold above) correspond to the numbers in the first sum (Site A) and second sum (Site B) of the numerator. Secondly, the sum of all minimum path lengths are divided by the sum of the total number of species at each site to give TD, the taxonomic difference between Sites A and B. Thirdly, TD is divided by the total number of taxonomic levels minus 1 (i.e. maximum path length) to give a dissimilarity index, which is subtracted from 1 for conversion to the taxonomic similarity index, Δ_S (0.54)

Taxonomic similarity at different spatial scales and comparison with Jaccard similarity coefficient. Values of Δ_S were computed for comprehensive shallow-water (<30 m depth) echinoderm datasets for 3 geographical areas, increasing in scale from within-island, between-island up to province/ocean-scale (Table 1, Fig. 2). For comparison, values of Jaccard are also computed. The datasets are partly nested, since Pula Wé, Sumatra, and the Lakshadweeps lie within the Indo-West Pacific; but not fully nested (due to lack of suitable datasets), since Pula Wé, Sumatra, is not part of the Lakshadweeps island group.

Influence of sampling effort on taxonomic similarity. The influence of sampling effort on Δ_S and Jaccard

was determined by simulations using echinoderm presence/absence records from 3 randomly selected pairs of sites in (1) Pula Wé, Sumatra (above), and (2) the Atlantic from data used for the study of Price et al. (1999). For each pair-wise comparison of sites in each region, the full complement of species was listed, i.e. 'fixed', for the first site. Species found at the second site were then randomly selected and 'added', successively in increments of 1 species, so that species richness increased until the full species complement was reached. Values for the similarity coefficient were re-computed after addition of each successive species. Hence, the effect of species richness, and sampling effort, on our new Δ_S index could be determined and

Table 1. Characteristics of the 3 regions of the Indo-West Pacific for which values of taxonomic similarity (Δ_S) and Jaccard index were determined

Feature	Pula Wé, Sumatra	Lakshadweeps, or Laccadives	Indo-West Pacific
Area or region	Small/within island	Intermediate/between island	Large/province (oceanic)
Proximity of 'sites' to each other within region	≤10 km	10s–100 km	100s–1000s km
No. of 'sites' within each comparative region	16	10	16
Source(s) for echinoderm records	Price & Reid (1985), Marsh & Price (1991), Price & Rowe (1996), Marshall-Crossland & Price (1999)	James (1989)	Clark & Rowe (1971)

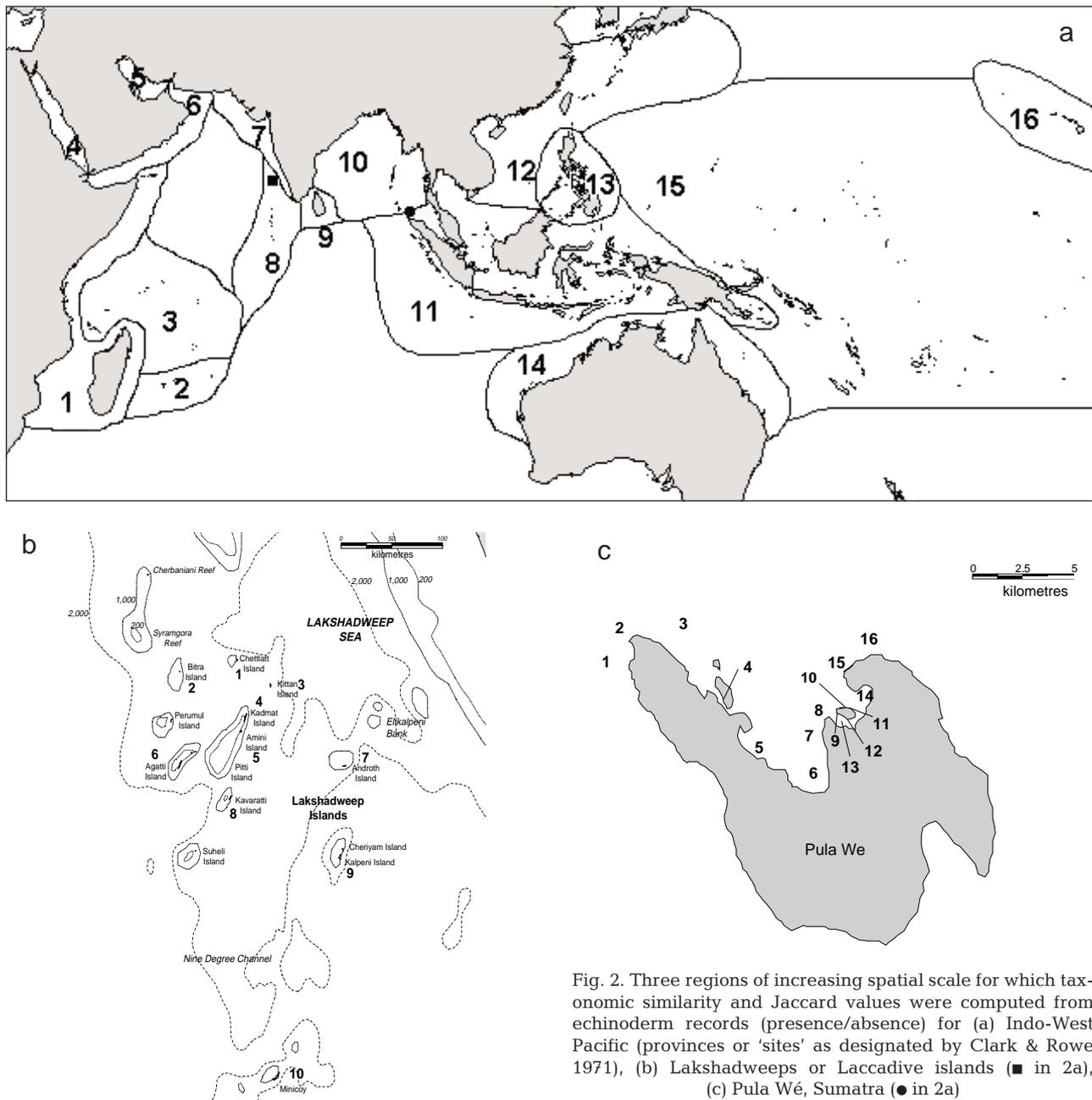


Fig. 2. Three regions of increasing spatial scale for which taxonomic similarity and Jaccard values were computed from echinoderm records (presence/absence) for (a) Indo-West Pacific (provinces or 'sites' as designated by Clark & Rowe 1971), (b) Lakshadweeps or Laccadive islands (■ in 2a), (c) Pula Wé, Sumatra (● in 2a)

compared with the behaviour of a conventional similarity index (Jaccard). The same procedure was undertaken by 'fixing' the complement of the second site of a pair, then successively adding species from the first site.

Detecting depth differences in β -diversity. We compare the ability of Δ_S and Jaccard to detect, qualitatively, differences in β -diversity between depth zones using the following species presence/absence datasets: (1) 3 different depth zones using echinoderm data for Pula Wé, Sumatra (above); (2) 3 different depth zones using Atlantic asteroid data (Price et al. 1999).

RESULTS

Taxonomic similarity of echinoderms and comparison with Jaccard index

Data on Δ_S and Jaccard from echinoderm records (presence/absence data) are shown for 3 regions of increasing size and distance between each site within the Indo-West Pacific (Fig. 3, Table 2). A greater range is evident for values of Δ_S (0.19 to 0.9) than Jaccard (0.03 to 0.58), and values of Δ_S are also higher than Jaccard. This might be expected on account of the inclu-

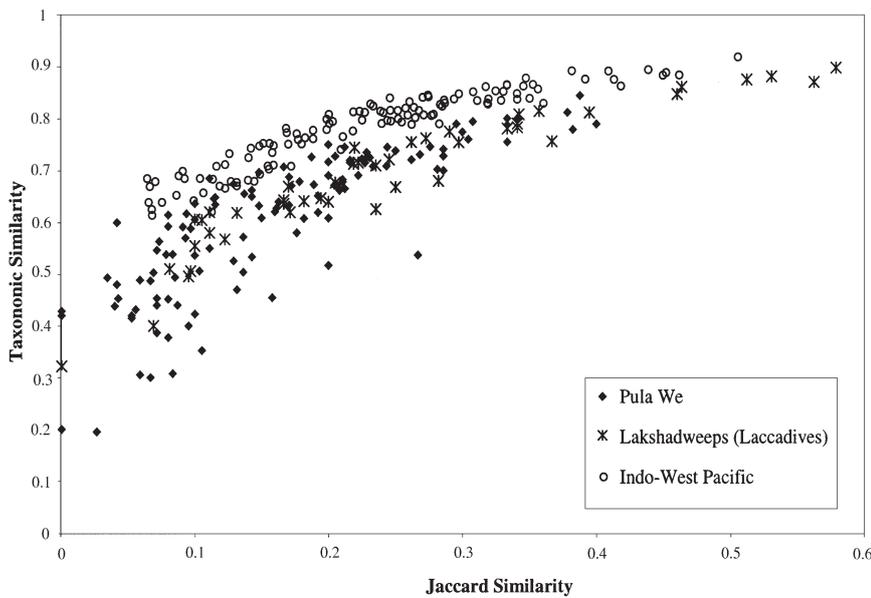


Fig. 3. Taxonomic similarity for 3 regions of increasing spatial scale for echinoderm records (presence/absence): Pula Wé, Sumatra, Lakshadweeps or Laccadive islands, and Indo-West Pacific. Jaccard values are shown for comparison

Table 2. Summary statistics for taxonomic similarity (Δ_S) and Jaccard index using echinoderm (presence/absence) records from Pula Wé (Sumatra), Lakshadweeps and Indo-West Pacific

	Pula Wé	Lakshadweeps	Indo-West Pacific
Taxonomic similarity			
Median	0.635	0.680	0.798
Variance	0.019	0.016	0.005
Range	0.649	0.575	0.303
Jaccard index			
Median	0.159	0.222	0.233
Variance	0.009	0.020	0.010
Range	0.400	0.579	0.441

Table 3. Summary statistics for taxonomic similarity (Δ_S) and Jaccard index using echinoderm (presence/absence) records from 3 depth zones on coral reefs of Pula Wé, Sumatra. Shallow: 0 to 10 m; medium: 11 to 20 m; deep: >20 m

	Shallow	Medium	Deep
Taxonomic similarity			
Median	0.491	0.434	0.570
Variance	0.025	0.034	0.008
Range	0.642	0.800	0.372
Jaccard index			
Median	0.093	0.071	0.077
Variance	0.008	0.007	0.005
Range	0.389	0.333	0.267

sion of common taxa above species rank in computations of Δ_S . Jaccard and Δ_S show strong correlation. Median similarity for both indices increases progressively from Pula Wé, Sumatra, to Lakshadweeps, to the Indo-West Pacific. A reverse pattern is shown for the variance and range in values of Δ_S , whereas no consistent pattern is shown for the Jaccard index across scales. These results suggest greater species turnover (Jaccard data), greater taxonomic turnover (Δ_S data), and hence higher β -diversity, at small spatial scales than over larger scales.

Sampling effort and taxonomic similarity

The effect of increasing species richness on Δ_S and the Jaccard coefficient is shown for selected echinoderm data from Pula Wé, Sumatra, in Fig. 4 and for asteroid data from the Atlantic in Fig. 5. The behaviour of Δ_S with increasing species richness is generally smoother than that shown by the Jaccard index, which shows greater fluctuations (Fig. 4a). In addition, Δ_S seems to approach an asymptote sooner than Jaccard (Fig. 4a). This suggests that Δ_S is less influenced by species richness, and hence sampling effort, than Jaccard. In instances of very few species held in common, a steady decline in Jaccard is evident, whereas there will always be some commonality with Δ_S , whose behaviour is little different to that when many species are shared (Fig. 4b). A further point is that the lack of any shared species between 2 sites results in '0' similarity for Jaccard, whereas Δ_S shows the same behaviour as when there are shared species (Fig. 5).

Detecting depth differences in β -diversity

Descriptive statistical data for Pula Wé, Sumatra, are shown in Table 3. Based on both Δ_S and Jaccard, β -diversity is greatest in intermediate depths. Using Δ_S , β -diversity is greater for shallow than deep water, whereas the reverse pattern is evident using Jaccard. Data for the Atlantic are shown in Table 4. Here again, β -diversity is greatest for intermediate depths for both indices. Using Δ_S , β -diversity is greater for deep than shallow water, whereas the reverse pattern is evident using Jaccard.

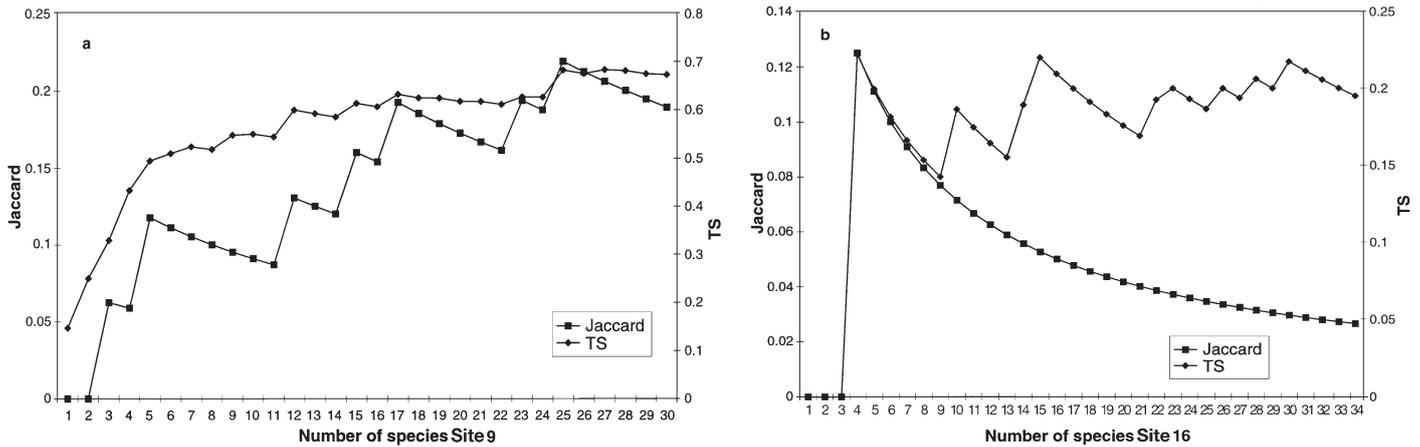


Fig. 4. Effect of increasing species richness, and hence sampling effort, on taxonomic similarity (TS) and the Jaccard index, based on pair-wise comparison of echinoderm records at sites in Pula Wé, Sumatra. (a) Species complement of Site 10 fixed with incremental additions of 1 species to Site 9; (b) species complement of Site 7 fixed with incremental additions of 1 species to Site 16 (see 'Methods' and Fig. 2c for site locations)

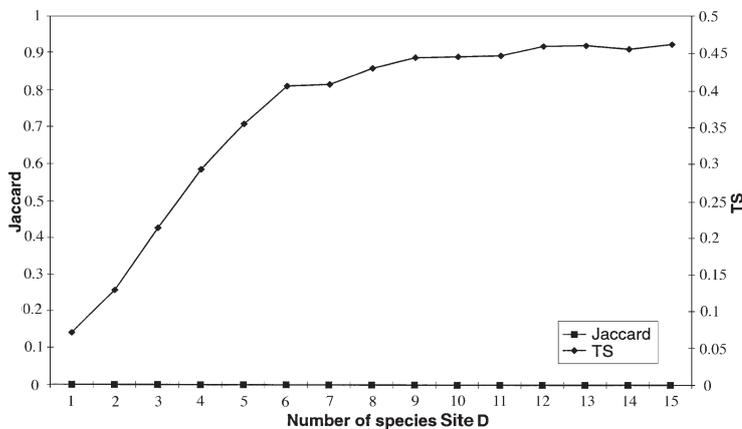


Fig. 5. Effect of increasing species richness, and hence sampling effort, on taxonomic similarity (TS) and the Jaccard index based on pair-wise comparison of asteroid records at sites in Atlantic. Species complement of Site N (South Angola to False Bay, South Africa) fixed with incremental additions of 1 species to Site D (Florida to Gulf of Mexico including Yukatan) (see 'Methods')

Table 4. Summary statistics for taxonomic similarity (Δ_S) and Jaccard index using asteroid (presence/absence) records from 3 depth zones in Atlantic. Intertidal/shelf: 0 to 200 m; upper bathyal: 200 to 500 m; lower bathyal: >500 m

	Intertidal	Upper bathyal	Lower bathyal
Taxonomic similarity			
Median	0.560	0.338	0.454
Variance	0.018	0.035	0.049
Range	0.584	0.847	0.814
Jaccard index			
Median	0.049	0	0.106
Variance	0.007	0.009	0.002
Range	0.400	0.523	0.250

DISCUSSION

Wilson & Shmida (1984) highlight the importance of β -diversity in indicating the extent to which habitats have been partitioned by species, as a means of comparing habitat diversity and, together with α -diversity, as a measure of overall biotic heterogeneity of an area. The importance of β -diversity for assessment of landscape diversity and, in turn, conservation value, has also been stressed recently (Tuomisto et al. 1995, Gray 1997). Compared with α -diversity, however, knowledge of β -diversity in the marine context is more limited (Gray 2000). Some recent exceptions addressing β -diversity explicitly include studies on sponges (Carballo et al. 1996), bryozoans (Clarke & Lidgard 1999), polychaetes (Paterson et al. 1998), asteroids (Price et al. 1999), ascidians (Naranjo et al. 1998), and associations between benthic habitats and β -diversity (Parry et al. 1999). Several authors have recently produced interesting plots of Bray-Curtis similarity against distance apart of the samples (Hull 1999, Kendall & Widdecombe 1999). Experimental work has included assessment of associations between bioturbation/feeding and β -diversity (Widdicombe & Austen 1998, 1999). Many other studies have examined species similarity (e.g. Price 1982, Sheppard & Sheppard 1991), although generally only implicitly as a means of estimating β -diversity.

Based on our preliminary studies, Δ_S appears to be less influenced by sampling effort than Jaccard. A likely reason is that Δ_S is a measure of average taxonomic relatedness, unlike conventional measures that depend only on (shared) species. This is analogous to the contrast between taxonomic diversity/distinctness

(Δ and Δ^* ; Warwick & Clarke 1995, Clarke & Warwick 1998a) and species richness. The optimal taxonomic mapping statistic, M (Clarke & Warwick 1998b), may be even less influenced by sample-size disparities.

Another possible practical advantage of Δ_S over other similarity coefficients concerns taxonomic robustness. As shown for Δ and Δ^* (Clarke & Warwick 1998a, Warwick & Clarke 1998), disparities in taxonomic rigour (e.g. misidentifications) are generally less likely to influence values of Δ_S than conventional similarity indices.

Moreover, we suggest that biodiversity measures are more comprehensive if based on all taxonomic levels, not just species. This is in closer accordance with the wider meaning and more recent definitions of biodiversity (e.g. Harper & Hawksworth 1994, Gray 1997, Clarke & Warwick 1998a): genetic (within-species), species and ecological (community/assemblage) diversity, particularly when species ('organismal' sensu Harper & Hawksworth 1994) diversity is taken to embrace taxonomic categories above species rank. Information on genetic diversity is seldom available for use in ecological analysis, except sometimes as records of sub-species (Clark & Rowe 1971, Price 1982, Clark & Downey 1992). In principle, however, such data could be incorporated into computations of taxonomic similarity (and taxonomic distinctness) (Clarke & Warwick 2001).

A dendrogram, or multidimensional scaling (MDS) plot, is commonly used to provide graphic representation of how species similarity changes along a gradient (e.g. between sites) in a particular area or environment. Longer branch lengths within a dendrogram denote relatively low similarity, and hence high β -diversity (e.g. Price et al. 1999). However, since quantitative comparison of dendrograms is difficult, we have used the species similarity matrix for computing and comparing similarity between sites. Comparisons of Δ_S (or Jaccard) can thus be made more readily between different environments, habitats, depths and spatial scales.

Our finding of increasing taxonomic (and species) similarity level at larger spatial scales initially seemed contrary to the observed, and expected, significant inverse correlation between geographical distance and species similarity, for example in Indian Ocean corals (Sheppard 1998), Atlantic ascidians (Naranjo et al. 1998) and Atlantic asteroids (Price et al. 1999). However, these patterns of similarity are evident for a particular (large) scale, whereas in this study we are comparing similarity *across* scales (small/intermediate/large-scale). The results also seem striking given that a wider range of habitats is represented for the large-scale (Indo-West Pacific) dataset, yet is associated with lowest β -diversity. In contrast, only 1 major habitat

(coral reef) is represented in the intermediate- (Lakshadweeps) and small-scale (Pula Wé, Sumatra) datasets, both of which are associated with higher β -diversity.

Assuming that the observed correlations between β -diversity and spatial scale are not due to chance (probability of ascending or descending rank order in 3 datasets is one-third), and that the availability of only partly nested datasets is not a major limitation, a possible explanation is the following. The Indo-West Pacific population may effectively be a metapopulation (Harrison 1994, 1998, May 1994) of echinoderms, with many species showing widespread distribution (Clark & Rowe 1971, Devaney 1973, Clark 1984, Price & Reid 1985). This reflects their relatively long larval duration (Devaney 1973) and excellent dispersal capability. Our study suggests that sites which are extensive in area and widely separated (Indo-West Pacific) are relatively homogeneous in terms of species composition. Any 'localised' species extinctions or migrations are probably unlikely to result in overall loss of that species from a site (i.e. area), due to its presence in other patches within the site. Hence, an overall high level of species similarity and Δ_S (i.e. low β -diversity) might be expected, and is observed, at large spatial scales.

In contrast, at sites that are small in area and in close proximity to each other (Pula Wé, Sumatra), 'localised' species extinctions or migrations may often equate to total loss of a species from that site. This might arise from effects of predation, competition or other effects of patch dynamics, resulting in collapse of species when too few fragments of habitat remain (Harrison 1994). Related to this, self-organised (by species) spatial heterogeneity is also known to influence the persistence of species (May 1994), and may be more prevalent over smaller than larger scales in the present context. These factors, invoking instability and unpredictability at small spatial scales (May 1994), might partly explain the low levels of similarity and high β -diversity observed, and the reverse pattern at larger scales. These apparent scaling effects are highly significant for taxonomic similarity, and less so but still discernible using the Jaccard coefficient. Biogeographical factors should also not be overlooked, although their possible influence on β -diversity is not completely clear. Pula Wé, Sumatra, lies at the intersection of 2 different nominal biogeographic provinces (10 and 11 in Fig. 2), as does the Lakshadweeps (between 7 and 8 in Fig. 2), and both are characterised by higher β -diversity than the Indo-West Pacific. High β -diversity related to geographical boundaries/ecotones has been reported for ascidians (Naranjo et al. 1998). However, relatively high β -diversity is also apparent for corals in the Arabian Gulf (see below), which does not lie close to a biogeographical boundary (Clark & Rowe 1971,

Sherman 1994). The relative interplay between biogeography and spatial scaling effects (e.g. greater uncertainty/unpredictability at smaller scales) needs further assessment. Further, even the definition of marine biogeographic areas and the boundaries between them is still debatable, and depends on the underlying criteria used (Sherman 1994).

Our findings are based on 1 set of comparative data for 1 faunal group (echinoderms). Any wider conclusions drawn would therefore be premature. The extent to which the same spatial patterns are also shown by other marine species groups, and the scale(s) at which β -diversity is maximal, require further study. Corals may show a pattern similar to echinoderms, with greater similarity (and lower β -diversity) at larger than smaller spatial scales. This is based on preliminary comparison between the wider Indian Ocean (Sheppard 1987, his Fig. 2) and 2 smaller regions: the Red Sea (Sheppard & Sheppard 1991, their Fig. 7) and the Bahrain coast of the Arabian Gulf (Sheppard 1988, his Fig. 1). The cluster analyses are all based on the same clustering method (group average). However, the similarity coefficient used is the same only for the first 2 regions (Dice coefficient), but different for the Gulf (Jaccard)—accentuating dissimilarity between sites. If the Dice coefficient is computed for the Gulf (data not shown), similarity between sites increases. While positive association between spatial scale and species similarity is discernible from qualitative comparison of the dendrograms, all based on Jaccard, comprehensive analysis of the data is needed for a clearer picture. The known interannual fluctuations and unpredictability of coral species from studies of 1 m² quadrats and coral fish species on small coral reefs (May 1994) would seem to support suggestions of greater β -diversity at small scales. For nematodes, which are small, relatively immobile and poor dispersers, positive association between spatial scale and species similarity may also occur. The scale at which dissimilarity and β -diversity are greatest for nematodes may be very small, possibly in the order of centimetres to metres (J. Lambshead pers. comm.).

It will also be useful to examine the utility of Δ_S for environmental monitoring and assessing environmental change. It is possible that Δ_S might have the benefits of a measure based heavily on average properties (like Δ/Δ^* , which in at least some studies has detected environmental degradation; Warwick & Clarke 1995, 1998, Clarke & Warwick 1999), and also carry the known advantages of multivariate techniques for detecting environmental impacts and community shifts (Clarke & Warwick 1999).

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