Oecologia (2001) 128:274–280
DOI 10.1007/s004420100643

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Beta and habitat diversity in marine systems: a new approach to measurement, scaling and interpretation

Received: 18 October 2000 / Accepted: 9 January 2001 / Published online: 1 March 2001

Abstract Habitat diversity is a widely used criterion for locating conservation activities such as protected areas. Most habitat diversity indices are measures of alpha diversity at the scale of habitats and are therefore insensitive to the underlying biological differences between habitats. To incorporate such inter-habitat differences, a new method is presented which calculates a measure of beta (β) diversity from pixels within a window passed throughout a habitat map. To avoid confusion with β diversity indices, the new measure is called β-dissimilarity. β-Dissimiliarity is calculated from the mean Bray-Curtis dissimilarity, D_m, of field data which comprise each habitat class. The variance of D_m distinguishes discrete β-dissimilarity distributions from homogenous patterns. The method also attempts to remove some of the arbitrary aspects of habitat mapping, can be scaled to other levels of diversity or measures of community structure, is readily interpretable and permits hypothesis testing. Its applications to ecosystem science and coastal management are discussed and illustrated.

Keywords Scale · Remote sensing · Coral reefs · Marine protected areas

Introduction

Biodiversity encompasses a wide range of biological, ecological and biogeographical scales including genetic, species, assemblage, functional, habitat and landscape perspectives (Magurran 1988; Gray 1997). Whilst each level of diversity has intrinsic importance (Ray 1991), the spatio-temporal scaling relationships between levels warrant investigation in order to identify the processes responsible for a given diversity (Levin 1992) and appropriate conservation measures. For example, workers in Australia have found that selecting marine protected areas using surrogate habitat-level measures is a cost-effective means of conserving species-level diversity which is expensive to survey (Ward et al. 1999).

The utility of surrogate diversity measures such as habitat diversity is appealing for marine conservation although unlike terrestrial systems, the literature is still in its infancy (examples of terrestrial papers include McKenzie et al. 1989; Williams and Gaston 1994). Difficulty in mapping marine habitats has, until recently, been the main reason for the paucity of habitat-scale studies in marine ecology (Gray 2000). However, spatial data on habitats are becoming increasingly available through high-resolution optical remote sensing (Green et al. 1996) and acoustic methods where light transmission is poor (Sotheran et al. 1997).

To most ecologists, the term "habitat" refers to the physical environment experienced by an organism. A more general definition is used when mapping habitats with remote sensing. In this case, the term habitat simply describes the features on the Earth's surface being mapped (Green et al. 2000). Depending on the objectives of the mapping, the focus may be biological, geomorphological, geological and so forth. The level of habitat detail revealed by a sensor is defined as its "descriptive resolution" and is a function of its spatial and spectral resolution (Green et al. 1996). In benthic marine systems, assemblages of macro-organisms and associated substrata are perhaps the highest descriptive resolution achievable. For example, coral reef assemblages have been defined using field data and mapped using high-resolution airborne imagery to a depth of about 20 m where horizontal visibility exceeds a Secchi distance of 20 m (Mumby et al. 1998).

Habitat mapping usually involves two multivariate analyses: classification of field data into habitat categories followed by discrimination of image data into habitat categories (Mather 1997). However, where habitats or assemblages vary along gradients, both multivariate methods may be partly arbitrary creating unavoidable er-

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rors in the structure and interpretation of output maps. First, field samples (e.g. species' abundances) may not cluster tightly within a dendrogram, indicating that the composition of some habitats is less distinct than in others. Arbitrary assignments of individual samples to clusters are more likely to have occurred where clusters are less distinct (Clarke and Warwick 1994a). Biologically, habitats derived from such clusters are less meaningful since they do not necessarily represent a natural grouping of samples. Second, a spectral discrimination rule may assign habitat classes arbitrarily where, for example, a pixel is equally similar to two habitat classes (Mumby and Harborne 1999). The pixel may actually represent an intermediate habitat but non-fuzzy classifiers cannot make this distinction.

Arbitrary decisions may be more prevalent in marine systems than in their terrestrial counterparts because the structuring effects of anthropogenic disturbance are usually more acute in the terrestrial environment. Agriculture, for example, imposes distinct boundaries on wheat, barley and maize fields, whereas (non-trawling) pelagic fisheries are less likely to affect benthic habitat structure directly. A second problem arises in the interpretation of habitat diversity from habitat maps. Like indices of species diversity, most indices of habitat diversity (O'Neill et al. 1988) involve the implicit assumption that each element (e.g. habitat, species) is equally different (Loehle and Wein 1994). However, an area containing three variants of seagrass habitat is arguably less diverse than one containing a seagrass, coral and macroalgal habitat. Thus, considering the underlying biological or physical similarities of habitats explicitly rather than treating habitats as binary variables (identical versus different) would be more instructive.

Maps of habitats do not explicitly reveal the underlying field data (e.g. species' abundance) from which habitats were defined. The method proposed here makes such underlying data spatially explicit in the form of beta (β) diversity. Whittaker (1960) identified two types of β diversity. The first, and most commonly adopted, compares the number of species in a large area to the number of species in a smaller area and yields *indices* of β diversity. The second type of β diversity, which is embodied here, examines how species' similarity changes along gradients (see also Pielou 1976). Since there has been confusion in the interpretation of β diversity (Gray 2000), the latter form of β diversity will be distinguished from indices by the term *β-dissimilarity* (the reason for using dissimilarity rather than similarity is discussed later).

The approach adopted here was inspired by the work of Loehle and Wein (1994) who used ordination scores to represent habitat similarity, and information theory to represent habitat diversity. The aim is to provide a method which interfaces with widely used multivariate analyses in marine ecology and is relatively easy to scale and interpret. Specifically, the method (1) accounts for inter-habitat differences, (2) attempts to remove some of the arbitrary aspects of mapping, (3) can be scaled to other levels of diversity or measures of community structure, (4) is readily interpretable and (5) permits hypothesis testing (e.g. effects of disturbance on diversity). Although the emphasis is on marine diversity, the methods are equally applicable to terrestrial systems. Gray (2000) noted that methods for measuring biodiversity have evolved separately in marine and terrestrial ecology and the intention here is to help bridge this gap by using a marine title in a journal which is not specialised in marine ecology. The method is described and illustrated and the applications to science and management discussed.

The method

Derivation of habitats

Habitats can be described using the most appropriate field variables for distinguishing habitat classes from remotely sensed data. The case study given here, for example, used airborne and high-resolution satellite sensors to map coral reefs and therefore the percent cover of macro-organisms and dead substrata were measured in 1-m^2 quadrats. Field data were categorised using agglomerative hierarchical classification with group-average sorting (Mumby and Harborne 1999). To link field data, habitat categories and β-dissimilarity, the Bray-Curtis similarity coefficient, S, is used to represent ecological similarities between samples (Eq. 1). The Bray-Curtis similarity coefficient is widely used in marine ecology (Clarke and Warwick 1994a) and has a number of biologically desirable properties: S is not a function of joint absences of variables, it takes a minimum value of 0 when two samples have no variables in common, and a maximum value of 100 when two samples are identical. Furthermore, S has been shown to be a robust estimator of ecological distance (Faith et al. 1987) and the weighting of individual variables (e.g. species) can be manipulated to reflect a priori notions of their importance (Mumby et al. 1996). In practice, either S or Bray-Curtis dissimilarity, D, (1- S) can be used to represent biological distances between samples.

$$\text{Bray} - \text{Curtis similarity, } S_{jk} = \left[1 - \frac{\sum_{i=1}^{p} |X_{ij} - X_{ik}|}{\sum_{i=1}^{p} |X_{ij} + X_{ik}|}\right] \quad (1)$$

Where X_{ij} is the abundance of the ith variable in the jth sample and where there are p variables overall.

Calculation of β-dissimilarity

The calculation of β-dissimilarity requires a thematic habitat (assemblage) map on a raster grid of pixels. A floating-square window comprising an odd number of pixels (3, 5, 7, etc.) is passed throughout the image at intervals of one pixel. β-Dissimilarity is calculated in each window in the following sequence: (1) all habitats pres-

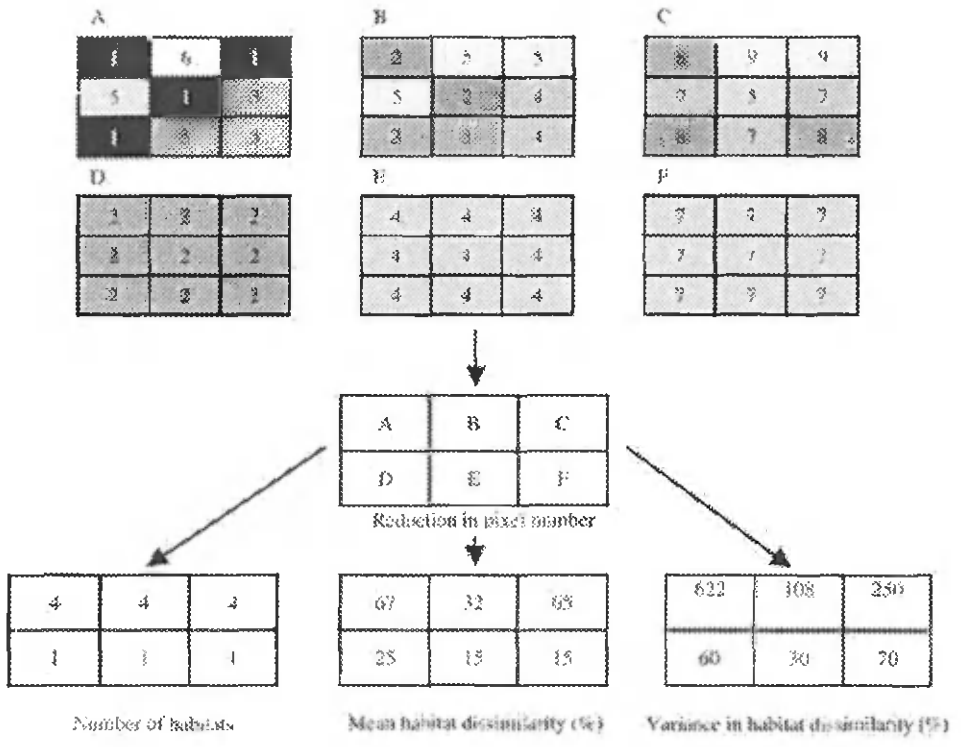

Fig. 1 β-dissimilarity and its variance based on six 9-pixel areas *A–F* (*top*). *Shading* indicates the degree of dissimilarity between habitats (which are *numbered*). The number of habitats, mean habitat dissimilarity and variance in habitat dissimilarity are displayed for each of the six areas (*below*). See Table 1 for interpretation

Table 1 Interpretation of the six habitat diversity scenarios illustrated in Fig. 1

Scenario	Description	Interpretation
A	High mean dissimilarity and high variance	Habitats have very different compositions (highest β diversity)
B	Approximately half the mean dissimilarity of A even though the number of habitats is identical; low variance	Habitats are consistently similar to one another (low β diversity)
C	Similar mean dissimilarity to A but the variance is much lower	Within-habitat dissimilarity is fairly high but all four habitats are quite similar (medium β diversity)
D	Single habitat with relatively high intra-habitat dissimilarity	Not a particularly cohesive cluster of samples from raw data (high α diversity)
E	Single habitat with low intra-habitat dissimilarity and low variance	Cohesive cluster of similar samples from raw data (low α diversity)
F	Single habitat with similar intra-habitat dissimilarity to E but higher variance	Samples comprising habitat F form sub-clusters although overall similarity is high (medium to low α diversity)

ent are identified, (2) raw sample data for each habitat (i.e. the percent cover values used to develop the initial habitat classification) are retrieved, (2) the mean Bray-Curtis dissimilarity (D_m) between *all* pairs of sample data is calculated (i.e. β-dissimilarity), and (4) the variance of dissimilarities between all pairs of sample data is calculated. D is a more intuitive measure of distance than S because greater D represents greater biological differences between habitats in the window and therefore greater β diversity. A new map is created in which each pixel constitutes the mean inter-habitat D_m (β-dissimilarity) at the centre of a window of n pixels (Fig. 1). A second map is created displaying the variance of inter-sample dissimilarities in each window. Variance is calculated to differentiate cases where intermediate values of D_m may result from (1) similar habitats whose intra-habitat $D \approx D_m$ but inter-habitat D is low, and (2) non-similar habitats where D_m is intermediate because intra-habitat D is low and inter-habitat D is high. The latter case would have substantially greater variance, indicating that the turnover resulted from a more discrete spatial distribution (i.e. greater biological contrast per unit area). A simple example of the method (Fig. 1, Table 1) demonstrates these cases and highlights the inadequacy of methods which treat habitats as equally different. In Fig. 1, habitat richness is 4 irrespective of the biological similarities between habitats (see Table 1 for explanation).

Table 2 Characteristic variables within habitat 1 (Fig. 1). The term *Average contribution* represents the average contribution of variable *i* to the average similarity within habitat 1 (overall average=28.9%). *Ratio*=contribution average/SD. The major discriminating features are the percent cover of bare substratum, *Lobophora variegata* and *Montastraea annularis*

Variable	Mean abundance	Average contribution	Ratio	Percent contribution	Cumulative percent
Bare substratum	58.1	11.5	2.5	39.7	39.8
Lobophora variegata	5.6	5.7	1.5	19.7	59.5
Montastraea annularis	12.4	3.5	1.3	12.1	71.6
Sand	1.0	2.4	0.8	8.3	79.9
Gorgonians	7.3	2.3	1.3	7.9	87.9
Madracis mirabilis	2.3	1.5	0.7	5.1	93.1
Dictyota spp.	4.1	1.3	1.4	4.5	97.6
Agaricia agaricites	0.7	0.7	1.4	2.4	100.0

Table 3 Discriminatory variables at β-dissimilarity scale between areas A and B (Fig. 1). The absence of habitat 1 in B is reflected in the discriminatory variables being similar to those that characterise habitat 1. D_m=82%. ANOSIM analysis: null hypothesis $D_{m\text{-}A}=D_{m\text{-}B}$; R-statistic=0.73, P=0.03 (i.e. fairly strong and significant differences in β-diversity between areas A and B)

Variable	Mean abundance		Average contribution	Ratio	Percent contribution
	A	B			
Bare substratum	55.2	26.7	29.3	3.4	35.7
Lobophora variegata	8.2	38.1	25.0	2.8	30.5
Montastraea annularis	11.1	2.3	15.3	1.6	18.7
Sand	3.2	1.1	9.2	0.8	11.2
Gorgonians	4.4	6.9	1.3	1.3	1.6
Madracis mirabilis	3.0	0	0.7	0.7	0.9
Dictyota spp.	5.2	9.2	0.6	1.4	0.7
Agaricia agaricites	0.3	0	0.6	1.4	0.7

Where an entire window is occupied by a single habitat, D_m is a measure of α-dissimilarity, or within-habitat diversity (Gray 2000). At the scale of the window, β-dissimilarity is zero and therefore the centre pixel can be replaced by zero. However, for investigations linking scales of diversity it is more appropriate to retain D_m (see below). In any event, such mono-habitat areas will be obvious as homogeneous patches with low variance (Fig. 1).

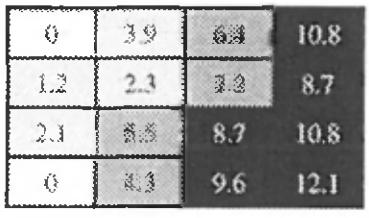

Fig. 2 Percent contribution of *Montastraea annularis* to S_m calculated using a 3×3 window. *Shading* helps identify an east-west pattern of greater contribution to species turnover

Linking scales of diversity and other measures of community structure

An advantage of using the Bray-Curtis similarity coefficient to represent inter-sample distance is that the contribution of each variable (e.g. species) can be quantified using similarity percentage (SIMPER) analysis (Clarke 1993). To identify characteristic features of a group of samples, SIMPER calculates the average S between all pairs of intra-group samples. Because S is the algebraic sum of contributions from each variable (Eq. 1), the average similarity between samples can be expressed in terms of the average contribution from each variable (Table 2). The standard deviation provides a measure of how consistently a given variable contributes to the similarity between samples. A good characteristic variable contributes heavily to intra-habitat similarity and has a small standard deviation (Table 2). To identify discriminating features between groups of samples, SIMPER calculates the mean D for all pairs of inter-group samples (e.g. all samples of the first group against all samples of the second group). Again, since D is the algebraic sum of contributions from each variable, the mean D between samples of the first two groups can be expressed in terms of the average contribution from each variable (Table 3). A good discriminating variable contributes heavily to inter-group dissimilarity (see Table 3). These routines have been formalised in the software PRIMER (Plymouth Routines in Multivariate Ecological Research; Clarke and Warwick 1994a).

SIMPER analysis of single habitats and groups of habitats allows both α- and β-dissimilarity to be examined using a common technique. Furthermore, analysis can focus on either single or multiple variables. At the simplest level, SIMPER provides a quantitative and variable-specific explanation of differences within and between habitats (Tables 2, 3). More advanced applications may focus on the contribution made by each variable to within- or between-habitat S. Examples include (1) plotting distribution curves (e.g. k-dominance curves; Lambshead et al. 1983) for different habitats or windows in which species' abundances are replaced by contributions, (2) mapping the number of variables responsible for a given threshold of S (habitats or windows with a greater number of variables have higher diversity) or (3)

mapping the contribution of important (e.g. keystone) species to β-dissimilarity (Fig. 2; see also Westman 1990).

Hypothesis testing

Hypotheses concerning β-dissimilarity may be tested using analysis of similarities (ANOSIM; see Clarke and Green 1988; Clarke 1993; Clarke and Warwick 1994b). ANOSIM yields a test statistic (R) which contrasts observed similarities between groups of samples with those within groups. R lies between 0 and 1 depending on the discrimination between groups. Permutations then evaluate the significance of the statistic. Providing that hypotheses are developed a priori, ANOSIM can be used to monitor change in β-dissimilarity or evaluate the significance and strength of spatial patterns in diversity (see legend to Table 3). Note that ANOSIM should be used in concert with SIMPER to describe the underlying causes of a test statistic.

Discussion and applications to science and management

The technique described here adapts widely used multivariate statistical methods (Clarke 1993) to explore spatial patterns of diversity. The key advantages of the method are (1) its consistency with existing statistical methods and therefore ease of interpretation, (2) the explicit nature with which habitat differences are incorporated and described, (3) the common framework with which different scales of community structure can be examined, (4) that hypotheses may be tested and (5) that the arbitrary aspects of habitat mapping can be mitigated. Habitat variables such as species, substrata and depth relate explicitly to the data recorded by remote-sensing instruments and are therefore appropriate for mapping. However, not all habitat variables need to be included in the calculation of β-dissimilarity. For example, β-dissimilarity could be derived from either (1) the living components of the habitats (e.g. assemblages of species), (2) the living and dead components (relevant for ecosystem functioning such as including the percent of settlement space available), or (3) a functional classification derived from the components of each habitat (e.g. primary productivity). The translation of habitat maps to ecosystem functions would strongly enhance understanding of ecosystem connectedness and guide the choice of scale to manage coastal processes.

As articulated, D_m is unaffected by the relative abundance and spatial arrangement of habitats within a given window. Relative habitat abundance can be incorporated explicitly into D_m by using the raw sample data for each habitat for *each pixel*. For example, if habitat 3 was derived from samples 23–32 of the raw sample data (used for the habitat classification), and is present in 6 pixels, then the calculation of D_m would use samples 23–32 six times. Spatial weightings are desirable if examining scales of diversity because the contribution of each variable to β-dissimilarity is weighted by habitat abundance, but spatial weightings should be used with caution. First, imposing explicit spatial structure within the window is at odds with the desire to mitigate arbitrary classification of samples to habitats and habitats to pixels. It is more conservative to interpret the presence/absence of habitats within a window rather than their relative abundances. By extension, further refinements to incorporate the spatial configuration of habitats within the window have not been attempted (but see Ricotta 2000 for such methods). Second, a simple mean of habitat dissimilarity is perhaps easier to interpret than a weighted mean, whose value is sensitive to minor differences in the relative abundance of habitats. An analogous situation can be found in α-diversity measures where the simplest measures such as species richness tend to be the most widely used and easily interpreted (Gotelli and Graves 1996).

In the marine environment, most remote sensing has focused on resource inventory and detecting changes in the overall cover of habitats (Green et al. 1996). However, remotely sensed data are becoming more widely available, easier to manage, and have ever greater spatial and spectral resolutions (reviewed in Mumby 2000). The time has come, therefore, to enhance the tool box of spatial analyses (e.g. Farina 1998) and strengthen the uptake of such analyses to the science underpinning coastal management. The combination of field data and habitat maps provides a synoptic and multi-scale vista of β-dissimilarity. Thus, β-dissimilarity can be investigated at multiple scales simultaneously and a variety of spatial analyses can be applied which adjust the grain (window size), lag (distance between pixels) and extent (overall coverage) of an area (see Farina 1998). For example, spatial patterns of semi-variance and autocorrelation in β-dissimilarity can be investigated using variograms (Rossi et al. 1992). Figure 3 demonstrates how a reef habitat map reveals that β-dissimilarity is spatially autocorrelated (aggregated) at short distances of <200 m. By matching the scales of pattern to those of putative processes (Wiens 1989; Levin 1992; Underwood et al. 2000), such information is useful for developing hypotheses about the processes structuring β-dissimilarity. The role of anthropogenic processes (e.g. sewage discharge) in modifying diversity patterns (e.g. a trend towards spatial homogeneity of β-dissimilarity) are of particular concern (Gray 1997).

Maps of β-dissimilarity also have direct relevance to coastal management planning even though the underlying science is often lacking. The notions of protecting representative habitats (see McNeill 1994) and high habitat diversity (Salm and Clark 1984; G. Llewellyn, personal communication) implicitly treat habitats as distinct units. In the former case, it may be more appropriate to protect examples of biologically dissimilar habitats at the expense of the protected area of similar habitats. In the latter case, hotspots of habitat diversity should not be identified solely using standard landscape diversity indi-

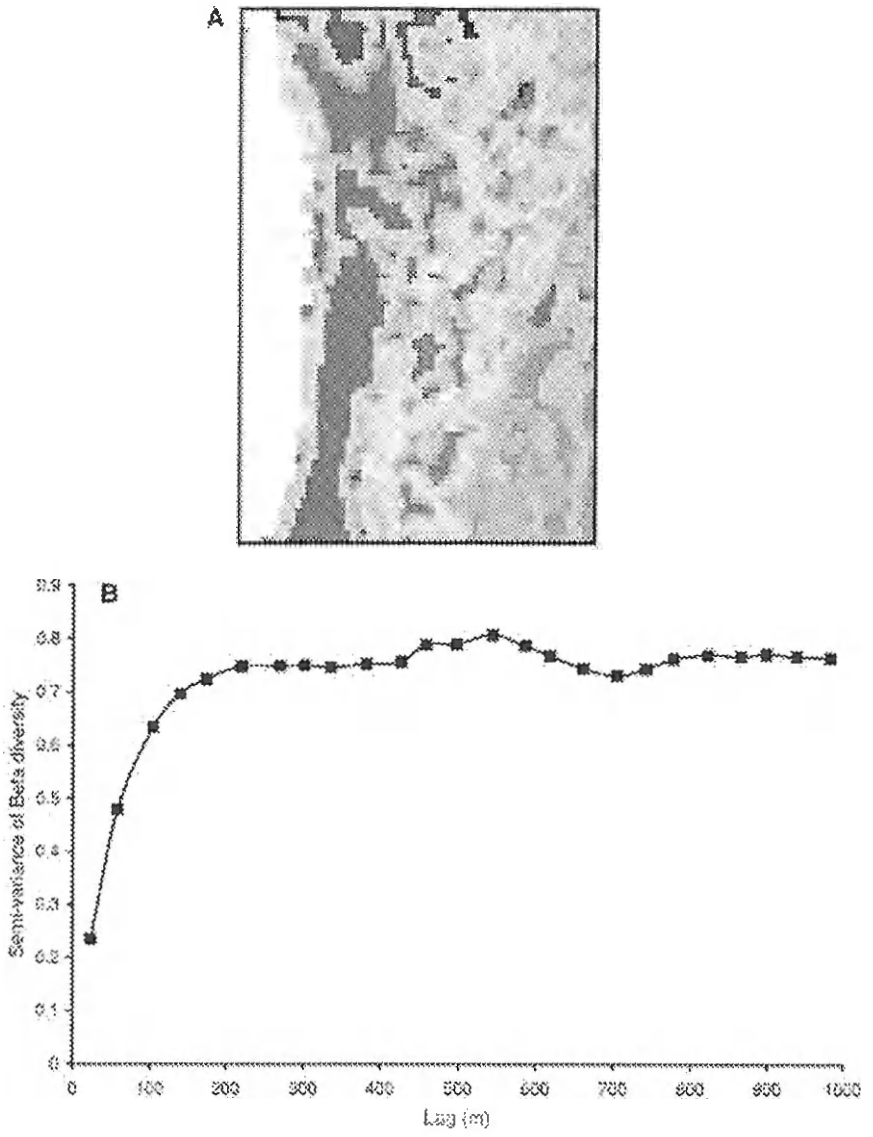

Fig. 3 **A** Map of β-dissimilarity calculated from a total of 13 reef habitats using a 3×3 pixel window. The *white area* is land (excluded). *Brighter pixels* have greater β-dissimilarity. Large mono-habitat zones occur in the vertical plane on both left and right sides of the image. The α-dissimilarity (within-habitat diversity) of habitats to the left (seagrasses) is lower (displayed as *darker*) than that of mono-habitat patches (corals) to the right. Greatest habitat diversity occurs approximately midway between pure seagrass and pure coral habitats. **B** Variogram examining spatial patterns of β-dissimilarity in a north-south plain. β-Dissimilarity is aggregated (low variance) at scales of <200 m

ces because incorporating β-dissimilarity and its associated variance will provide greater insight into diversity patterns. It must be borne in mind that no single diversity statistic is all-encompassing (Gotelli and Graves 1996) and that informed decisions should be based on a suite of methods, each of which should be readily interpretable. For example, if candidate locations for a 25-km^2 marine protected area were being evaluated, it would be appropriate to pass a 5×5 km window over a habitat map and generate a range of statistics in map form. Diversity hotspots would have high habitat richness, high β-dissimilarity and a high variance of D_m. Unfortunately, the utility of concepts such as hotspots and representativeness for conserving marine biodiversity are poorly understood and little is known of the scale dependency of processes affecting diversity. Exploratory use of the methods described here may shed light on putative processes by, for example, evaluating how windows of varying size (scale) would capture β-dissimilarity. In short, the utility of empirical measures of diversity may be greatest in the matching of pattern to putative processes (e.g. scales of dispersion of marine taxa).

Acknowledgements This work was funded by a NERC Fellowship and (later) a Royal Society University Research Fellowship. I thank Bob Clarke and Bob Foster-Smith for helpful discussions on the idea. John Gray and an anonymous reviewer improved the manuscript.

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