

MODELING THE BETA DIVERSITY OF CORAL REEFS

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Abstract. Quantifying the beta diversity (species replacement along spatiotemporal gradients) of ecosystems is important for understanding and conserving patterns of biodiversity. However, virtually all studies of beta diversity focus on one-dimensional transects orientated along a specific environmental gradient that is defined a priori. By ignoring a second spatial dimension and the associated changes in species composition and environmental gradients, this approach may provide limited insight into the full pattern of beta diversity. Here, we use remotely sensed imagery to quantify beta diversity continuously, in two dimensions, and at multiple scales across an entire tropical marine seascape. We then show that beta diversity can be modeled ($0.852 \geq r^2 \geq 0.590$) at spatial scales between 0.5 and 5.0 km², using the environmental variables of mean and variance of depth and wave exposure. Beta diversity, quantified within a “window” of a given size, is positively correlated to the range of environmental conditions within that window. For example, beta diversity increases with increasing variance of depth. By analyzing such relationships across seascapes, this study provides a framework for a range of disparate coral reef literature including studies of zonation, diversity, and disturbance. Using supporting evidence from soft-bottom communities, we hypothesize that depth will be an important variable for modeling beta diversity in a range of marine systems. We discuss the implications of our results for the design of marine reserves.

Key words: beta diversity; biodiversity; coral reefs; landscape ecology; marine reserves; St. John; St. Thomas; U.S. Virgin Islands; wave exposure.

INTRODUCTION

Establishing a theoretical framework for understanding the patterns and controls of biodiversity is a major focus of ecology. A key component of this framework is understanding variations in the diversity of species, but research has tended to focus on the diversity of species at local (alpha diversity) or regional (gamma diversity) scales, and beta diversity has received relatively little attention (Gaston and Williams 1996). Since the term was introduced by Whittaker (1960), “beta diversity” has grown to incorporate a range of concepts but is generally regarded as referring to some component of how two or more sampling units vary across spatial or temporal axes (e.g., Magurran 2004). Even with this relatively simple concept, there has been extensive debate on the most appropriate scales and metrics for quantifying beta diversity (Wilson and Shmida 1984, Gray 2000, Koleff et al. 2003, Magurran 2004). However, it is clear that beta diversity is an important property of ecosystems (Harrison et al. 1992, Tuomisto et al. 1995, Condit et al. 2002). Beta diversity provides insights into the partition of habitats by species (Wilson and Shmida 1984) and constitutes an empirical and theoretical link between alpha and gamma diversity

(e.g., Cornell and Lawton 1992, Loreau 2000). Beta diversity is also important in conservation planning because it can be measured at scales appropriate for management (Condit et al. 2002) and is a potential proxy for a range of ecosystem functions and processes.

Empirical studies of beta diversity have typically been conducted along transects or environmental gradients (Magurran 2004) that are appropriate for particular research questions. Such approaches inevitably limit examination of beta diversity to axes that may not be the most important for all the taxa of interest and potentially confound investigations by not explicitly considering all the factors that may influence species turnover across a landscape. Here we examine beta diversity both continuously in two dimensions and at a variety of spatial scales across seascapes, and link the resulting patterns to putative controlling variables. Such an unconstrained perspective, where it is unnecessary to predefine transects or gradients of interest, is made possible by advances in our ability to map ecosystems and generate continuous data layers of a range of environmental factors using remotely sensed imagery.

The study focused on the beta diversity of coral reefs. Like all ecosystems, investigation of the beta diversity of the coral reef ecosystem is limited (but see Price 2002, Connell et al. 2004), which is surprising given their high alpha diversity and setting within regions of high gamma diversity (e.g., Cornell and Karlson 2000) and long-standing use as a model system for studies of diversity

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and community structure (Sale 1977, Connell 1978, Sheppard 1982, Huston 1985, Karlson et al. 2004). Coral reefs are also particularly appropriate for mapping because clear waters permit high light penetration, and the coastal shelf is often sufficiently shallow to allow discrimination of benthic habitats (Green et al. 1996). The areal coverage, pattern, and context of reef habitats can now be mapped over a continuum of spatial scales using high-resolution hyperspectral sensors mounted on aircraft (Mumby et al. 2001).

Coral reef communities and ecosystem processes are structured by a range of variables acting over a hierarchy of scales (Hatcher 1997, Harborne et al. 2006). To facilitate development of statistical models of beta diversity we focus on two key variables: depth and wave exposure (e.g., Sheppard 1982, Done 1983, Huston 1985). While not directly influencing community structure, depth is a proxy for numerous environmental gradients such as light intensity, temperature, and salinity (Buddemeier and Kinzie 1976). Although wave energy and depth are correlated, with deeper areas being generally less exposed than shallower areas, exposure embodies the variation in aspect, which is important at the scale of seascapes; a section of reef at a depth of 5 m may be exposed to the prevailing winds or in a sheltered bay.

This study generates multiple-scale, two-dimensional maps of beta diversity for the first time. We find that beta diversity can be modeled effectively using two variables and consider the ecological and conservation implications of the results.

METHODS

Study site

The study was carried out around the islands of St. Thomas and St. John in the U.S. Virgin Islands (USVI). The U.S. Virgin Islands form part of the Lesser Antilles, a Tertiary island arc system lying at the eastern boundary of the Caribbean plate (Adey et al. 1977). Reefs within this area are found on metamorphosed volcanic bedrock (Donnelly 1966) and typically slope to a depth of 10–15 m before merging into a reef shelf (Witman 1992). St. John and St. Thomas are ideally suited to our objectives because a wide range of biological communities are present (Adey et al. 1977, Beets et al. 1986), but the islands are small enough (St. Thomas is 82 km² and St. John is 52 km²) and close enough (<5 km apart) to ignore intrahabitat variations in community structure.

Community composition

A total of 402 sites around both St. John and St. Thomas were visited between 2 and 16 April 2001; geographical coordinates, depth, and benthic community type were recorded to facilitate ground-truthing of remotely sensed imagery and assessment of benthic community structure. A classification scheme of 19 benthic communities in the USVI was established based

on knowledge of the spectral capabilities of the remote-sensing instrument used (CASI; see Mumby et al. 2001), previous Caribbean fieldwork, and classification schemes (Mumby and Harborne 1999, Green et al. 2000), and discussions with local researchers. A subset of ~10% of sites, haphazardly placed 0.25-m² quadrats were used to quantify the species composition of each benthic community. The subset of sites was chosen to ensure (a) representation of data from each benthic community, (b) replicate data from benthic communities at different sites around both islands, and (c) more data from more diverse (typically reef) communities. The content of quadrats was filmed in 10-cm swathes, using a high-resolution digital video camera. Following completion of all the swathes within a given quadrat, cryptic organisms and areas of high relief (e.g., under ledges and the sides of large mounds) were filmed in more detail. A mean of 12 quadrats (maximum 45) were sampled per habitat, depending on the diversity of the community. The digital video of each quadrat was projected onto a large television monitor for analysis. Analysis consisted of identification (presence/absence) of species of scleractinian corals (minimum diameter one centimeter), macroalgae, macroscopic mobile invertebrates, sponges, and gorgonians to the highest taxonomic resolution possible. Data were then converted to frequency of occurrences (number of times present divided by number of quadrats) for each taxon at each site. Frequencies of occurrence were averaged across replicates to provide mean values for each benthic community.

Habitat maps

The Compact Airborne Spectrographic Imager (CASI) is a state of the art remote sensing instrument capable of mapping coral reef communities accurately (Mumby et al. 1998). Over 410 km² of CASI imagery were collected around St. John and St. Thomas between the 31 March and 18 April 2001. CASI data were collected at pixel sizes of either 1 × 1 m or 2 × 2 m with 19 spectral bands. CASI imagery was supplied as a series of geometrically corrected flight lines. Sun glint (specular reflection of the sun on non-flat water surfaces) on each line was reduced to maximize the observable detail of benthic habitat types; the land and clouds were masked to leave only marine communities. Sun glint removal was achieved using the method of Hedley et al. (2005). Maps were prepared using unsupervised classification with contextual decision rules (see Mumby et al. 1998). Pixels were then resampled to 10 × 10 m to filter out aberrant pixels that had been caused by sensor noise and specular reflection (Appendix A).

The study focused explicitly on shallow lagoon and forereef environments with a maximum depth of ~15 m. Beyond this depth, the distribution of many features (e.g., patches of hard-bottom) are probably the result of antecedent topography rather than biophysical structuring in the Holocene, for which we have data (i.e., present-day depth and wave exposure). Therefore, the

deepwater shelf was represented as a homogeneous soft-sediment community.

Measurement of bathymetry

Bathymetry was mapped using Landsat 5 TM imagery (collected on 7 February 1991) and the “depth of penetration” method of Jupp (1988). Briefly, the method exploits differences in the penetration of water by light of different wavelengths. The four bands of shortest wavelength can be used to segment the water column into four depth of penetration zones (DOPZ), each representing pixels where light is reflected in one band but not the next and hence representing water between particular minimum and maximum values. Further analysis and calibration for the water quality characteristics of the study area facilitates interpolation of spectral signals within each DOPZ and assignment of each pixel to a specific depth (± 1 m). Landsat TM pixels measure 30×30 m so each bathymetric map was rescaled to a common 10×10 m grid, generating a depth for every pixel on the habitat map but only discerning features at the larger spatial scale.

Measurement of wave exposure

Wave exposure in marine ecological studies is typically measured at a few sites using one of many available techniques (e.g., current meters, de Boer et al. 2000). For this study we required continuous, spatially explicit estimates of wave energy for each pixel. Ekeboom et al. (2003) provide a method for assessing physical exposure at any point by measuring fetch and then using linear wave theory to convert fetch to wave height and period, and then wave power. This approach is utilized here with additional revisions that will be detailed in a future article but are outlined in Appendix B. Note that the two key revisions to the method are (1) a clear theoretical framework for when to change from using the equations appropriate for a “fetch-limited” sea (when increasing the fetch will increase wave height) to those for a “fully developed” sea (when wave height does not increase with increasing fetch because wind energy input is balanced by dissipation from wave breaking and turbulence) and (2) the dependence of wave energy on water depth.

Beta diversity algorithm

Beta diversity was calculated using bespoke scripts written in MATLAB 6.1. For each pixel in the map, an algorithm assessed the composition of habitats within an area (“window”) of given size centered on that pixel. The window of pixels grew outwards from the focal “seed” pixel in a method analogous to conducting a pixel-to-pixel random walk in all possible directions simultaneously. The walk was iterated until the desired area of the window was achieved. This algorithm generated circular windows when no land was present but was able to “grow” around headlands and islands when necessary.

The algorithm returned the number of pixels in each habitat category within the window and beta diversity (B_d) was calculated as follows:

$$B_d = \log_{10} \sum_{i=1}^{i=H-1} \sum_{j=i+1}^{j=H} (100D_{ij})^2 \times \frac{-\sum_{i=1}^H P_i \ln P_i}{\ln H} \quad (1)$$

where H is the number of habitats within the window, D_{ij} is the the Bray-Curtis dissimilarity coefficient (Bray and Curtis 1957) between the i th and j th habitats following a square root transformation of the community composition data, and P_i is the the proportion of the window consisting of the i th habitat.

Eq. 1 is a modification of the metric proposed by Mumby (2001). Note that the additional second term in Eq. 1 is analogous to the Shannon equitability index, J , for species evenness (Shannon and Wiener 1963). The modified measure of beta diversity has the following properties: (1) beta diversity increases with an increasing number of habitats; (2) for a given number of habitats, beta diversity is largest for those combinations where the differences between community compositions are greatest; and (3) for a given combination of habitats, beta diversity is highest where the habitat coverage is most equitable within the target window. The use of dissimilarity coefficients to assess beta diversity is widely recognized (Magurran 2004).

Spatial scales of windows

The beta diversity algorithm can be applied to windows of any size, but in this study was limited to sizes of 0.5, 1.0, 2.5, and 5.0 km² around each pixel. The same windows were used to calculate the mean and variance of depth and wave exposure around the same pixel. The benthic community “sand” was excluded from all analyses because its virtual absence of epibenthic species contrasted with all other communities (mean Bray-Curtis dissimilarity of 0.93). Such high values skew beta diversity, and the aim of this study was to examine patterns of contrasting habitats, rather than identifying areas with a high beta diversity simply because of the presence of a unique community that is very different because of its *lack* of species. Therefore, after the window growing algorithm returned the number of pixels of each benthic community, “sand” pixels were discounted prior to calculating beta diversity (Eq. 1).

Statistical analysis

Window generation at each spatial scale created a beta diversity value and values for each of the four explanatory variables (mean and variance of depth and wave exposure) for every pixel. Modeling beta diversity with respect to the four explanatory variables utilized a generalized least squares (GLS) model in NLME package for R (Pinheiro and Bates 2000). The GLS model allowed patterns of spatial autocorrelation to be added explicitly to the model. To find the most suitable model



PLATE 1. Beta diversity is high where hard- and soft-bottomed habitats coexist, such as this patch reef within a seagrass bed. Photo credit: Jonathon Ridley (Coral City Conservation).

for the correlation structure for each window size for each island, we first calculated residuals for the data set (1545 points for St. John, 1756 for St. Thomas, systematically derived from the full data set) using a full model (all variables included) without any correlation structure. Ideally these residuals would be used to generate a semivariogram, but calculating the distance, and subsequently incorporating a correlation matrix, between every pair of samples was computationally prohibitive. Distance values had to be calculated using a bespoke algorithm which finds the shortest path, without crossing land, between pairs of points. Note that the “within sea” distance does not imply any notion of direction and hence there is an assumption of isotropy.

For tractability, the data were separated into nine systematically derived sub-samples and distances calculated between each pair of points in each subsample. Nonparametric, robust estimates of spatial correlation (Cressie 1991) were then calculated for each of the nine semivariograms. The Matérn function (Matérn 1986) was used to model the correlation structure in the data because it provides a wide class of possible correlation structures. Firstly, the parameters of the function were estimated from the nonparametric semivariograms by weighted least squares (WLS) for each data subset. In some cases (for the smallest scale of window [0.5 km²] around St. John and for the two largest scales [2.5 and 5.0 km²] around St. Thomas), the parameters in the Matérn function were restricted to ensure that the correlation did not increase rapidly outside the considered range; this was consistent with patterns seen for other window sizes. Secondly, a single pooled estimate of semivariogram parameters was obtained from all nine subsets using WLS.

GLS models incorporating correlation structure were then fitted to each subsample of data, and a “pooled” estimate of the coefficient and significance of each term

was obtained as a weighted combination of all nine estimates. Models were chosen so that they included all the significant linear, quadratic, logarithmic, and pairwise interaction terms. Even though, for tractability reasons, the models take into account only the correlation within subsets, diagnostic plots of normalized residuals vs. fitted values and Q–Q plots revealed no serious departures from the model assumptions. Models were assessed by calculating the coefficient of determination, r^2 . Finally, to provide some insight into the generality of the results, models from one island were fitted to data from the other island and assessed using r^2 . Statistical techniques used in this study are described in more detail in Appendix C.

RESULTS

Community compositions and environmental settings

The eighteen benthic communities used in this study contained 150 taxa (Appendix D details the frequency of each taxon in each habitat and the dissimilarity between each pair of habitats) and inter-habitat differences are significantly greater than intra-habitat variations (ANOSIM, $R = 0.847$, $P = 0.001$). A nonmetric, multidimensional scaling (MDS) ordination provided insight into the functioning of the beta diversity algorithm (Fig. 1); for example, the coral dominated communities were relatively similar to each other but were very different from soft-bottom communities. Therefore, windows containing an even mix of soft-bottom and coral-dominated habitats have high beta diversity (beta diversity ranged from 0 to ~4.5; Fig. 2) (see Plate 1). Such “hotspots” of beta diversity can be seen within seagrass-dominated bays along the south coast of St. John (Fig. 2). It is difficult to provide a succinct summary of the contribution of each taxon to beta diversity because contributions vary throughout the

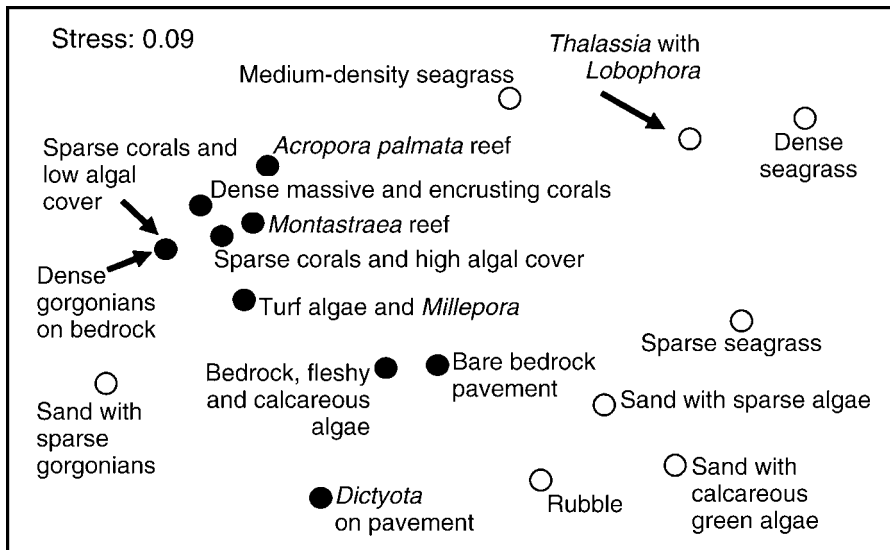


FIG. 1. Ordination from nonmetric multidimensional scaling of benthic community composition data used for beta diversity calculations around St. John and St. Thomas, U.S. Virgin Islands. The relatively low stress (0.09) indicates that the two-dimensional distances are a good representation of the multidimensional similarity between communities. Closed circles represent hard-bottom habitats; open circles represent soft-bottom habitats.

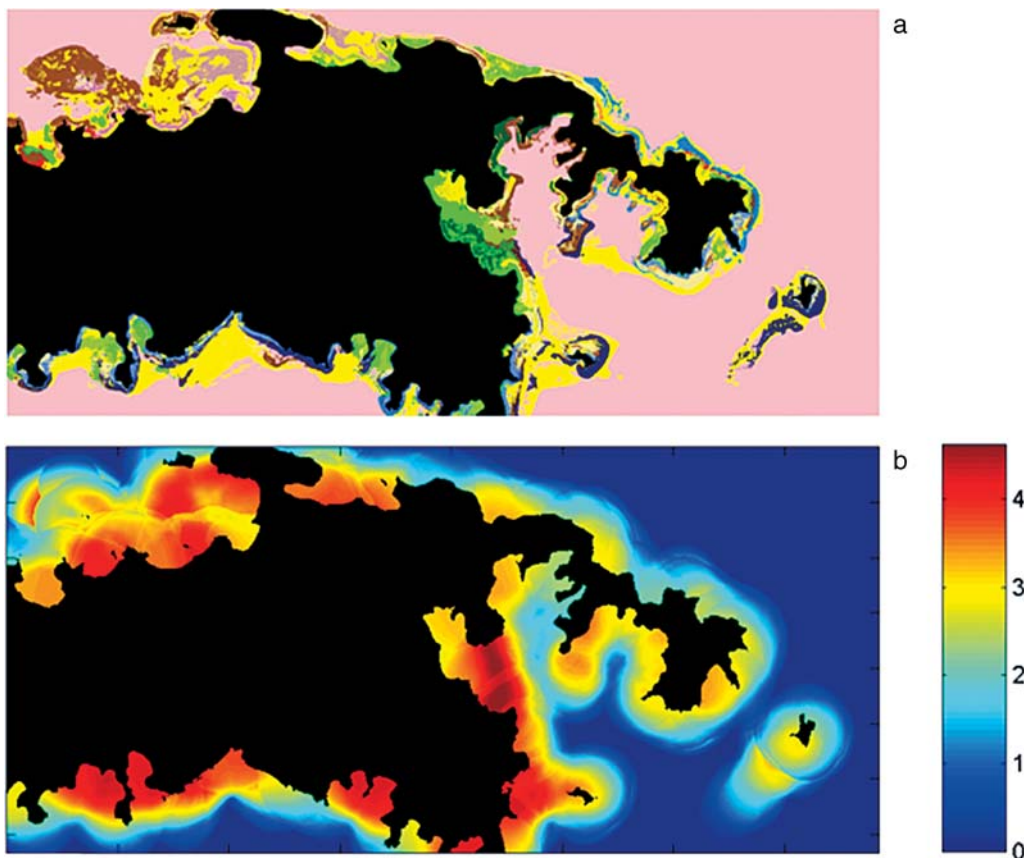


FIG. 2. A comparison of (a) habitat map and (b) map of beta diversity for St. John. (a) Coral-rich habitats are shown in blue, reef crest in red, hard-bottom habitats in brown, seagrass habitats in green, soft-bottom habitats in pink, and sand in yellow (maps with full legends are provided in Appendix A). (b) Beta diversity (key at right) was calculated using a window of 1 km². The area bounded by the map is 7.3 × 15.7 km.

TABLE 1. Mean depths and exposures (SE in parentheses) of each habitat type around St. John and St. Thomas, U.S. Virgin Islands.

Habitat type	St. John			St. Thomas		
	<i>n</i>	Depth (m)	Exposure (J/m ³)	<i>n</i>	Depth (m)	Exposure (J/m ³)
Dense massive and encrusting corals	15 222	14.62 (0.05)	0.003 (0.001)	22 470	13.94 (0.03)	0.186 (0.009)
Turf algae and <i>Millepora</i>	12 878	5.79 (0.04)	0.002 (0.0003)	20 067	6.13 (0.03)	1.013 (0.020)
<i>Acropora palmata</i> reef	754	3.55 (0.10)	2.530 (0.146)
Sparse corals and low algal cover	23 418	8.38 (0.03)	0.074 (0.005)	25 452	7.95 (0.03)	0.443 (0.012)
Sparse corals and high algal cover	11 124	9.53 (0.05)	0.112 (0.008)	55 077	14.20 (0.03)	0.629 (0.010)
<i>Montastraea</i> reef	7226	12.58 (0.06)	0.005 (0.001) NS	3283	10.77 (0.05)	0.020 (0.007) NS
Medium-density seagrass	19 645	7.03 (0.04)	0.115 (0.006)	32 676	8.97 (0.03)	0.006 (0.0003)
Rubble	79	6.75 (0.40) NS	3.19 × 10 ⁻¹² (1.74 × 10 ⁻¹²)	404	7.98 (0.11) NS	0.137 (0.050)
Sparse seagrass	13 432	8.19 (0.04)	0.020 (0.002)	10 439	7.00 (0.04)	0.002 (0.0003)
Dense seagrass	5149	6.65 (0.06)	0.0001 (1.09 × 10 ⁻⁵)	20 921	7.85 (0.04)	0.00009 (3.42 × 10 ⁻⁵)
Dense gorgonians on bedrock	25 365	10.48 (0.04)	0.449 (0.011)	4060	8.35 (0.11)	3.141 (0.070)
Sand with sparse gorgonians	4749	4.65 (0.04)	0.164 (0.009)	409	6.08 (0.20)	0.002 (0.0002)
Bare bedrock pavement	2616	5.35 (0.07) NS	0.103 (0.013) NS	7151	5.24 (0.04) NS	0.554 (0.026) NS
Sand with sparse algae	1 566 925	19.97 (0.002)	0.003 (0.0001) NS	1 495 777	18.44 (0.003)	0.006 (0.0002) NS
<i>Dictyota</i> on pavement	1817	9.39 (0.09)	0.013 (0.002)	7467	10.30 (0.04)	0.165 (0.014)
Bedrock, fleshy and calcareous algae	2768	8.71 (0.05)	0.001 (0.001)
Sand with calcareous green algae	8117	14.38 (0.07)	0.010 (0.001)	8341	13.15 (0.02)	1.94 × 10 ⁻⁷ (1.94 × 10 ⁻⁷)
<i>Thalassia</i> with <i>Lobophora</i>	849	12.72 (0.03)	1.09 × 10 ⁻²⁸ (4.16 × 10 ⁻²⁹)

Notes: Sample size, *n*, is the number of pixels containing each habitat type and indicates the areal extent of each habitat (see Appendix A for habitat maps). Comparisons (e.g., mean exposure of *Montastraea* reefs on St. John vs. St. Thomas) that are not significantly different ($P > 0.05$) are denoted ns.

seascape and depend on the specific combination and relative areas of habitats found within a window. However, a comprehensive table of key discriminatory taxa between each pair of habitats is provided in Appendix D. In general, most taxonomic groups, including hard corals, gorgonians, algae, and seagrasses are well represented in driving patterns of beta diversity. The main exceptions are sponges and other invertebrate groups such as Actinaria, Annelida, and Ascidiacea, which offer weak discriminatory power among habitats (Appendix D). *Thalassia* and *Syringodium* are particularly important discriminating species in any comparison including a seagrass community. Corals, gorgonians, and algae tend to drive the differences between hard-bottom communities.

The mean depth and exposure of each benthic community around each island provides a summary of their environmental settings (Table 1). With the exception of those highlighted, almost all communities differ significantly in their depth and exposure between islands (Mann-Whitney test, $P < 0.05$).

Modeling beta diversity

GLS modeling can incorporate a range of terms (e.g., linear, quadratic, and logarithmic) for each putative explanatory variable considered. Exploratory analysis of the relationship between beta diversity and each variable aids model construction and in this study revealed

similar relationships for all window sizes. Scatter plots suggested that the relationships between beta diversity and mean depth and variance of depth were quadratic (Fig. 3a, b) but were logarithmic with the mean and variance of wave exposure (Fig. 3c, d). The form of such relationships may not be borne out by the GLS because of interactions among variables. However, all four independent variables contributed significantly to the models of beta diversity, and the terms generally (26 of 29 terms) matched those suggested by the scatter plots (Table 2). Models for St. John explained a large proportion of the variance of beta diversity ($0.852 \geq r^2 \geq 0.590$) but were less appropriate when applied to data from St. Thomas ($0.574 \geq r^2 \geq 0.502$). Coefficients of determination for models from St. Thomas were similar ($0.652 \geq r^2 \geq 0.598$) but generally lower than those for St. John. When models for St. Thomas were applied to data from St. John, r^2 ranged from 0.405 to 0.213.

Only at the largest spatial scales (St. John, 2.5 and 5 km²; St. Thomas, 5 km²) was the logarithm of variance of exposure excluded from the model, which might be caused by the high dependence between this variable and its mean. For the reefs of St. John, the dependence on the mean and variance of depth was quadratic for all spatial scales. Similar quadratic terms were found for St. Thomas but were replaced by linear terms on a few occasions (linear for variance of depth at 1 km² and 5 km², linear for mean depth at 2.5 km²). Interactions

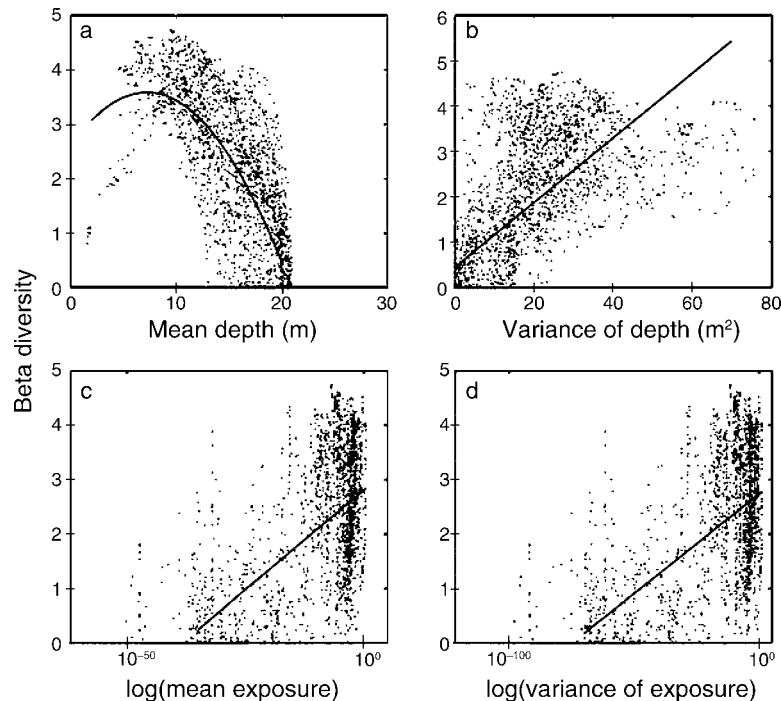


FIG. 3. Scatter plots of beta diversity against (a) mean depth, (b) variance of depth, (c) log mean exposure (measured in J/m^3), and (d) log variance of exposure (measured in J/m^6) for a window size of 0.5 km^2 around St. John. Trend lines are quadratic (mean depth), linear (variance of depth), and logarithmic (mean and variance of exposure). For mean depth, $r^2 = 0.684$; for variance of depth, $r^2 = 0.488$; for mean exposure, $r^2 = 0.517$; and for variance of exposure, $r^2 = 0.515$ ($P < 0.001$ in all cases).

between depth and exposure were significant in most models (Table 2) and, in some cases, the interaction between mean of depth and variance of depth was also included (e.g., St. John, 5 km^2).

DISCUSSION

Using high-resolution remote sensing together with detailed field survey, we mapped and modeled beta diversity across an entire seascape and at multiple spatial scales. GLS models for each island explicitly account for spatial correlation and with only two environmental variables explain $\geq 59\%$ of the variance in the data.

Impact of depth and exposure on beta diversity

Community structure varies across coral reefs and associated habitats because of the biotic and abiotic requirements of each species. These multivariate niches combine and often form feedback loops with environmental gradients to produce the well-established patterns of vertical zonation on coral reefs (e.g., Geister 1977, Sheppard 1982, Done 1983). Beta diversity will, therefore, increase as a greater proportion of any particular gradient is sampled, yielding a greater range of benthic communities. While not necessarily expressed in terms of beta diversity, this principle is enshrined in a variety of coral reef studies including the literature on zonation, patterns of coral diversity across reefs (e.g., Huston 1985, Cornell and Karlson 2000), and the

intermediate disturbance hypothesis (Connell 1978, Aronson and Precht 1995). Indeed, the many coral reef papers that use multivariate statistical techniques to discriminate benthic communities are measuring an aspect of beta diversity, but few make the link explicit (Mumby 2001, Price 2002, Connell et al. 2004 are exceptions). Crucially, however, by considering continuous seascapes, we are able to represent many of the patterns established in the literature in two dimensions by combining the dissimilarity between, and distribution of, benthic communities. Of the many processes and environmental factors that contribute to such patterns (e.g., carbonate bioconstruction, antecedent topography, currents, sedimentation, and biotic interactions) we investigated how just two proxy variables explained the patterns of beta diversity and, therefore, provide an empirical framework for a more integrated understanding of previous observations.

Beta diversity increased with increasing variation of depth. Windows with a low variance of depth will tend to incorporate homogeneous environmental conditions and few benthic communities. In contrast, windows with a high variance of depth will span a series of environmental gradients, incorporate a range of different benthic communities, and contain high beta diversity. The quadratic term for variance of depth was surprising and may indicate that steeply sloping forereefs (which have the highest values of variance) only support a limited number of habitats compared to the greater

TABLE 2. Summary of the generalized least-squares models for the beta diversity of reefs around St. John and St. Thomas.

Window size and island	Correlation at 1 km	Model variables (with coefficients in parentheses)	r^2 (source island)	r^2 (other island)
0.5 km ²				
St. John	0.672	M_d (0.002), M_d^2 (-0.007**), V_d (0.044**), V_d^2 (-0.001**), $\log(M_e)$ (-0.962**), $\log(V_e)$ (0.520**), $M_d \times \log(M_e)$ (0.044**), $M_d \times \log(V_e)$ (-0.024**)	0.590	0.523
St. Thomas	0.496	M_d (0.052), M_d^2 (-0.010**), V_d (0.080**), V_d^2 (-0.0004**), $\log(M_e)$ (-0.181**), $\log(V_e)$ (0.092**), $M_d \times V_d$ (-0.002**), $V_d \times \log(V_e)$ (0.0002*)	0.598	0.390
1.0 km ²				
St. John	0.547	M_d (-0.017), M_d^2 (-0.006**), V_d (0.044**), V_d^2 (-0.0004**), $\log(M_e)$ (-1.315**), $\log(V_e)$ (0.719**), $M_d \times \log(M_e)$ (0.062**), $V_d \times \log(M_e)$ (0.007**), $M_d \times \log(V_e)$ (-0.034**), $V_d \times \log(V_e)$ (-0.004**)	0.775	0.573
St. Thomas	0.577	M_d (0.088*), M_d^2 (-0.012**), V_d (0.035**), $\log(M_e)$ (-0.093**), $\log(V_e)$ (0.049**)	0.610	0.293
2.5 km ²				
St. John	0.542	M_d (0.038), M_d^2 (-0.013**), V_d (0.019**), V_d^2 (-0.0004**), $\log(M_e)$ (0.100**), $M_d \times \log(M_e)$ (-0.005**), $V_d \times \log(M_e)$ (-0.001**)	0.822	0.502
St. Thomas	0.690	M_d (-0.297**), V_d (-0.030*), V_d^2 (-0.001**), $\log(M_e)$ (-0.606**), $\log(V_e)$ (0.312**), $M_d \times V_d$ (0.005**), $M_d \times \log(M_e)$ (0.033**), $M_d \times \log(V_e)$ (-0.017**)	0.648	0.213
5.0 km ²				
St. John	0.748	M_d (0.175), M_d^2 (-0.011*), V_d (0.157**), V_d^2 (-0.001**), $\log(M_e)$ (0.168**), $M_d \times V_d$ (-0.006**), $M_d \times \log(M_e)$ (-0.008**), $V_d \times \log(M_e)$ (-0.002**)	0.852	0.574
St. Thomas	0.692	M_d (-1.454**), M_d^2 (0.032**), V_d (-0.103**), $\log(M_e)$ (0.005**), $M_d \times V_d$ (0.009**), $V_d \times \log(M_e)$ (-0.0004**)	0.652	0.405

Notes: The r^2 values represent explanatory power of model when applied to the same data set from which it was derived ("source island") and when applied to data from the other island. Order of variables is arbitrary; "×" symbols indicate interaction terms. M_d = mean depth; V_d = variance of depth; M_e = mean exposure; V_e = variance of exposure. The intercept term within models was always significant ($P \ll 0.01$) except for the 5 km² model for St. John.

* $P < 0.05$; ** $P < 0.01$.

zonation (higher beta diversity) of gently sloping forereefs. Beta diversity also increased with increasing variance of wave exposure. Windows with high variance of exposure exhibit a wide range of aspect, such as the exposed and lee sides of a headland where zonation patterns could be very different, or spanning a low-energy lagoon, high-energy reef crest, and moderately exposed forereef. Such areas contain a range of environmental conditions and hence a variety of habitats and high beta diversity. Logarithmic terms suggest that a given change in variance of exposure has a greater influence on beta diversity when variance is low (<0.1 joules/m³) than when it is high. Such terms highlight the existence of discontinuities in exposure, such as those found either side of a reef crest, which can create strong nonlinearities between variance of exposure and beta diversity.

The inclusion of terms for mean depth (quadratic) and exposure (logarithmic) can be explained by the topography of the U.S. Virgin Islands. Windows with a low mean depth will tend to encompass *only* a few shallow habitats (e.g., seagrass beds) while windows with a high mean depth will contain *only* the homogeneous bank habitat so that variance of depth and beta diversity will be low. Beta diversity will be highest when windows span the entire reef profile (high variance of depth), and

this occurs when mean depth is intermediate (~10–15 m). This quadratic relationship between mean and variance of depth will vary between reefs, such as where the seaward edge of the reef terminates with an escarpment descending to the abyssal plain.

St. John and St. Thomas were selected for this study because of their similar size and proximity. Despite their similarities, the fit of models of beta diversity differed, with the coefficient of determination being generally higher for St. John. It is clear that most habitats differ in their mean depth and wave exposure between islands, and this may be linked to factors such as St. Thomas being sheltered from prevailing easterly winds by St. John, the large south-facing bay in eastern St. John which is not present on St. Thomas (and differs in zonation from other sections of reef; Appendix A), or differences in antecedent topography so that depth and exposure alone were able to explain less of the variance in beta diversity around St. Thomas. Factors such as antecedent topography could be added in future models to explain some of the remaining variance. In addition, the history of hurricane disturbance, which may strongly impact benthic community structure (Rogers et al. 1991, Witman 1992, Bythell et al. 2000, Edmunds 2002), could be added to models to explain the remaining variance in beta diversity. However, it is difficult, a priori, to select

appropriate spatial or temporal scales to quantify hurricane impact and a series of exploratory analyses would help generate specific hypotheses concerning these acute disturbances.

To examine patterns of beta diversity in two dimensions and over a range of spatial scales, it was necessary to combine state-of-the-art remote sensing and intensive field survey. This approach implicitly assumes that the averaged descriptions of community structure are adequate representations of each habitat type, i.e., that patterns of community structure within a given habitat type are similar throughout the seascape. The assumption is necessary because it is not logistically feasible to survey every habitat patch in a seascape and because the relationship between patch size and alpha diversity has not yet been quantified. Though the assumption is yet to be tested, it should not obscure the interpretation of results at the relatively small extent studied here (tens of kilometers). Systematic patterns of intra-habitat community structure are relatively unlikely and a random sampling of habitats should capture much of the variation. Furthermore, the use of relatively large window sizes, in which individual habitat patches may exceed 0.5 km², should minimize variability in alpha diversity. However, more sophisticated methods would be required if the extent of the study breached biogeographic boundaries. In this case, the beta diversity algorithm should allow inter-habitat dissimilarity to adapt to local changes in community structure along appropriate gradients, such as latitude.

Efficacy of environmental predictors of beta diversity

In the present study, a combination of just two variables explained up to 85% of the variance in beta diversity. Many biological and ecosystem processes in tropical coastal ecosystems are driven by light, the flux of nutrients, and physical disturbance, all of which are influenced by depth or wave exposure. Of the five major ecosystem processes reviewed by Hatcher (1997) (accretion, biological production, organic decomposition, biogeochemical cycling, and maintenance of biodiversity), all would be expected to be influenced by depth or exposure, making these variables excellent proxies. Although the lack of analogous studies of beta diversity limits the number of comparisons that can be drawn, it would be instructive to quantify the degree to which processes in other ecosystems can be represented by surrogates. Overarching variables that act as proxies for many processes, as depth and exposure do on coral reefs, may not be present in many systems. We would, therefore, expect models for such systems to be more complex than those demonstrated here. For example, although not directly comparable, Duivenvoorden et al. (2002) required five factors (distance [the dispersal process], elevation, precipitation, age of forest stand, and the type of bedrock) to explain 41% of the variation of beta diversity in tropical forests. The level of surrogacy

for ecosystem processes may prove to be fundamentally different between marine and terrestrial systems.

Depth may be a key environmental proxy for most marine systems. Studies of the beta diversity of macrobenthos in soft sediments also found depth to be an important factor. Ellingsen and Gray (2002) found that Bray-Curtis similarity among discrete sediment samples was higher when their depths were similar. Community similarity halved, indicating an increase in beta diversity, over a depth change of ~130 m. Therefore, the data of Ellingsen and Gray (2002), together with the data reported here, generate the hypothesis that depth is an important control, or at least an excellent proxy for controlling variables, of beta diversity in marine systems. The great explanatory power of depth implies that changes in sea level could have profound impacts on the beta diversity of marine ecosystems.

Implications for biodiversity conservation

Beta diversity is an intrinsic component of biodiversity, and its consideration can assist in achieving conservation targets during the selection of reserves. Firstly, beta diversity lends itself to conservation planning because it can be measured, and potentially conserved, at the scale of management units (Condit et al. 2002), which in the case of marine reserves may comprise several square kilometers. Secondly, areas of high beta diversity typically encapsulate strong environmental gradients that control and maintain patterns of species diversity (Reyers et al. 2002). Thirdly, areas with high beta diversity would be expected to be rich in "transitional communities" across ecotones, which might be expected to have distinct species assemblages and perhaps particular ecological functions. Ecotones are well studied in terrestrial ecosystems (Ries et al. 2004 provide a review and predictive model of habitat edge responses) but have received little attention in seascapes. Finally, beta diversity may prove to be an effective scale of diversity to represent ecosystem functions and processes; areas with a rich diversity of habitats may have greater overall productivity because the range of biotopes facilitates trophic cascades across the seascape. For example, Mumby et al. (2004) show that mangroves in Belize enhance the biomass of reef fish communities. When mangroves are present (higher beta diversity seascape) the biomass of several commercially important species is more than doubled on neighboring reefs compared to reef systems where mangroves are absent (lower beta diversity).

Habitat maps generated from remotely sensed imagery are routinely used in marine conservation (Cendrero 1989). Despite the cost of generating these maps, the tools available to conservation scientists for translating patterns seen across seascapes into optimal strategies for siting marine reserves are limited. We have shown that beta diversity can be quantified across seascapes forming an explicit link between mapped information and the species level data collected within

habitats. Maps of beta diversity have immediate use in reef conservation planning by identifying areas with a high diversity of contrasting habitats at a given spatial scale. Providing that the scale is not so small that individual habitat patches lose alpha diversity, this approach increases the likelihood that many species and transitional habitats (e.g., ecotones) would be incorporated within the site selection process. Reyers et al. (2002) provide a terrestrial example of how consideration of beta diversity resulted in an optimal network of conservation areas. Future studies will examine the link between beta diversity and ecosystem processes in greater detail.

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APPENDIX A

Habitat maps of St. John and St. Thomas (*Ecological Archives* E087-174-A1).

APPENDIX B

Description of protocol for calculation of wave exposure (*Ecological Archives* E087-174-A2).

APPENDIX C

Details of statistical techniques used to model coral reef beta diversity: model framework, selection and diagnostics, models of covariance, calculating the distance between data points, and estimates of coefficients (*Ecological Archives* E087-174-A3).

APPENDIX D

Tables showing mean frequency of abundance of each taxon within each benthic community around St. John and St. Thomas, a Bray-Curtis dissimilarity matrix between habitats, and the five taxa with the largest influence on the Bray-Curtis dissimilarity between each pair of habitats (*Ecological Archives* E087-174-A4).