VOL. 366, NOS. 1–2 15 NOVEMBER 2008 ISSN 0022-0981

ELSEVIER

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

Special Issue

Marine Ecology: A Tribute to the Life and Work of John S. Gray

Guest Editor

R. Warwick

Journal of Experimental Marine Biology and Ecology 366 (2008) 28–36

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Scaling up beta diversity on Caribbean coral reefs ☆

Jesús Ernesto Arias-González [a,*], Pierre Legendre [b], Fabián Alejandro Rodríguez-Zaragoza [a]

[a] Laboratorio de Ecología de Ecosistemas de Arrecifes Coralinos, Departamento de Recursos del Mar, Centro de Investigación y de Estudios Avanzados del I.P.N.-Unidad Mérida, Antigua Carretera a Progreso Km 6, A.P. 73 CORDEMEX, 97310, Mérida, Yucatán, México

[b] Département de Sciences Biologiques, Université de Montréal, Montréal, Québec H3C 3J7, Canada

ARTICLE INFO

Keywords:
Beta diversity
Caribbean Sea
Coral reefs
Coral reef fish
MesoAmerican Reef System (MAR)
Spatial patterns
Yucatan Peninsula

ABSTRACT

The objective of this paper is to find good proxies that are important to explain the spatial variation of beta/delta diversity in coral reefs. To reach that objective, we looked for and identified the environmental and spatial variables most strongly related to variation in fish and coral species richness and composition. We studied variation in fish and coral species diversity at two spatial scales: among geomorphology classes (reef lagoons, fronts, slopes and terraces) within reefs (beta diversity), and among eleven reefs across a 400-km latitudinal diversity gradient (delta diversity) in the western Caribbean Sea. The variation of species richness and community composition was partitioned between environmental and spatial variables. Two-way ANOVA (for richness) and MANOVA (for presence-absence community composition) were used to test for the influence of reefs and geomorphology classes on fish and coral species richness and community composition. The results show that for both fish and coral, differences among geomorphology classes were strong whereas there were no significant differences among the reefs. We identified additional spatially-structured environmental variables that explained the spatial variation of fish and coral species richness and community composition at the various scales. Geomorphological structure, "reefscape" attributes at different scales, and depth are important variables for shaping beta/delta diversity. We discuss the impact of our results with respect to regional ecomanagement strategies and the creation of marine reserves.

1. Introduction

Revealing the causes of variation in species diversity has traditionally been a primary goal of ecology. During the last two decades, the interest of scientists for explaining the causes of spatial variation of species diversity has increased considerably (e.g. Ormond and Roberts, 1997; Condit et al., 2001; Connell et al., 2004).

Whittaker (1960, 1972, 1977) originally defined beta diversity as a measure of the variation in diversity among samples along transects or across environmental gradients. Beta diversity is a central concept for the control of diversity in ecological communities (Condit et al., 2001) and a potential proxy for a range of ecosystem functions and processes (Harborne et al., 2006). Beta diversity increases as the similarity in species composition among sites decreases; therefore it is a measure of the extent to which the diversity of two or more spatial units differs (Magurran, 2004). Specifically on coral reefs, environmental variables seem to play an important role in determining patterns of community similarity (Dornelas et al., 2006). Patchy habitats in coral reef ecosystems constructed mainly by corals and the relative composition of associated benthic reef communities across depth gradients, produce particular reefscape characteristics in small surfaces. These particular characteristics may be one of the causes why community similarity is generally low among sites in coral reef ecosystems, beta diversity being high.

A range of variables, acting over a hierarchy of scales, structure coral reef community and ecosystem processes (Hatcher, 1997; Harborne et al., 2006). Macro-scale variation in reef area has been the major factor explaining variation in coral and coral reef fish assemblages in the Indo-Pacific (Bellwood and Hughes, 2001; Bellwood et al., 2005). In the West Indies, spatial patterns of fish community structure and composition seem to be controlled mostly by latitudinal and hydrologic gradients, by habitat type and, with a lower influence, by depth (Bouchon-Navaro et al., 2005; Nuñez-Lara et al., 2005). Reef geomorphology plays an important role to shape fish and benthos coral reef communities (Andréfouët and Guzmán, 2005; Núñez-Lara et al., 2005). Local-scale variations in live coral cover, topographic complexity and reef structure seem to be the major factors explaining the variation in diversity of coral reef fishes (Jones et al., 2004; Almany, 2004; Arias-González et al., 2006). Local variation in coral richness and composition has been related to coral cover (Tomascik et al., 1996; Guzmán et al., 2004) and direct damage by storms and elimination in competition (Connell et al., 2004). Other plausible factors operating at local scale are species interactions, disturbance, and productivity (Cornell and Karlson, 2000). It is also known that coral diversity correlates very closed with reef fish biodiversity (Harmelin-Vivien, 1989). At seascape scale, Harborne et al.

☆ This paper is dedicated to the memory of John Gray, Professor of Marine Biology, University of Oslo, Norway, who passed away on October 21, 2007. Professor Gray was a leader of minds, working on the development of a predictive benthic ecology based on ecological theory.

* Corresponding author.
E-mail addresses: earias@mda.cinvestav.mx (J.E. Arias-González), pierre.legendre@umontreal.ca (P. Legendre), fabian@mda.cinvestav.mx (F.A. Rodríguez-Zaragoza).

0022-0981/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2008.07.035

(2006) found in the Caribbean an increase in benthic species turnover with an increase in depth. Despite the large number of diversity studies in coral reefs, much of our understanding of biodiversity is based on local (alpha diversity) or macro-scale (gamma diversity) studies, whereas variation in species diversity at landscape scale (beta diversity) remains poorly understood. Studies on beta diversity in coral reefs are few (Connell et al., 2004; Harborne et al., 2006); it is therefore necessary to analyze and understand the processes that control beta/delta biodiversity at different levels of differentiation, that is, at different scales.

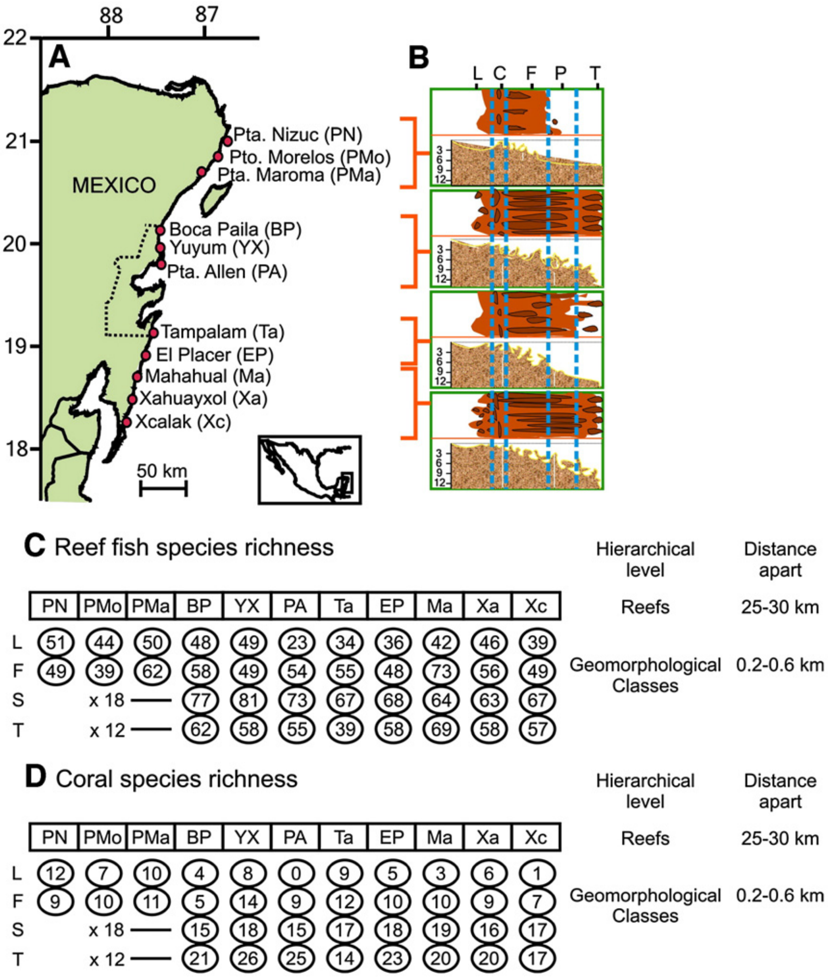
In this study, we analyzed the variation in fish and coral species richness and community composition at two different scales: (1) among geomorphology classes (reef lagoons, fronts, slopes and terraces) within reefs (beta diversity); and (2) among eleven reefs (we call *delta diversity* this type of beta diversity to mark the difference in scale) across a 400-km latitudinal diversity gradient in the western Caribbean Sea. Our objective is to find good proxies that are important to explain the spatial variation of beta/delta biodiversity in coral reefs. To reach that objective, we will look for and identify the environmental and spatial variables most strongly related to variation in fish and coral species richness and community composition. This study will produce several proxies at different scales to evaluate beta/delta diversity from a variety of reefs with different forms, shapes, depths and evolutionary histories. We will find that beta/delta diversity can be shaped, depending on the scale, by the geomorphology of the reef, the reefscape characteristics, and depth. We will discuss the impact of our results for developing regional ecomanagement strategies and the creation of marine reserves.

2. Background

We studied variation of the fish and coral species richness and composition on 11 reefs located in a 400 km track in the northern part of the Mesoamerican Reef System (MAR). Overall, the north sector of the MAR provides a good testing ground for exploring beta diversity. Geomorphology and reefscape differ substantially, changing in a systematic way along the reef system: from north to south there is a marked increase in reef area, live coral cover, and habitat complexity, and the reef platform gradually widens (Fig. 1).

Reefs from Punta Nizuc to Xcalak have different geomorphological structures. The northern reefs are small in area and have an identifiable reef lagoon, back reef and reef front, but there is no reef extension of the "buttress and canyon", systems which is very well developed in the reef systems located in the central and southern parts of the study area.

Another important factor in the area is anthropogenic pressure. Beta diversity is not only simply a consequence of ecological patterns (Magurran, 2004); it can also be influenced by human pressure. Human development in the area follows a gradient from north to south. The highest human development is in the northern part of the study area while the central part is a Biosphere reserve (delimited by dotted lines in Fig. 1A) and the southern part has little human development. In this study, both geomorphology and differential human pressure can shape the variation patterns in coral reef communities; the reefs highly used by tourists (i.e. Punta Nizuc, Puerto Morelos and Punta Maroma) can experience phase shifts in coral cover and changes in coral species patterns;



C Reef fish species richness

												Hierarchical level	Distance apart
	PN	PMo	PMa	BP	YX	PA	Ta	EP	Ma	Xa	Xc	Reefs	25-30 km
L	51	44	50	48	49	23	34	36	42	46	39	Geomorphological Classes	0.2-0.6 km
F	49	39	62	58	49	54	55	48	73	56	49		
S		x 18	—	77	81	73	67	68	64	63	67		
T		x 12	—	62	58	55	39	58	69	58	57		

D Coral species richness

												Hierarchical level	Distance apart
	PN	PMo	PMa	BP	YX	PA	Ta	EP	Ma	Xa	Xc	Reefs	25-30 km
L	12	7	10	4	8	0	9	5	3	6	1	Geomorphological Classes	0.2-0.6 km
F	9	10	11	5	14	9	12	10	10	9	7		
S		x 18	—	15	18	15	17	18	19	16	17		
T		x 12	—	21	26	25	14	23	20	20	17		

Fig. 1. Study area location in the North Sector of the Mesoamerican Barrier Reef System: (A) eleven studied reefs; (B) top and lateral views of the geomorphology of the reefs: L: Reef Lagoon, C: Reef Crest, F: Reef Front, S: Reef Slope, T: Reef Terrace. (C) Number of fish species and (D) coral species per reef. Redraw from Nuñez-Lara et al. (2005).

reefs used by coastal fisheries (i.e. Mahahual, Xcalak) can experience changes in fish species patterns.

We had *a priori* knowledge of the relative effects of reef geomorphology and tourism-fisheries pressures on spatial patterns of fish communities in the study area (Nuñez-Lara et al., 2005). These authors examined the spatial patterns of reef fish communities and tested ecological models concerning the relative importance of reef geomorphology and anthropogenic pressure possibly driving community structure. They concluded that, in the Yucatan Peninsula, spatial variation in reef fish community composition at the time of the study was mainly influenced by the geomorphology of the fringing reef system. Significant differences among regions were found for the lagoon, slope and terrace fish communities, consistent with the geomorphological model, but it is only in the reef lagoon that they were consistent with the anthropogenic model. This means also that tourism and fisheries activities had greater impact in the lagoon than on the fore reef, and that fishing practices on the reefs were so similar that they did not generate recognizable differences in fish community structure among anthropogenic-pressure regions.

From that previous work, we learned that in the study area: 1) a division of the reef based on their geomorphology (geomorphologic model) explained more of the variation of fish composition that a model describing anthropogenic pressure, but the difference between the two models was small; 2) there were significant differences in community composition between adjacent geomorphology classes and among reefs (<30 km apart), which suggest low physical connectivity; 3) the results indicated that fish communities of the fringing reef systems were well described by a meta-population model; 4) fish on the reef front exhibited significant spatial variation at the reef scale, not at the regional scale; this suggests a natural response of the fish species to the reefscape structure.

3. Methods

3.1. Study area

Eleven reefs distributed along the eastern coast of the Yucatan Peninsula were studied (Fig. 1). These reefs form part of a semi-continuous fringing reef running close and parallel to the coast, beginning in Punta Nizuc, in the Mexican state of Quintana Roo, and connecting in the south with the fringing reefs of Belize. This area is part of the MesoAmerican Reef System (MAR), one of the major biodiversity hotspots of the Caribbean Sea.

Reefs in this area present a clear zonation into four main habitats (geomorphology classes): lagoon (L), front (F), slope (S), and terrace (T) (Fig. 1). Punta Nizuc, Puerto Morelos and Punta Maroma contained two geomorphology classes (reef lagoon and reef front); all four classes were present on the other 8 reefs (reef lagoon, reef front, slope and terrace); 3 reefs × 2 geo-classes + 8 reefs × 4 geo-classes = 38 study units.

3.2. Sampling design, variables

The eleven reefs were sampled between June and September in 1999 and 2000 (Ruiz-Zárate and Arias-González, 2004; Núñez-Lara et al., 2005). We assessed biodiversity patterns using a two-way spatial sampling design: transects were the sampling units in geomorphology classes (2 or 4 habitats per reef, see previous paragraph: lagoon, front, slope and terrace), and the geomorphology classes were crossed with the reefs (11); 18 L-transects × 11 reefs + 18 F-transects × 11 reefs + 18 S-transects × 8 reefs + 12 T-transects × 8 reefs = 636 transects in total (Fig. 1). We counted the total number of species of corals and coral reef fish along each transect. We pooled the species transect information in each geomorphology class of each reef in order to reduce sampling variance, which was very high, due to the random presence of individual species on small transects surveyed once only, and also because we were interested in analyzing/explaining the variation in species composition at the level of geomorphology and reefs and not for individual transects. We also estimated the percentage cover of morpho-functional groups for several types of benthic assemblages. We obtained different morpho-functional groups that together with topographic complexity, reef structure area and depth were used as explanatory variables for corals and coral reef fishes species richness and composition variability.

Fish and coral (On-line Appendices A and B) were identified to species on each individual transect. The data from all transects of a geomorphology class within a reef were then summed, forming 38 study units (SU, Fig. 1B). The data were further summed by reef. We analyzed these tables of community composition (species presence-absence), and species richness values computed for each study unit and per reef, for fishes and corals, separately.

3.2.1. Fishes

Reef fishes were surveyed along belt transects (50 m long, 2 m wide) set parallel to the coast (Núñez-Lara et al., 2005), located at a similar depths in corresponding geomorphology units. Eighteen transects were surveyed on the reef lagoons, fronts and slopes, and 12 on the reef terraces at each location, for a total of 636 transects. All transects within a habitat were approximately at the same depth; the distance between neighbouring transects was about 50 m.

3.2.2. Topographic complexity

Along each belt transect, topographic complexity was estimated by laying an 18-m-long chain following the rugosity of the bottom, following Risk (1972). Topographic complexity (TC) was calculated as $1-(d_m/L_t)$ where d_m is the straight-line distance from the beginning to the end points of the chain and L_t is the chain length (18 m). The mean, over all transects of each site, was calculated and produced a single TC value for the site.

3.2.3. Coral and benthic morpho-functional group cover and richness

A video was recorded over most of the belt transects, 50 m in length and about 0.4 m in width (total number of video transects: 474). The videotapes were examined using a high-resolution monitor. Forty frames spread evenly along each video transect were paused and the coral species and morpho-functional groups found in each frame were recorded. The proportion of live coral and morpho-functional groups was estimated at 13 points marked systematically on each frame (520 points in total per video transect). The benthos under each point sampled was identified to the lowest taxonomic group and life form possible. For some analyses, the data were grouped into major benthic categories, i.e. hard coral, soft coral, sponge and other benthos. For each transect, the points for each benthic category were summed and expressed as a percentage of the total number of frames sampled along the transect.

3.2.4. Estimation of reef area

We analyzed Landsat TM remote sensing images of a 1.8 km section centred on each site to estimate reef area in the approximate depth range of 3 to 20 m. We used the ERDAS GIS program (ERDAS, Inc.) in a supervised classification approach.

3.2.5. Spatial patterns

Spatial patterns were modelled in two different ways. (1) Since the reefs are approximately positioned along a straight line (Fig. 1A), the first principal component of their geographic coordinates, which represented 99% of the variation, was used to display the geographic positions of the study units. We created a cubic polynomial from this variable, called *Y*, in order to model nonlinear responses of the species to the geographic gradient; see for example Legendre and Legendre (1998, Section 13.2). (2) The reefs were also divided into 3 regions. The 3 northern reefs (PN, PMo, PMa) belong to the tourist region (Reg.1), the next four (BP, YX, PA, Ta) to the Sian Ka'an Biosphere Reserve (Reg.2), and the four southernmost reefs (EP, Ma, Xa, Xc) are in the fishing region

(Reg.3). Variable *Regions* was represented by 3 dummy variables in the analysis.

3.2.6. Estimation of diversity

Local diversity is the diversity at a given location, here our 38 elementary sampling units (Fig. 1). Macro-scale diversity was obtained by computing species richness and composition after combining the data from the elementary sampling units across a reef. Reefscape diversity was the variation in richness (Fig. 1C, D) or in species composition (On-line Appendices A and B) among geomorphology classes or reefs. Whittaker (1972) proposed various indices to synthesize beta diversity in single numbers, including the well-known index $b=S/\bar{\alpha}$, where S is the number of species in the whole area of interest while $\bar{\alpha}$ is the mean number of species observed at individual sites.

The index proposed by Legendre et al. (2005) is used in this study. This index is the sum, over all species and sites, of the squared abundance deviations from the species means. This index is a direct measure of the variation in species composition among the sites in the area of interest, which corresponds to the concept of beta diversity. This approach offers the advantage of allowing the partitioning of the variation in species composition between tables of environmental and spatial explanatory variables.

We followed that method in the present paper, where we studied the differentiation in diversity of fishes and corals at three levels: summed by reef (11 reefs), across the study area (38 SU), and per habitat type across reefs (11, 11, 8, and 8 SU per table), using either the tables of species presence-absence or the computed values of species richness.

3.3. Data analyses

We partitioned coral reef fish and coral diversity variation at each of the studied scales among groups of explanatory variables (Legendre and Legendre, 1998; Legendre et al., 2005). Each diversity measure was analyzed against a set of environmental and two sets of spatial variables: the polynomial of the geographic axis Y and the *Regions*. For environmental analysis, we used live coral cover, other benthic group covers (fire corals, soft corals, sponges, algae and sea grasses), substrate cover (sand, rubbles, and calcareous substrate), and reef structure area. For spatial analysis, we used as explanatory variables the X (latitude) and Y (longitude) geographic coordinates measured as distances (km) (Legendre and Legendre, 1998). More advanced methods of spatial modelling by eigenfunction maps, such as PCNM analysis (Borcard and Legendre, 2002; Borcard et al., 2004), could not be used here because they required a more regular spacing of the reefs that was the case in the present study. Forward selection (permutation tests, at the 5% significance level, of the increase in R^2 at each step) was applied to the environmental and spatial variables to identify parsimonious subsets of variables that significantly explained the community composition data. The variation of the community composition data was partitioned between the environmental and spatial variables (Borcard et al., 1992; Borcard and Legendre, 1994; Legendre and Legendre, 1998) using canonical redundancy analysis (RDA: Rao, 1964). All partitioning results are expressed in terms of adjusted multivariate R-squares (R_a^2) as recommended by Peres-Neto et al. (2006). Tests of significance were computed using simple and partial RDA. Two-way ANOVA (for richness) and MANOVA (for community composition) were computed using partial RDA, as described by Legendre and Anderson (1999).

The variation partitioning (function 'varpart'), canonical analyses (function 'rda'), and tests of significance of the fractions (function 'anova.cca') were computed using the 'vegan' library (Oksanen et al., 2008) of the R statistical language (R Development Core Team, 2008). Forward selection was computed using the 'packfor' package of Stéphane Dray (Laboratoire de Biométrie et Biologie Évolutive, UMR CNRS 5558, Université Lyon I, France).

4. Results

4.1. Variation related to geomorphology classes

Two-way ANOVA (for richness) and MANOVA (for community composition) for the 38 study units (lagoon: 11 SU; front: 11 SU; slope: 8 SU; terrace: 8 SU) were computed with respect to the crossed factors "geomorphology classes" and "reefs". The results, reported in Table 1, show that, for both fishes and corals, differences among geomorphology classes were strong, whereas the differences among the reefs were weaker. Geographic differences among the reefs will be modelled more efficiently in the next subsections. The proportion of the response variable's variance (R^2 or R_a^2) explained by geomorphology classes was always lower for community composition than for richness because of the high inherent variability of community composition data. This high variability, reported by many authors, is due to the small size of the survey transects compared to the size of the reefs under study. For fishes, it is also due to their mobility and the presence of many species observed with low frequencies; their presence on or near survey transects is highly stochastic (On-line Appendix A).

4.2. Variation partitioning, 11 reefs

The variation of richness and community composition among the reefs was related to potential explanatory variables by variation partitioning (Tables 2 and 3). The models for fish and coral richness had very high explanatory power, with R_a^2 of 0.95 for fish and 0.90 for coral. The best explanatory variables for fish richness were: reef area (RA), fire coral cover (FC), and sponge cover (SP); for coral richness: live coral cover (LCC) and sand cover (SA). The variation in richness among the reefs was fairly well described by the geographic axis (GeoAxis in Tables 2 and 3) and by the *Regions* variable (R_a^2 of 0.68 to 0.79), but that geographic variation was well expressed by the environmental variables (see fraction [b] in Tables 2 and 3) which were much better predictors of fish and coral species richness. Graphs of richness as a function of GeoAxis (not shown) indicate that the geographic model essentially captured differences between the tourist region (Reg.1 in Tables 2 and 3) and the other two regions.

The situation was about the same for the fish and coral community composition data, except for the fact that the R_a^2 coefficients were much lower, due to the high variability of the community composition data mentioned in the previous subsection. Among the available environmental variables, live coral cover (LCC) and calcareous substrate cover (CS) were selected for fish community composition, and live coral cover (LCC) and soft coral cover (SC) for coral community composition.

Table 1
Two-way ANOVA (for richness) and MANOVA (for community composition) for 38 study units, computed by RDA, with respect to the crossed factors *geomorphology classes* and *reefs*

Anova factors	Geomorphology classes (4 levels)	Reefs (11 levels)
Fish richness	$R^2=0.585$, $R_a^2=0.548$ $F=19.832$, $P=0.001^{***}$	$R^2=0.147$, $R_a^2=-0.168$ $F=1.500$, $P=0.208^{\mathrm{NS}}$
Fish community composition	$R^2=0.226$, $R_a^2=0.158$ $F=28.394$, $P=0.001^{***}$	$R^2=0.248$, $R_a^2=-0.031$ $F=2.798$, $P=0.054^{\mathrm{NS}}$
Coral richness	$R^2=0.788$, $R_a^2=0.770$ $F=53.882$, $P=0.001^{***}$	$R^2=0.087$, $R_a^2=-0.252$ $F=1.778$, $P=0.112^{\mathrm{NS}}$
Coral community composition	$R^2=0.360$, $R_a^2=0.303$ $F=54.611$, $P=0.001^{***}$	$R^2=0.200$, $R_a^2=-0.096$ $F=2.741$, $P=0.235^{\mathrm{NS}}$

Notes: R^2 is the bimultivariate redundancy statistic, or RDA R-square, computed in RDA; R_a^2 is the corresponding adjusted R-square. Because the design was unbalanced, the *F*-statistics were computed from type III sums-of-squares. Probabilities (P) were computed using permutation tests (999 random permutations of the residuals of the reduced model). ***: $P \le 0.001$, $^{\mathrm{NS}}$: $P > 0.05$.
The interaction could not be tested because there were no replicates of the 38 study units.

Table 2

Fish variation partitioned between the environmental (Environ.) and spatial (GeoAxis: polynomial of the geographic axis *Y*) data tables

					Total explained	Environ.	GeoAxis	*Regions*
	[a]	[b]	[c]	[d]	[a+b+c]	[a+b]	[b+c]	
Fish species richness								
1. 11 reefs	**0.269**	0.686	−0.005	0.050	**0.950**	**0.955**	**0.681**	**0.764**
						RA,FC,SP	Y^2,Y^3	Reg.1
2. 38 study units (SU)	**0.475**	0.000	0.000	0.525	**0.475**	**0.475**	0.000	0.000
						SG,SC,SP	*nil*	*nil*
3. 11 or 8 reefs (SU) per habitat type								
3.1. Lagoon (11 SU)	**0.443**	0.000	0.000	0.557	**0.443**	**0.443**	0.000	0.000
						LCC	*nil*	*nil*
3.2. Front (11 SU)	**0.415**	0.000	0.000	0.585	**0.415**	**0.415**	0.000	0.000
						RU	*nil*	*nil*
3.3. Slope (8 SU)	0.030	0.506	**0.224**	0.240	**0.760**	**0.536**	**0.730**	0.000
						FC,CS	*Y*	*nil*
3.4. Terrace (8 SU)	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
						nil	*nil*	*nil*
Fish community composition								
1. 11 reefs	**0.108**	0.050	0.063	0.779	**0.221**	**0.158**	**0.109**	**0.109**
						LCC,CS	Y^2,Y^3	Reg.1
2. 38 study units (SU)	**0.169**	0.007	0.005	0.818	**0.182**	**0.176**	**0.012**	**0.018**
						LCC,TC,ALG,SG,SC,DE	Y^3	Reg.1
3. 11 or 8 reefs (SU) per habitat type								
3.1. Lagoon (11 SU)	**0.039**	0.012	0.036	0.914	**0.086**	**0.051**	**0.048**	**0.058**
						LCC	*Y*	Reg.1
3.2. Front (11 SU)	0.038	0.000	0.000	0.962	0.038	0.038	0.000	0.000
						RU	*nil*	*nil*
3.3. Slope (8 SU)	**0.059**	0.000	0.000	0.941	**0.059**	**0.059**	0.000	0.000
						TC	*nil*	*nil*
3.4. Terrace (8 SU)	**0.045**	0.000	0.000	0.955	**0.045**	**0.045**	0.000	0.000
						LCC	*nil*	*nil*

Notes. **Y**=richness or community composition data, **X**=table of selected environmental variables, **W**=table of selected spatial monomials. *Fractions of variation:* [*a*] is the pure environmental variation, [*b*] is the spatially-structured environmental variation, [*c*] is the pure spatial variation, [*d*] is the unexplained (or residual) variation, [*a*+*b*+c]=R_a^2 of the analysis of **Y** against **X** and **W** together, [*a*+*b*]=R_a^2 of the analysis of **Y** against **X**, [*b*+c]=R_a^2 of the analysis of **Y** against **W**. When the explanatory variables explain no more of the response's variation than random predictors would, the value of R_a^2 is near zero. It can be negative on occasion; in that case, it is interpreted as zero.

Habitat variables: LCC=live coral cover, TC=topographic complexity, RA=reef structure area, ALG=algal cover, SG=sea grass cover, FC=fire coral cover, SC=soft coral cover, SP=sponge cover, SA=sand cover, RU=rubble cover, CS=calcareous substrate cover, DE=depth.

Geographic coordinate monomials: X, Y, X^2, XY, Y^2, X^3, X^2Y, XY^2, Y^3; *nil*: no variable selected.

The explanatory power of variable *Regions* (3 dummy variables) is also tabulated. First line of each entry: fractions of variation (R_a^2). Bold values: significant fractions (5% level). Fraction [b] cannot be tested for significance. Second row: environmental and spatial variables retained by forward selection at the 5% level. Permutation tests: 999 random permutations.

4.3. Variation partitioning, 38 study units

The variation among the 38 study units (SU) was modelled in much the same way as the data for the 11 reefs (previous subsection). The models for fish and coral richness were highly predictive, with R_a^2 of 0.48 for fishes and 0.86 for corals. The environmental variables selected to explain fish richness were: sea grass cover (SG), soft coral cover (SC), and sponge cover (SP); for coral richness: live coral cover (LCC), topographic complexity (TC), sea grass cover (SG), rubble cover (RU), and depth (DE). The geographic variables did not succeed in modelling the variation in species richness at that level.

The models for community composition had lower R_a^2 statistics: 0.18 for fish and 0.39 for coral. Live coral cover (LCC), topographic complexity (TC), algal cover (ALG), sea grass cover (SG), soft coral cover (SC), and depth (DE) were selected for the fish community composition; live coral cover (LCC), topographic complexity (TC), sea grass cover (SG), fire coral cover (FC), soft coral cover (SC), rubble cover (RU), and depth (DE) were selected for the coral community composition. As in the previous paragraph, the geographic variables had little (R_a^2=0.01-0.02 for fish) or no success (for coral) in modelling the variation at that level.

We wondered if these relationships could be due, mostly or solely, to the strong differences among the geomorphology classes. To test this hypothesis, we recomputed the models with dummy variables representing geomorphology classes as covariables. All relationships remained highly significant (P=0.001 to 0.009) when controlling for the differences among geomorphology classes.

4.4. Variation partitioning recomputed within each geomorphology class

The models per geomorphology classes only involved 11 SU (lagoon, front reef) or 8 SU (slope, terrace). Tests of significance with small numbers of observations have low power; for that reason, the species-environment or species-geography relationships did not reach significance in some models. For the richness data, the fish model identified a significant relationship with live coral cover (LCC, R_a^2=0.44) for the lagoon habitat, with rubble cover (RU, R_a^2=042) for front reefs, and with fire coral cover (FC, R_a^2=0.54) for slopes. Geographic variation was only found among reefs for the slope habitat. The coral models identified significant relationships with the environmental variables in three geomorphology classes: lagoon (R_a^2=0.99), slope (R_a^2=0.98), and terrace (R_a^2=0.86). Geographic variation among reefs was only found for the lagoons.

The models of community composition had much lower R-square values. For fishes, all four models found a weak albeit significant relationship with an environmental variable. For coral, all four models also identified significant species-environment relationships. Only the lagoon models showed a significant differentiation of region 1 (Reg.1 in Tables 2 and 3). Núñez-Lara et al. (2005) had noted that the reef lagoons are more strongly impacted in the tourist region.

5. Discussion

Variation partitioning of the fish and coral biodiversity data provided a better understanding of the factors responsible for variation of species richness and composition at the studied scales. Coral species variation is more strongly spatially structured than fish species variation. This

Table 3
Coral variation partitioned between the environmental (Environ.) and spatial (GeoAxis: polynomial of the geographic axis *Y*) data tables

					Total explained	Environ.	GeoAxis	*Regions*
	[a]	[b]	[c]	[d]	[a+b+c]	[a+b]	[b+c]	
Coral species richness								
1. 11 reefs	**0.119**	0.721	0.060	0.099	**0.901**	**0.840**	**0.781**	**0.790**
						LCC,SA	Y,Y^2	Reg.1
2. 38 study units (SU)	**0.859**	0.000	0.000	0.141	**0.859**	**0.859**	0.000	0.000
						LCC,TC,SG,RU,DE	*nil*	*nil*
3. 11 or 8 reefs (SU) per habitat type								
3.1. Lagoon (11 SU)	**0.550**	0.444	−0.001	0.007	**0.993**	**0.994**	**0.443**	**0.348**
						LCC,RA,SP,CS	Y^3	Reg.1
3.2. Front (11 SU)	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
						nil	*nil*	*nil*
3.3. Slope (8 SU)	**0.978**	0.000	0.000	0.022	**0.978**	**0.978**	0.000	0.000
						RA,ALG,FC,SP	*nil*	*nil*
3.4. Terrace (8 SU)	**0.864**	0.000	0.000	0.136	**0.864**	**0.864**	0.000	0.000
						LCC,RA	*nil*	*nil*
Coral community composition								
1. 11 reefs	0.094	0.204	0.078	0.624	**0.376**	**0.298**	**0.282**	**0.261**
						LCC,SC	Y,Y^2	Reg.1
2. 38 study units (SU)	**0.371**	0.000	0.000	0.629	**0.371**	**0.371**	0.000	0.000
						LCC,TC,SG,FC,SC,RU,DE	*nil*	*nil*
3. 11 or 8 reefs (SU) per habitat type								
3.1. Lagoon (11 SU)	**0.304**	0.067	0.061	0.567	**0.433**	**0.371**	**0.129**	**0.109**
						LCC,FC,CS	Y^3	Reg.1
3.2. Front (11 SU)	**0.131**	0.000	0.000	0.869	**0.131**	**0.131**	0.000	0.000
						LCC,SC	*nil*	*nil*
3.3. Slope (8 SU)	**0.083**	0.000	0.000	0.917	**0.083**	**0.083**	0.000	0.000
						LCC	*nil*	*nil*
3.4. Terrace (8 SU)	**0.370**	0.000	0.000	0.630	**0.370**	**0.370**	0.000	0.000
						TC,CS	*nil*	*nil*

Notes: see Table 2.
The explanatory power of variable *Regions* (3 dummy variables) is also tabulated. First line of each entry: fractions of variation (R_a^2). Bold values: significant fractions (5% level). Fraction [b] cannot be tested for significance. Second row: environmental and spatial variables retained by forward selection at the 5% level. Permutation tests: 999 random permutations.

suggests that coral communities are more structured by the geomorphology classes across both the latitudinal and depth gradients than fish communities. The corals, which are sessile organisms, may have fewer possibilities to disperse across scales than fish.

5.1. Variation related to geomorphology classes

Partitioning the biodiversity data by ANOVA (richness species) and MANOVA (species composition) provided a clearer picture of the roles of geomorphology classes in determining species turnover (Table 1). Geomorphological variation (lagoon, reef front, slope and terrace) is responsible for the highest proportion of the variation in the coral and fish richness and species composition patterns along the 400 km gradient under study.

Geomorphological characteristics in the study area vary considerably; reefs located in the north are small and are structured by a lagoon and a reef front, while reefs located in the south are large with large outer slope and terrace extensions with buttress and canyon systems. This type of spatial extension, where it exists, increases the topographic complexity of the reef as well as reef patch size; this is extremely important because these structures host a high number of species. This result is consistent with work by others in the Caribbean (Núñez-Lara et al., 2005; Andréfouët and Guzmán, 2005), which suggested that reef geomorphology was the main factor explaining the variability of fish and benthic coral reef communities. Buttress and canyon reefscapes are variable along the 400 km track that we studied, but maximum development is found in the Boca Paila, Yuyum, and Mahahual reefs where we obtained maximum total fish and coral species richness.

Reef lagoons are also extremely variable in the study area and some have considerable extensions of sea grass beds and coral reef patches (i.e. Boca Paila), other reef lagoons are more homogeneous (i.e. Mahahual). This spatial habitat variation produces high variation in species richness and composition and may be an important cause of biodiversity variation among reef geomorphology classes. Sea grass beds are widely distributed in the Caribbean, and seem to be a dominant factor structuring reef biodiversity. These habitats have several functional roles when they interact with reef front reefscapes and influence nutrient fluxes, trophic transfers, and fishery production (Duffy, 2006). Paradoxically, sea grass bed reefscapes are the most vulnerable to fragmentation by coastal tourism and urban development or pollution. Sea grass fragmentation decreases the probability of new recruit settlement and of the development of new cohorts in the population. In the study area, tourism and urban development are considerably affecting reef lagoons in all reefs located in the northern areas like Punta Nizuc, Puerto Morelos and Punta Maroma. Núñez-Lara et al. (2005) suggested that fish community variation in reef lagoon systems in the study area might be strongly associated with tourism development.

5.2. Variation partitioning, 11 reefs

Partitioning reef biodiversity between the environmental and spatial explanatory variables highlighted the role played by various environmental variables in creating spatial biodiversity structures within geomorphology classes (Tables 2 and 3). Variation of fish species richness among reefs is highly related to reef area (RA), fire coral (FC) and sponge cover (SP). Reef fish richness associated to reef area is consistent with the ecological premise that the larger the total reef area, the more types of habitats there are likely to be (MacArthur and Wilson, 1969; Rosenzweig, 1999), i.e. geomorphology classes. These in turn can support a higher number of fish species, populations, progeny, and genetic diversity (Palumbi, 1997). Large reefs with more geomorphology classes also have a high coral cover over a sufficiently large area. Similar patterns, although not as clear, were found by Ormond and Roberts (1997). Within tropical latitudes, these authors found that the latitudinal gradient in fish diversity was not clear, although they found pronounced gradients in coral reef area. Bellwood and Hughes (2001) examined four variables (latitude, longitude, area of shallow-water habitat, and reef type) that may explain the variation in taxonomic composition of Indo-Pacific fish and coral assemblages. Of these, regional-scale variation in habitat area was the major factor, explaining 57% of the variation in coral assemblages and 42% in fishes. The results reported in the present paper for fish species richness agree with these results; the variation in richness among the reefs was well expressed by RA (see fraction [b] in Tables 2 and 3), which was a much better predictor of fish species richness that the geographic coordinates were.

Interesting is the association of variation of the reef fish richness to fire corals and sponges. Sponges in Caribbean coral reefs are important contributors to reef complexity because some species can reach large sizes and complex structures (Wulff, 2006). Sponges have several biological and ecological properties that make them an influential part of Caribbean coral-reef ecosystems (Diaz and Rützler, 2001). Associated effect of sponges on variation of the fish species richness has received minimal attention in coral reef studies; our results suggest that sponges are an important structural element for regulating fish species richness across latitudinal gradients. Fire corals colonies may be abundant locally on coral reefs but they usually cover less than 10% of the overall surface (Lewis, 2006). Fire coral produce morphologically complex skeletons (Edmunds, 1999) that can influence associations of fish species. In the studied reefs, fire corals were abundant in some areas, producing a reefscape and associated increased fish richness species variation.

For corals, live coral cover and sand cover (SA) were the main variables that shaped species richness turnover among reefs. Corals, which are sessile organisms, are more dependent on habitat structure and live coral cover than fish, which are mobile and can actively seek available habitats, rather than sufficient coral cover as we have documented in the previous paragraph. Sand plains parallel to the coast divide Caribbean coral reefs. Sand channels that run perpendicular to the coast (grooves) also divide reefs into buttress and canyonsystems. Sand plains function as ecotones and in fact they divide, in general, reef fronts form outer slopes and terraces trough the depth gradient. Live coral cover highlights its importance on coral species richness and distribution patterns across large scales. Our results agree with previous work of Tomascik et al. (1996) and Guzmán et al. (2004) who found high coral cover and high diversity on an Indonesia and Caribbean coral reef. However, our results contrast with Connell's (1978) study who suggested that diversity was low at the extremes of coral coverage, while highest diversity was apparent at moderate coral cover. As stated by Van Woesik (2000), these kinds of results indicate that Connell's premise breaks down in very diverse environments and is not applicable to all situations.

Even though reef area explains the variation of fish species richness, it does not explain the variation of the species composition, but live coral cover (LCC) and calcareous substrate cover (CS) do. Live coral cover (LCC) also shaped variation of the coral community composition; together with soft coral cover (SC). These results highlight the importance of live coral cover, both from massive and soft corals, on fish and coral community variation along latitudinal gradients. Within the coral habitat, the strong correlation between live coral cover and richness of corals and fish and coral species composition is suggestive of a potential cause and effect relationship (Bell and Galzin, 1984; Jones et al., 2004). Most reef fish species seem to recruit and establish themselves among live coral (Munday et al., 1997; Booth and Beretta, 2002; Jones et al., 2004). Other studies suggest that more than 60% of the total reef fish species prefer to inhabit zones with some level of live coral (Ormond and Roberts, 1997; Bell and Galzin, 1984; Jones et al., 2004). The presence of abundant live coral also influences the species composition of reef-associated fishes (Bell and Galzin, 1984). For example, some species are strict corallivores (Hixon, 1997) or permanent inhabitants of coral structures (Munday et al., 1997); others depend on prey whose occurrence and abundance are related to live coral cover and/or morpho-functional groups (Bell and Galzin, 1984; Munday et al., 1997; Booth and Beretta, 2002; Arias-González et al., 2006).

5.3. Variation partitioning, 38 study units

Variation among the 38 SU was successfully modelled by the available environmental variables. The environmental variables selected to explain the variation of fish richness are variables that produce particular reefscapes: sea grass (SG), soft coral (SC), and sponge (SP). Sea grass beds are less complex systems located in the reef lagoon. They host fewer species than coral patches or coral reef structure, i.e. reef front, slopes and terraces; thus there is great variation in fish richness between habitats that are associated and not associated to coral. These two reef components give an extra dimension to massive coral builders and are excellent attractors for fish species. Sponges and soft coral could be associated to reef slope sites, characterized by high massive and encrusting coral coverage and pronounced vertical relief. It seems that the most important reefscape elements that produce a change in coral species richness are live coral cover (LCC), topographic complexity (TC), sea grass beds (SG) and depth gradient (DE). This suggests that dispersal patterns of coral species within reefs may be strongly associated to these variables.

Topographic complexity (TC), algal cover (ALG), sea grass cover (SG), soft coral cover (SC), fire coral cover (FC), and rubble cover (RU) variation contribute to fish and coral species composition patterns across variation of the geomorphology classes within reefs. The fish and coral species turnover is also associated to a depth (DE) gradient and live coral cover (LCC). Fish and corals vary systematically with changes in wave energy across reefs, which are in turn related to depth and position on the reef and to three-dimensional reefscape architecture (Done, 1982; Arias-González et al., 2006). It is important to stress the change in the fish or coral species richness and composition across those gradients and with the benthic substratum. A recent study in Davies reef on the Great Barrier Reef showed that variation of fish assemblages and diversity are related to reefscape structure (Arias-González et al., 2006). Maximum biodiversity was found in coral-dominated reefscapes; coral morphology was also important and had a strong influence on fish assemblages and functional groups. The type of corals and the coral cover in Caribbean reefscapes is given by different elements that create a spatial three-dimensional matrix with soft, fire, branching, and massive corals, and sponges as the most conspicuous elements. This structure is an excellent substrate to host several reef fish species, but the assemblage of species will depend on the type of benthic assemblage. This result is extremely important; for example we have some evidence of how coral reefs of the Caribbean have changed since 1970 (Hughes, 1994; Aronson et al., 2002) suffering a phase shift from coral to algae dominated systems, or from one coral species to another, e.g. from *Acropora cervicornis* to *Agaricia tenuifolia*. These phase shifts may produce a change in species richness and composition in both coral and fish assemblages. This can also influence coral species richness. Our results suggest that fish and coral species composition are not shaped by the variation of reef area, which means that species composition turnover between geomorphology classes may be strongly associated to variation of reefscape composition and vertical relief. Additionally, these results indicate that benthic environmental variables are determinant for fish and coral species composition across depth gradients.

5.4. Implications for conservation and management

Our results have important implications for conservation. With phase shifts (Done, 1992; Hughes, 1994: replacement of corals by seaweeds), reef areas or geomorphology classes are not reduced, but live coral cover and other benthic components are. Apparently, this has a direct impact on the biological and functional diversity of fishes and corals (Hughes, 1994; Gardner et al., 2003), and on species composition. Phase shifts in coral cover and benthic structure may in turn cause phase shifts on fish species assemblages, i.e. from carnivorous dominant to herbivorous dominant. The existence of 'bottom-up' causative links from reefscape to fishes and corals is an important message for conservation planners and managers (Jones et al., 2004). Management strategies for coral reefs should not only be framed in terms of top-down strategies such as the temporary closure of fisheries or area restrictions for protecting over-exploited species. They should also take into account geomorphology classes and reefscape characteristics. For example, fish species composition, as well as coral richness and species composition, is associated with a guild of benthic variables, while fish richness species turnover is mainly associated with reef area. This two-directional approach will ensure that biodiversity values associated with intact complex habitat are not overlooked. Our results demonstrate that beta diversity is related to reefscape structure (i.e. vertical relief) and characteristics (i.e. live coral, sponge, soft coral, algae, etc.), health conditions of benthic communities, number of geomorphology classes, and depth. Variation in fish diversity measured as species richness is associated to reef area.

Reefscape degradation (loss of sea grass, three-dimensional coral architecture, sponge and coral cover), phase shift (i.e. increasing percentage of "algae reefs") and fragmentation (smaller areas of sea grass, mangroves) may have a significant and slow-to-reverse effect on species turnover. Therefore, by focusing protection onto locations with large or healthy coral areas, high habitat diversity (i.e. different geomorphology classes, sea grass, mangroves, and coral cover), managers in the Caribbean should better capture the associated biological diversity at different spatial scales, with its potential to impart added resilience to the reef community. For the Caribbean, it may be possible to create regional coral reef networks of fully protected areas that would permit species movements among habitats and among reefs of different local compositions and diversities, and therefore help conserve regional biodiversity. This strategy of protecting strategically-located sea grass beds connected to 'good' reefs would improve prospects for regional resilience by maximizing opportunities for source-sink connections, species turnover, and recruitment of reef species. This has been done during the recent re-zoning of the Great Barrier Reef, Australia (Fernandes et al., 2005).

6. Conclusions

Geomorphology classes (lagoon, front, slope and terrace), "reefscape" attributes (i.e. sea grass cover, live coral cover, sponge cover, etc.), and depth were shown to be good proxies for variation in coral and fish species richness and composition at different spatial scales. Geomorphology classes and reefscape attributes were found to be useful predictors of biodiversity values for reef areas where data are scarce. The diversity of reef geomorphology was significant to explain variations of species richness and composition: reefs with four geomorphology classes hosted more species than reefs with two geomorphology classes. We identified additional environmental variables (i.e. algae (ALG), sea grass (SG), fire coral (FC), soft coral (SC), sponges (SP), sand (SA), rubble (RU), and calcareous substrate (CS)) that explained the spatial variation of species richness and composition at various scales of resolution, i.e. among geomorphology classes within reefs and among reefs. Live coral cover was not a significant predictor for fish richness variation, but it explained fish and coral species composition and coral richness. Reef geomorphology, several "reefscape" attributes (see above), and depth were good proxies for critical coral and fish reef species richness and composition values; they can be used to predict biodiversity values for reef areas where data are sparse. Such predictions can prove invaluable in the development of guidelines for regional eco-management. The environmental variables in our models were partly the same as those found in other models to explain diversity patterns, but our models incorporated additional variables that had been little studied as predictors for biodiversity patterns.

Acknowledgements

We are grateful to P. Sale, P. Mumby, T. Done, and A.R. Harborne for comments on a draft of this paper. RA values were obtained by GIS analysis conducted by G. Acosta-González. This research was funded by CONACYT and by NSERC grant no. 7738 to P. Legendre. F. Rodríguez-Zaragoza thanks CONACYT for a Ph.D. scholarship, and the WWF, Russell E. Train Education for Nature Program for grant M22. **[SS]**

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2008.07.035.

References

Almany, G.R., 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia 141, 105–113.

Andréfouët, S., Guzmán, H.M., 2005. Coral reef distribution, status and geomorphology–biodiversity relationship in Kuna Yala (San Blas) archipelago, Caribbean Panama. Coral Reefs 24, 31–42.

Arias-González, J.E., Done, T.J., Page, C.A., Cheal, A., Kininmonth, S., Garza-Pérez, J.R., 2006. Towards a reefscape ecology: relating biomass and trophic structure of fish assemblages to habitat at Davies Reef, Australia. Marine Ecolology. Progress Series 320, 29–41.

Aronson, R.B., Macintyre, I.G., Precht, W.F., Murdoch, T.J.T., Wapnick, C.M., 2002. The expanding scale of species turnover events on coral reefs in Belice. Ecological Monographs 72, 233–249.

Bell, J.D., Galzin, R., 1984. Influence of live coral cover on coral reef fish communities. Marine Ecolology. Progress Series 15, 265–274.

Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science 292, 1532–1534.

Bellwood, D.R., Hughes, T.P., Connolly, S.R., Tanner, J., 2005. Environmental and geometric constraints on Indo_Pacific coral reef biodiversity. Ecology Letters 8, 643–651.

Booth, D.J., Beretta, G.A., 2002. Changes in a fish assemblage after a coral bleaching event. Marine Ecology. Progress Series 245, 205–212.

Borcard, D., Legendre, P., 1994. Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). Environmental and Ecological Statistics 1, 37–53.

Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbor matrices. Ecological Modelling 153, 51–68.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Borcard, D., Legendre, P., Avois-Jacquet, C., Tuomisto, H., 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85, 1826–1832.

Bouchon-Navaro, Y., Bouchon, C., Louis, M., Legendre, P., 2005. Biogeographic patterns of coastal fish assemblages in the West Indies. Journal of Experimental Marine Biology and Ecology 315, 31–47.

Condit, R., Pitman, N., Leigh Jr., E.G., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., Hubbell, S.P., 2001. Beta-diversity in tropical forest trees. Science 295, 666–669.

Connell, J.H., 1978. Diversity in tropical rainforests and coral reefs. Science 199, 1302–1310.

Connell, J.H., Hughes, T.P., Wallace, C.C., Tanner, J.E., Harás, K.E., Kerr, A.M., 2004. A long-term study of competition and diversity of corals. Ecological Monographs 74, 179–210.

Cornell, H.V., Karlson, R.H., 2000. Coral species richness: ecological versus biogeographical influences. Coral Reefs 19, 37–49.

Diaz, M.C., Rützler, K., 2001. Sponges: an essential component of Caribbean coral reefs. Bulletin of Marine Science 69, 535–546.

Done, T.J., 1982. Patterns in the distribution of coral communities in the central Great Barrier Reef. Coral Reefs 1, 95–107.

Done, T.J., 1992. Phase changes in coral reefs and their ecological significance. Hydrobiologia 247, 121–132.

Dornelas, M., Sean, R.C., Hughes, T., 2006. Coral reef diversity refutes the neutral theory of biodiversity. Nature 440, 80–82.

Duffy, E.J., 2006. Biodiversity and the functioning of seagrass ecosystems. Marine Ecology. Progress Series 311, 233–250.

Edmunds, P.J., 1999. The role of colony morphology and substratum inclination in the success of *Millepora alcicornis* on shallow coral reefs. Coral Reefs 18, 133–140.

Fernandes, L., et al., 2005. Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. Conservation Biology 19, 1733–1744.

Gardner, T.A., Côté, M.I., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-Term Region-Wide declines in Caribbean corals. Science 301, 958–960.

Guzmán, H.M., Guevara, C.A., Bredy, O., 2004. Distribution, diversity, and conservation of coral reefs and coral communities in the largest marine protected area of Pacific Panama (Coiba Island). Environmental Conservation 31, 111–121.

Harborne, A.R., Mumby, P.J., Zychaluk, K., Hedley, J.D., Blackwell, P.G., 2006. Modeling the beta diversity of coral reefs. Ecology 87, 2871–2881.

Hatcher, B.G., 1997. Coral reef ecosystems: how much greater is the whole than the sum of the parts? Coral Reefs 16, S77–S91.

Harmelin-Vivien, M.L., 1989. Reef fish community structure: an Indo-Pacific comparison. In: Harmelin-Vivien, M.L., Bourliere, F. (Eds.), Vertebrates in Complex Tropical Systems. Springer-Verlag, New York, USA, pp. 21–60.

Hixon, M.A., 1997. Effects of reef fishes on corals and algae. In: Birkeland, C. (Ed.), Life and Dead of Coral Reefs. Chapman and Hall, New York, USA, pp. 230–248.

Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551.

Jones, G.P., McCormick, M.I., Srinivasan, M., Eagle, J.V., 2004. Coral decline threatens biodiversity in marine reserves. Proceedings of the National Academy of Science U.S.A. 101, 8251–8253.

Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd English ed. Elsevier, Amsterdam.

Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecological Monographs 69, 1–24.

Legendre, P., Borcard, D., Peres-Neto, P.R., 2005. Analysing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75, 435–450.

Lewis, J.B., 2006. Biology and ecology of the hydrocoral Millepora on coral reefs. Advances in Marine Biology 50, 1–55.

MacArthur, R.H., Wilson, E.O., 1969. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey, USA.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, United Kingdom.

Munday, P.L., Jones, G.P., Caley, M.J., 1997. Habitat specialisation and the distribution and abundance of coral-dwelling gobies. Marine Ecology Progress Series 152, 227–239.

Núñez-Lara, E., Arias-González, J.E., Legendre, P., 2005. Spatial patterns of Yucatan reef fish communities: testing models using a multi-scale survey design. Journal of Experimental Marine Biology and Ecology 324, 157–169.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H., 2008. vegan: community ecology package version 1.11-0. http://cran.r-project.org/.

Ormond, R.F.G., Roberts, C., 1997. The biodiversity of coral reef fishes. In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity: Patterns and Processes. Cambridge University Press, pp. 216–257.

Palumbi, S.R., 1997. Molecular biogeography of the Pacific. Coral Reefs 16, S47–S52.

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87, 2614–2625.

R Development Core Team, 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rao, C.R., 1964. The use and interpretation of principal component analysis in applied research. Sankhya. Series A 26, 329–358.

Risk, M.J., 1972. Fish diversity on a coral reef in the Virgin Islands. Atoll Research Bulletin 193, 1–6.

Rosenzweig, M.L., 1999. Ecology – Heeding the warning in biodiversity's basic law. Science 284, 276–277.

Ruiz-Zárate, M.A., Arias-González, J.E., 2004. Spatial study of juvenile corals in the northern region of the Mesoamerican Barrier Reef System (MBRS). Coral Reefs 23, 584–594.

Tomascik, T., Van Woesik, R., Mah, A.J., 1996. Rapid coral colonization of a recent lava flow following a volcanic eruption, Banda Islands, Indonesia. Coral Reefs 15, 169–175.

Van Woesik, R., 2000. A metacommunity model predicts coral diversity regulated by post-settlement mortality. Biodivesity and Conservation 9, 1219–1233.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30, 279–338.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.

Whittaker, R.H., 1977. Species diversity in land communities. Evolutionary Biology 10, 1–67.

Wulff, J.L., 2006. Rapid diversity and abundance decline in a Caribbean coral reef sponge community. Biological Conservation 127, 167–176.