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Scaling up beta diversity on Caribbean coral reefs ☆

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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.

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(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;

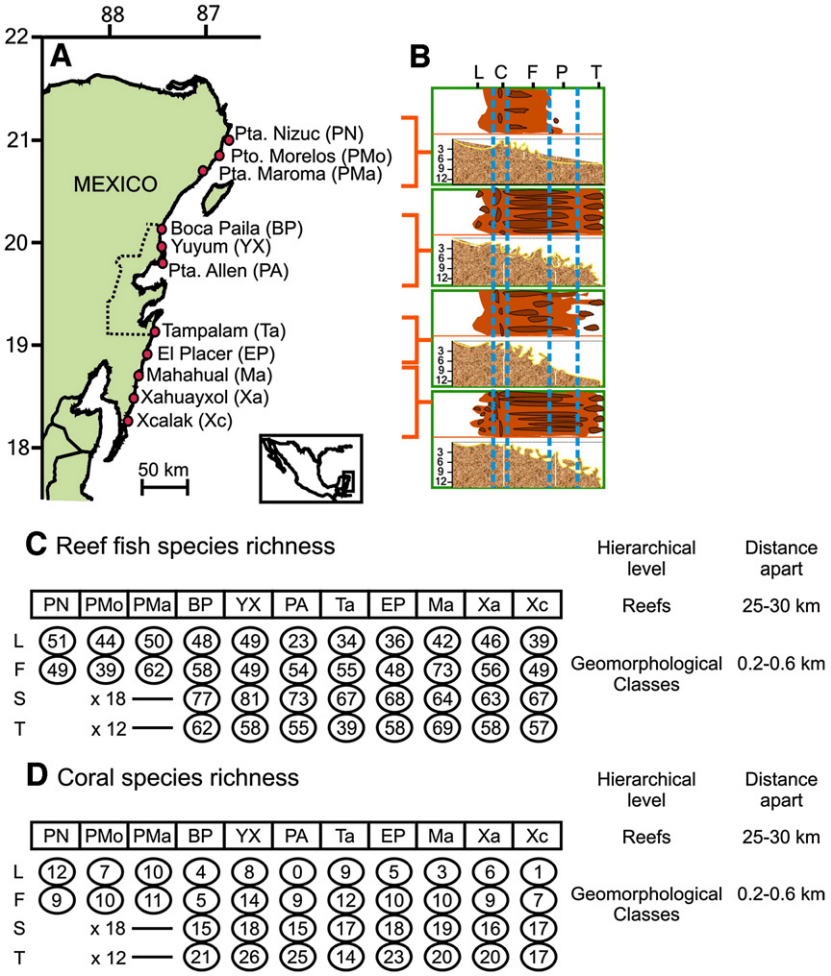

Fig. 1. Study area location in the North Sector of the Mesoamerican Barrier Reef System: (A) eleven studied reefs; (B) top and lateral views of the geomorphology of the reefs: L: Reef Lagoon, C: Reef Crest, F: Reef Front, S: Reef Slope, T: Reef Terrace. (C) Number of fish species and (D) coral species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