Landscape patterns of reef coral diversity: A test of the intermediate disturbance hypothesis

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Abstract

The intermediate disturbance hypothesis predicts that species diversity within habitats will be maximal at intermediate levels of disturbance, because competitive exclusion will be balanced by destruction of the competitive dominant(s). Previous tests of the hypothesis on coral reefs have produced variable results, in part because they were conducted at the small spatial scale of the quadrat. This study tested the intermediate disturbance hypothesis on a landscape scale, over an area >10^4 m^2 within a single reef habitat. Among replicate shallow reef spurs in Belize, coral species diversity was maximal at intermediate levels of disturbance, as measured by the topographic complexity of the substratum. Increased diversity at intermediate disturbance levels was due primarily to increased evenness rather than to increased species richness. The impacts of storm-generated debris appear to have reduced the cover of the competitively dominant coral, Agaricia tenuifolia Dana, allowing competitively subordinate coral species to increase on some spurs. This landscape-scale analysis provides the first rigorous, quantitative support for the hypothesis in a reef coral assemblage.

Keywords: Coral; Coral reef; Disturbance; Diversity; Intermediate disturbance hypothesis; Landscape ecology; Scale

1. Introduction

According to the nonequilibrium “intermediate disturbance hypothesis”,

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species diversity should be low at both low and high frequencies and intensities of
disturbance, and maximal at intermediate levels of disturbance (Paine & Vadas,
1969; Richerson et al., 1970; Grassle & Sanders, 1973; Grime, 1973; Grigg &
Maragos, 1974; Osman, 1977; Connell, 1978; Lubchenco, 1978; Huston, 1979,
1994). At low levels of disturbance, the dominant competitors eliminate or
severely limit most of the other species. At high levels of disturbance, all but the
most resistant or earliest successional species are excluded. At intermediate levels
of disturbance, however, a balance is struck between the competitive exclusion of
early colonists and the destruction of competitive dominant(s) by disturbance (see
Petraitis et al., 1989, and Caswell & Cohen, 1993, for recent theoretical treat­
ments). The result is a successional mosaic that supports a higher diversity than at
either extreme of the disturbance continuum. Similar arguments apply to the time
course of recovery from disturbance: diversity should be maximal at intermediate
stages of succession. Support for the intermediate disturbance hypothesis has
come from studies of competition for hard substratum in temperate zone benthic
communities and tropical algal assemblages (Lubchenco, 1978; Sousa, 1979;
Carpenter, 1981; Paine & Levin, 1981; Hixon & Brostoff, 1983; Hay, 1985; Sebens,
1985). In other situations, the predicted pattern has occurred for reasons other
than the proposed mechanism, has been obscured by other effects, or has not
occurred at all in the absence of the proposed mechanism (Dayton, 1973;
Connell (1978) used this hypothesis to explain the high within-habitat diversity
observed in tropical forest communities and in the sessile biotas of coral reefs (see
also Grassle, 1973). However, there is considerable debate over the model's
applicability to reef corals (Karlson & Hurd, 1993; Tanner et al., 1994). Fortuitous
observations of uncontrolled disturbances have yielded a variety of community
responses (Grigg & Maragos, 1974; Porter et al., 1981; Dollar, 1982; Huston, 1985;
Brown & Suharsono, 1990; Rogers et al., 1991; Dollar & Tribble, 1993; Rogers,
1993). The most important finding to emerge from these studies is that the
system-wide effects of disturbance on coral diversity depend on the history of the
particular reef ecosystem (Hughes, 1989; Done et al., 1991; Witman, 1992; Dollar
& Tribble, 1993; Rogers, 1993; see Sammarco, 1982, for historical effects on coral
reef algal assemblages).
Jackson (1991) suggested that the intermediate disturbance hypothesis may not
hold for reef corals at the small scale of square meters, because reef dynamics can
be unpredictable at that "quadrat scale". In many reef habitats, coral colonies are
larger than the scale of observation, routinely covering several square meters of
substratum. Jackson suggested that the search for pattern and process be undertaken
at larger spatial scales. Thus far, however, the model has not been tested formally on coral reefs at scales above the quadrat (Jackson, 1991). Here
we report such a test at the scale of the landscape, over an area $>10^4$ m$^2$.
Diversity was measured and the extent of disturbance inferred along discrete,
replicate landscape features of a coral reef, encompassing a wide range of
disturbance regimes.
2. Study area and species

The fore reef along the outer margin of the Belizean Barrier Reef in the vicinity of Carrie Bow Cay (16°48'N, 88°05'W) and nearby Curlew Bank (Fig. 1) is characterized by a shallow spur-and-groove zone, as described by Rützler and Macintyre (1982). This zone is actually composed of two sub-zones: a shallower set of spurs (0–3 m depth) dominated by elkhorn coral (Acropora palmata [Lamarck]) and hydrocorals (Millepora spp.), and a slightly deeper set of spurs (3–6 m depth). Spurs in the latter sub-zone were the subject of this study; all discussion that follows concerns these slightly deeper spurs. Note that the two shallow sub-zones described above are distinct from the deep spur-and-groove zone at 10–18 m depth (Rützler & Macintyre, 1982).

The spurs examined in this study occur over a linear distance >1 km. They are ≈2 m wide and are separated by distances of 3–10 m. They can be >50 m long and stand up to 4 m above the surrounding substratum. Agaricia tenuifolia Dana, a scleractinian coral, forms much of the framework of the spurs at 3–6 m depth (Rützler & Macintyre, 1982; Chornesky, 1991).

Chornesky (1991) showed that Agaricia tenuifolia exploits and retains space better than co-occurring species of hard corals (Scleractinia and Milleporina). The predominance of Agaricia tenuifolia arises from the ability of contiguous, genetically distinct colonies to modify their skeletons so that they become anchored against each other. The thin, vertical blades that characterize this species join to form relatively stable boxworks of coral skeleton that monopolize space on the spurs (Chornesky, 1991).

Other branching, fragile species of hard corals that grow on the spurs include the scleractinians Acropora cervicornis (Lamarck) and Porites spp., which are competitively inferior to Agaricia tenuifolia, and the milleporine hydrocorals, Millepora spp. Millepora spp. are capable of killing and overgrowing Agaricia tenuifolia (Chornesky, 1991). However, Millepora spp. were virtually absent from the spurs at 3–6 m depth, accounting for only 2% of hard coral cover (data from this study).

Visual surveys at Carrie Bow Cay and Curlew Bank revealed that corals growing on the spurs are disturbed by the impacts of storm-generated debris. This debris consists primarily of boulder-sized plates of Acropora palmata, broken from colonies growing in adjacent, shallower water. Many of these allochthonous plates rest on or against the spurs, with trails of smashed coral extending behind them (Fig. 2). The impact events evidently shatter the skeletons of Agaricia tenuifolia and break and kill other corals, opening space on the spurs for recolonization.

Growth rates of Agaricia tenuifolia, measured in the shallow spur-and-groove at Carrie Bow Cay, are rapid enough that the 4-m high spurs probably accreted within several decades (K.P. Sebens, unpubl. data). Anecdotal evidence also suggests that spurs accrete rapidly following severe disturbance; well-developed spurs were observed at Turneffe Islands, Belize, 30 yr after the shallow spur-and-
Fig. 1. Map of the Belizean Barrier Reef, showing the locations of Carrie Bow Cay and Curlew Bank (solid arrows), as well as nearby islands and banks.
groove habitat was completely leveled by Hurricane Hattie in 1961 (Stoddart, 1969; I.C. Feller, pers. comm., 1993).

3. Methods

3.1. Coral cover and diversity

Twenty haphazardly-chosen spurs off Carrie Bow Cay and Curlew Bank were examined in June 1993. For each spur, the percent cover of each species of hard coral was measured using the linear point-intercept (LPI) method (Ohlhorst et al., 1988). A 10-m transect line, marked at 1-cm intervals, was placed along the center of the top surface of each spur. One end of the transect was positioned haphazardly on the spur, and the tape was then extended in the seaward direction. The sessile organisms underneath every 10-cm mark were identified and recorded. Coral cover was calculated as the percentage of points under which hard corals were observed.

Species richness, $S$, was assessed by recording all coral species within 0.5 m on either side of the transect. Shannon-Wiener diversity, which takes into account both species richness and evenness, was calculated as $H' = -\sum p_i \ln(p_i)$, where $p_i$ is the proportional cover of the $i$th species along the transect and $\Sigma$ denotes the
summation over all $i$ coral species. Shannon evenness was calculated as $E_h = H'/\ln S$ (Buzas & Gibson, 1969; Magurran, 1988).

There are many field methods for measuring coral cover and diversity (e.g. Loya, 1978; Dodge et al., 1982; Chiappone & Sullivan, 1991). The LPI method is time-efficient and sufficiently accurate for comparative purposes, particularly on "simplified reefs" with low species richness (Ohlhorst et al., 1988). The spur system examined in this study qualifies as a "simplified reef" since no more than four coral species were recorded under a single transect line.

Assessing the species diversity of corals is problematic. Vast size differences among coral colonies and colony fragmentation and fusion obscure the meaning of $H'$ calculated from numbers of "individuals". Since it was not possible to establish the genetic identity of all ramets in this study, $H'$ was not calculated based on numbers of colonies. Rather, proportional cover was used to calculate $H'$, as described above (Aronson et al., 1994).

3.2. An integrated measure of disturbance

Historical records of disturbance do not exist for most coral reefs. Even where such records do exist, there is no obvious way to sum the different disturbances to reflect the total disturbance regime; one cannot simply score three disturbance points for a hurricane and two for a coral bleaching event. Topographic complexity (= substratum rugosity) can be used as an integrated, though indirect, estimate of the relative degree of disturbance in some reef habitats.

Where foliose and fragile, branching corals predominate, disturbances decrease topographic complexity. Complexity declines either directly, through the breakage of corals during storms, or indirectly, through the bioerosion and subsequent collapse of dead coral skeletons (Rogers et al., 1982; Kaufman, 1983; Hallock & Schlager, 1986; Tomascik & Sander, 1987; Hallock, 1988; Glynn, 1990). The spur-and-groove sub-zone at 3–6 m depth in Belize is dominated by fragile corals susceptible to breakage, including the most abundant, competitively dominant species, *Agaricia tenuifolia*. In fact, *Agaricia tenuifolia* is so fragile that colonies were damaged by turbulence from the fin kicks of careless divers (R.B. Aronson & W.F. Precht, pers. obs.). Following disturbance, topographic complexity increases as corals recolonize the spurs (e.g. the recovery at Turneffe Islands discussed above). Complexity therefore integrates the total disturbance regime experienced by the spurs.

During the course of our investigation, we noticed that the spurs most exposed to wave action (those on the northeast-facing portions of the Carrie Bow Cay and Curlew banks) had lower coral cover and lower topographic complexity than spurs in more protected positions. This qualitative observation supports a causal link between disturbance and topographic complexity. Although the precise history of each spur remains unknown, flatter terrain indicates more intense, more frequent and/or more recent disturbance in this habitat (Aronson et al., 1994).

No measure of disturbance is perfect, including topographic complexity. The mortality of coral tissue does not by itself necessarily lead to the immediate loss of
structure, because bioerosion takes time. This error should be minimal in the shallow spur-and-groove since *Agaricia tenuifolia* is thin and fragile and therefore easily bioeroded and broken. Note that topographic complexity would not be useful as an indicator of disturbance in certain other reef habitats such as shallow-water hardground areas, which are characterized by isolated head corals on limestone pavements.

Topographic complexity was measured along each transect by carefully conforming a 5-m length of brass chain (links 17 mm long) to the substratum along the central portion of the transect, beginning 10 m seaward of the beginning of the tape. The chain was fine enough to be laid over and between the closely spaced blades of *Agaricia tenuifolia* and the branches of *Porites* spp. and the other hard corals. Complexity was calculated as $C = 1 - \frac{d}{l}$, where $d$ is the horizontal distance covered by the chain when conformed to the substratum and $l$ is the length of the chain when fully extended (Risk, 1972; Rogers et al., 1982; Aronson & Harms, 1985; Hubbard et al., 1990).

### 3.3. Statistics

Putative causal relationships between variables were explored by computing linear and second-order polynomial regressions. All second-order relationships were predicted to be concave downward, reflecting hypotheses of high values at intermediate disturbance levels. The coefficients of determination, $r^2$, of these linear and polynomial regressions are reported below. In addition, $t$-tests were employed to determine if the regression coefficients (for linear regressions) or second-order coefficients (for polynomial regressions) were significantly different from zero ($df = 18$ and $df = 17$, respectively).

The significance level reported is for a one-tailed $t$-test if the direction of the relationship was predicted a priori. Significance levels for all second-order regressions are one-tailed. The directions of several hypothesized linear relationships were not predicted a priori, and so the significance levels are for two-tailed tests.

Shannon-Wiener diversity data are normally distributed and do not require transformation (Magurran, 1988). In contrast, coral cover, topographic complexity and Shannon evenness are percentage or proportional data. The arcsine transformation is recommended for percentages and proportions to make the data conform to the assumptions of parametric statistics (Sokal & Rohlf, 1981). Species richness data, which are in the form of counts, also require transformation. The calculations presented in the next section are based on the transformed data (arcsine transformation for percentages and proportions, logarithmic transformation for counts), although calculations using the untransformed data yielded the same results. Plots of the untransformed (raw) data and curves fitted to those data are presented for ease of interpretation.

Since topographic complexity was measured with error, regressions using $C$ as the independent variable are, strictly speaking, Model II problems (Sokal & Rohlf, 1981). However, the measurement error associated with $C$ was small
compared to natural variation in the diversity measures that were regressed on \( C \). The error in \( C \) can therefore be ignored, reducing these problems to Model I (least squares) regressions (Draper & Smith, 1981).

4. Results

Percent coral cover on the 20 spurs ranged from near zero to \( >60\% \), and topographic complexity ranged from \(<0.20\) to \( >0.80 \) (Fig. 3). Topographic complexity, \( C \), was positively correlated with coral cover \( (r = 0.876, \text{df} = 18, p < 0.0005 \) [one-tailed]; Fig. 3), which has also been used to estimate disturbance (Jackson, 1991; see also Sebens, 1985).

A second-order polynomial regression between \( H' \) and \( C \) was concave downward and highly significant \( (r^2 = 0.599, t = -4.941, p < 0.0005 \) [one-tailed]; Fig. 4A). A linear relationship was not significant and accounted for almost none of the variance \( (r^2 = 0.023, t = -0.646, p > 0.50 \) [two-tailed]). Likewise, a second-order polynomial relationship between \( E_H \) and \( C \) was highly significant \( (r^2 = 0.423, t = -3.413, p < 0.002 \) [one-tailed]; Fig. 4B), and a linear relationship was not significant \( (r^2 = 0.027, t = -0.712, p > 0.45 \) [two-tailed]). Regressions were also calculated between \( S \) and \( C \). A second-order polynomial regression was concave downward but marginally non-significant \( (r^2 = 0.115, t = -1.430, 0.05 < p < 0.10 \) [one-tailed]; Fig. 4C); a linear relationship was not significant and explained even less of the variance \( (r^2 = 0.009, t = 0.401, p > 0.30 \) [two-tailed]). These results suggest strong effects of topographic complexity on Shannon-Wiener diversity and Shannon evenness, but at best weak effects on species richness. Second-order regressions using coral cover rather than topographic complexity to estimate disturbance yielded analogous results, although the one-tailed \( t \)-tests gave lower \( p \)-values \( (H' \) regression: \( r^2 = 0.203, t = -1.822, p < 0.05 \); \( E_H \) regression: \( r^2 = 0.149, t = -1.440, 0.05 < p < 0.10 \); \( S \) regression: \( r^2 = 0.015, t = -0.435, p > 0.30 \)).

The percent cover of \textit{Agaricia tenuifolia} was strongly and positively dependent

![Fig. 3. Relationship between percent coral cover and topographic complexity, \( C \).](image-url)
5. Discussion

Many authors have stressed the need to determine that patterns consistent with particular models are in fact due to the proposed mechanisms (Dayton, 1973;

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**Fig. 4.** (A) Relationship between Shannon-Wiener diversity, $H'$, and topographic complexity, $C$. Equation of the best-fit parabola is $H' = -0.42 + 5.70C - 5.85C^2$. (B) Relationship between Shannon evenness, $E'$, and topographic complexity, $C$. Equation of the best-fit parabola is $E' = -0.11 + 2.54C - 2.64C^2$. (C) Relationship between species richness, $S$, and topographic complexity, $C$. Equation of the best-fit parabola is $S = 2.12 + 19.49C - 17.81C^2$.

on $C$ (linear regression: $r^2 = 0.785$, $t = 8.117$, $p < 0.0005$ [one-tailed]; Fig. 5A). In contrast, the cover of corals other than *Agaricia tenuifolia* was highest at intermediate values of $C$ (second-order polynomial regression: $r^2 = 0.276$, $t = -1.915$, $p < 0.05$ [one-tailed]; Fig. 5B). The cover of those other corals was also highest at intermediate values of *Agaricia tenuifolia* cover (second-order polynomial regression: $r^2 = 0.281$, $t = -2.145$, $p < 0.025$ [one-tailed]).
Fig. 5. (A) Relationship between percent cover of Agaricia tenuifolia and topographic complexity, C. Equation of the best-fit line is Cover = −15.37 + 66.22C. (B) Relationship between percent cover of competitively subordinate corals and topographic complexity. Equation of the best-fit parabola is Cover = −8.08 + 63.20C − 55.19C².

Underwood & Denley, 1984; Connor & McCoy, 1979; Connor & Simberloff, 1979; McGuinness, 1984; Elner & Vadas, 1990). Apart from any consideration of process, this study demonstrates the utility of topographic complexity as a predictor of abundance and diversity in a coral assemblage. More importantly, the observations reported here and information from previous studies support the hypothesis of intermediate disturbance effects on the landscape scale. This evidence comprises four steps in a logical sequence.

First, Agaricia tenuifolia was identified as competitively dominant, highly susceptible to disturbance, and highly complex structurally. Second, a link between disturbance and topographic complexity was established. Third, the source of disturbance and the mechanism of competitive dominance were known. Fourth, where disturbance removed the competitive dominant, thereby decreasing topographic complexity, diversity varied in a particular pattern. That pattern was not predictable a priori given only the information in steps 1–3. Rather, the pattern was in many ways consistent with the intermediate disturbance hypothesis. Landscape-scale variations in water flow and other forcing functions may have influenced coral assemblages on the spurs; however, the primary determinant of coral diversity appears to have been the interaction of competition and physical disturbance, as inferred from the strong regressions with topographic complexity.

The diversity of hard corals was higher at intermediate levels of topographic complexity/disturbance. Yet disturbance did not so much allow more species to coexist (regressions with S) as increase the evenness among species that were
already present (regressions with $H'$ and $E_H$). Disturbance limited the cover of the competitive dominant, *Agaricia tenuifolia* (Fig. 5A). Competitively subordinate corals increased in cover as disturbance increased from low to intermediate levels, and as *Agaricia tenuifolia* declined from high to intermediate percent cover (Fig. 5B). At moderate disturbance levels, this increased coral species diversity. Strong, frequent and/or recent disturbance removed virtually all coral colonies, whereas weak, infrequent and/or old disturbance permitted *Agaricia tenuifolia* to dominate.

The intermediate disturbance hypothesis may explain landscape-scale patterns of diversity in other reef habitats and on other coral reefs, provided the landscape exhibits a broad range of disturbance regimes and the competitive dominant is susceptible to that disturbance. Rogers (1993) independently predicted that the hypothesis would most likely be applicable to shallow reef zones dominated by fragile corals. In contrast, diversity and disturbance could exhibit no relationship if the entire landscape is heavily disturbed by large-scale events such as strong hurricanes or mass mortalities of herbivores, or if the competitive dominant is disturbance-resistant (Lubchenco, 1978; Hughes et al., 1987; Hughes, 1989; Jackson, 1991; Knowlton, 1992; Rogers, 1993). Landscape- or larger-scale variations in coral recruitment (Connell, 1973; Bak & Engel, 1979; Highsmith et al., 1980; Rogers et al., 1984) and growth (Huston, 1985) may also influence diversity-disturbance relationships.

This observational study provides the first rigorously quantitative evidence for intermediate disturbance effects in a coral assemblage. Understanding the interaction of disturbance and other processes, on multiple scales, will be necessary to formulate a unified theory of biological diversity (Huston, 1994; Ricklefs & Schluter, 1994).

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