Change in Coral Community Diversity and Structure Surrounding El Niño and Unidentified Stress Disturbances, Thousand Islands, Indonesia 1981-1988

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ABSTRACT

The rates of modern extinctions across a variety of ecosystems are considerably higher than background levels due to a combination of anthropogenic influences and global environmental change. As threats become more widespread, repeated selective extinctions at a local level may amplify into global-scale biotic homogenization. In high-diversity coral reefs, climate change results in coral bleaching, a phenomenon that leads to a drastic reduction in coral abundance and species richness. However, the mechanisms underlying biodiversity loss are poorly understood. In this study, I used published data on live coral richness and abundance in Indonesia between 1981-1988 to measure changes in coral species richness and occupancy surrounding two distinct disturbance events: the El Niño event that led to widespread bleaching in 1982-1983, and an unidentified stress in 1986-1987. Using a null model based on random extinction, I compared null-expected and observed changes in coral species richness and occupancy. Both disturbances showed many significant changes in coral species occupancy independent of their original occupancies, indicating selective extinctions. By 1987, the community recovered to pre-stress regional species richness but not to pre-El Niño regional species richness. By exploring patterns of coral extinctions and recovery surrounding different types of stress, my study provides insights into how coral communities will react to global environmental change and highlights the importance of conservation strategies for coral biodiversity.

INTRODUCTION

A variety of ecosystems are experiencing modern extinction rates considerably higher than background levels due to a combination of anthropogenic and natural disturbances (Brook et al. 2008; Nystrom et al. 2000). Although extinction threats may be regionally uniform, local extirpations within the community are often non-random with respect to taxonomy or phylogeny (McKinney 1987; Purvis et al. 2000; Smith et al. 2009). Analyzing extinctions based on patterns, rather than processes, identifies the extinctions that are non-random and possibly leading to the loss of evolutionary history (Smith et al. 2009; Brook et al. 2008). Non-random patterns of local extirpation, when repeated across many localities, may have similar impacts as regional or global extinctions.

Both natural and anthropogenic disturbances may lead to drastic changes in community structure. Local extirpations can be stochastic, due to random chance, or deterministic, non-randomly selecting species with certain evolutionary history or phylogeny (Brook et al. 2008; Chase 2003). Deterministic threats may cause repeated, selective small-scale extirpations translating to increased regional extinctions and community similarity, or "biotic homogenization" (Smith et al. 2009). Biotic homogenization refers to the dominance of a few species and disappearance of endemics (McKinney and Lockwood 1999). In the process of biotic homogenization, community disassembly often leads to severe reduction in the regional species pool, with reassembly depending on interspecific interactions, abiotic aspects of the environment, and the remaining species pool (Chase 2003; Diamond 1975). In analysis of disturbances, we

must identify extinction patterns and processes to assess the threat of biotic homogenization on a regional scale.

The extent of community similarity amongst localities in a given region is reflected in the measure of beta diversity as repetitive patterns in non-random local extirpations (Smith et al. 2009; Harborne et al. 2006; Cornell et al. 2007; Anderson et al. 2011) Beta diversity combines the concepts of turnover (the change in community structure) and heterogeneity (the variation in species identities) among spatial, temporal, or environmental gradients, linking species richness at local sites (alpha diversity) and regional scales (gamma diversity). However, beta diversity can be calculated in different ways (Anderson et al. 2011). Beta diversity is an important measurement tool for conservation strategies; by linking species turnover from local to regional scales, it involves many ecosystem functions and processes present on the large scale appropriate for management (Smith et al. 2009; Harborne et al. 2006; Condit et al. 2002).

Modern extinction threats have a large influence on coral reefs, jeopardizing the highly productive ecosystem that serves as coastal protection and habitat for important fisheries resources (West 2003; Reaka-Kudla 1997; Wilkinson and Buddemeier 1994). Coastal degradation and global climate change are increasingly affecting seawater quality and temperature, causing the fluctuation of environmental conditions beyond the limited threshold for coral reef health (Wilson et al. 2006; Reaka-Kudla 1997; Goreau and Hayes 1994). Coral bleaching, the expulsion of symbiotic algae and subsequent whitening (Goreau and Hayes 1994), is a common stress response to increased sea surface temperatures (SST) (Jimenez et al. 2001; Podesta and Glynn 2001; Glynn et al 2001; Chavez et al. 1999; Brown 1997; Goreau and Hayes 1994; Gates et al. 1992; Glynn and

D'Croz 1990) and other local stressors such as overfishing, eutrophication, and pollution (Cote and Darling 2010; Carilli et al. 2009; Wilson et al. 2006; Nystrom et al. 2000; Brown 1997; Wilkinson and Buddemeier 1994). The El Niño event of 1982-1983 was the first sign that El Niño-Southern Oscillation (ENSO) may lead to coral bleaching and mortality, confirmed by correlations between extensive coral community disturbance and high magnitude SST changes of El Niño (Glynn 1990). Although recent studies report details of coral bleaching and mortality surrounding disturbances, few have examined repeated patterns of extirpations as possible signs of regional or global extinction and biotic homogenization (Glynn et al. 2001; Jimenez et al. 2001; Podesta and Glynn 2001). As disturbances leading to coral bleaching and mortality become more severe and widespread, we must consider repeated extirpation patterns that could amplify to global extinctions.

This study examines patterns of coral community disassembly and reassembly surrounding two disturbance events in the Thousand Islands, Indonesia. The study period between 1981-1988 encompassed a severe El Niño event (1982-1983) and unidentified stress (1986-1987). The study region, consisting of ten transects or "sites", experienced increased SST due to El Niño between 1982 and 1983. The severe El Niño event resulted in coral bleaching and coral death, decreasing the regional species pool and resulting in high community similarity (decreased beta-diversity) (Warwick et al. 1990). In preliminary analyses Warwick et al. found initial progression to recovery to pre-El Niño conditions (observed by close coincidence in 1981 and 1985 k-dominance species curves), with an interruption between 1986-1987 due to unidentified stress resulting in some extirpations (Brown and Suharsono 1990). My ecological questions ask if

disturbances amongst the coral community result in a non-random pattern of extinctions and how the community recovers. Analyzing both El Niño and stress allows comparison between acute temperature change and bleaching with the confounding effects of general pressures (Brown and Suharsono 1990, Cote and Darling 2010).

Considering periods of temperature and stress disturbance in the coral reef ecosystem, I examine the null hypothesis that extinctions are random against the alternate hypothesis that extinctions are non-random and selective. For both the El Niño and unidentified stress events, I tested for statistically significant patterns in local extirpations, regional extinctions, and species occupancy that would indicate selective extinction or recovery using a null model to compare observed species richness and occupancies with those expected by random chance. My results help explain the stages of disassembly and reassembly surrounding disturbance. I found that the coral community had a much more severe and long-lasting level of species richness loss surrounding El Niño than unidentified stress. I discuss the implications of increasingly widespread disturbances and repeated extirpation patterns on worldwide extinctions amongst coral reef ecosystems.

METHODS

The dataset used in this study includes physical and biological data previously published in: (1) an assessment of percentage of live coral cover damage and recovery (Brown and Suharsono 1990); (2) a comparison of various statistical analyses (Warwick et al. 1990); and (3) explorations of beta diversity calculations (Anderson et al. 2011). I am now using this dataset to identify local and regional extinction patterns using incidence matrices

applied to a null model of random extinction and occupancy distributions. See Table 1 for a clear list of my independent and dependent variables.

Study Site

The study site is located in the Thousand Islands of Indonesia, specifically the Pulau Pari island complex. Fringing reef surrounds the islands, including habitats of sand flat, reef flat, reef edge, and reef slope. Of the corals, *Acropora* and *Montipora* species dominate the fringing reef (Brown and Suharsono 1990).

Overview of Data Collection

Ten transects were established in the Pulau Pari island complex by 1981. For this study, each transect is considered a "site," or local community, and the region encompasses all ten sites. Each 30-m^2 (3x10-m) transect was laid across the reef flat, or the shallowest, flattest area of the reef. Adjacent transects are separated by one meter. Placement of cement blocks at each site made transects permanent. Although slight movement of the cement bricks was possible annually, the error is estimated to be only half a meter from the original placement (Brown and Suharsono 1990).

Throughout the study period, Brown, Suharsono, and Sya'rani measured percentage live coral cover along the transects (Brown and Suharsono 1990). The coral measure is planar rather than three-dimensional, ignoring live coral surfaces along the sides of colonies. From November 1982 to June 1987, sea surface temperatures were measured daily at a reef flat area in the north of Pulau Pari Island at the Center for Oceanology marine laboratory (Brown and Suharsono 1990).

Overview of Analytical Methods

Null Model

I created a null model of random extinctions similar to that of Smith, Lips, and Chase in their study of homogenization of amphibian biota (2009). The null model predicts the number of species expected to have gone extinct randomly based on observed local extirpation rates. For reference, "random extinctions" are those that could be expected under conditions of random chance, while "local extirpations" refers to species that disappear at local sites and "regional extinctions" are those that disappear from the entire study area. To differentiate between responses of coral species, I use the terms "extinct" or "extirpated" in reference to species that disappear regionally or locally immediately post-disturbance and never return throughout the study period, while "absent' refers to species that disappear but reappear in future years.

Each incidence matrix is specific to one year, detailing species presence or absence at each of the ten sites. From the incidence matrix, I calculated total occupancy (the number of sites each species inhabits), local richness (the number of species present at each site) and regional richness (the total number of species that occupy at least one site). I also created incidence matrices grouping the species into their respective families to identify patterns that are not as apparent at the species-level.

To model random local extirpations and regional extinction, I assigned each species or family present at each site in the year prior to disturbance a fixed and equivalent probability of local extinction. These probabilities are based on the observed local loss of species at a given site between two years. For example, the local species

richness in 1981 at Site 1 was 30 species, but dropped to only 4 species in 1983. The local extirpation rate at Site 1 between 1981-1983 was then about 0.87. The regional extinction rate would then be the average of all ten local extirpation rates. The null model assigns each species or family present in the year prior to disturbance (1981 for El Niño analyses and 1985 for stress analyses) a number between 0 and 1 representing a randomly generated extirpation rate. If the randomly generated extirpation rate is less than or equal to the observed extirpation rate, the species or family is predicted to go extinct at that site. If the random number is greater than the extirpation rate, it is predicted to survive the disturbance. For each simulation, I chose a dependent variable: regional richness, average local richness, or the occupancy of a species or family. I then applied a Monte Carlo simulation, conducting 10,000 iterations of the random extinction process.

In order to identify non-random extinction patterns, I compared the observed data with what would be expected under random extinctions. The results of each simulation calculate the expected outcome of the dependent variable (the average of all 10,000 generated values) and the number of iterations that resulted in a value greater than or equal to the observed dependent variable post-disturbance. The observed regional richness, average local richness, or species or family occupancy that are significantly different from the null-expected outcome indicates any potential patterns of non-random extinctions. To determine which results were significantly different than observed, I calculated a p-value as the proportion of the 10,000 iterations where the expected dependent value is less than or equal to the test statistic (the observed value). For example, if the observed regional species richness were 23, the p-value would be 0 if

none of the iterations produced a dependent variable less than or equal to 23. If 100 iterations were less than or equal to 23, the p-value would be 0.010.

Occupancy Distribution

I also utilized the incidence matrix data to represent the occupancy distribution in each year. I created the occupancy distribution by ranking each species according to the number of sites they occupy (1-10). By comparing occupancy distributions between years, I can see how disturbances affect community structure in terms of relative abundance. For each year, species or families are placed into occupancy categories based on the number of sites they occupy: rare (occupancy 1 or 2), somewhat rare (occupancy 3 or 4), somewhat common (occupancy 5 or 6), common (occupancy 7 or 8) or very common (occupancy 9 or 10). Because species' occupancies often fluctuated by one or two sites, I grouped two occupancies into each category to identify patterns of general occupancies more apparent at a slightly broader level. I can then more easily compare each species or family's occupancy throughout the years.

Ecological Questions and Analysis

I use the null model and occupation distribution described above to address several ecological questions over two time periods corresponding with two types of disturbance.

Beta Diversity

To identify immediate impact of the two distinct disturbances on local and regional species richness, I applied the null model of random extinction using the observed local

extirpation rates between 1981-1983 (El Niño) and 1985-1987 (unknown stress). This analysis uses the species-level incidence matrices, consisting of the 54 species present in 1981 and 28 present in 1985 across the ten sites. I perform two simulations for each disturbance, choosing regional species richness and then average local species richness as the dependent variables. The results allow for a comparison between expected and observed values of species richness, and a casual comparison of the slope between regional and local species richness as a proxy for beta diversity.

Recovery

I also aimed to determine if coral species richness had recovered to pre-disturbance levels. I parameterized the null model for incidence matrices from 1981 (pre-El Niño) and 1985 (2-3 years post-El Niño), to compare observed local and regional species richness with the null-expected based on local extirpations between 1981 and 1985. A casual comparison of the 1985 data indicate that local and regional species diversity had still not recovered to pre-disturbance levels by 1985. My analysis will allow us to go beyond this observation to determine if the deviation from the random expectation between 1981 and 1983 (if any) had been ameliorated between 1983 and 1985, which would be indicative of partial recovery, perhaps owing to recolonization by extirpated species. The same analysis was performed for the stress disturbance, using the data from 1985 (pre-stress) and 1988 (1-2 years post-stress) to detect effective recovery to pre-stress conditions and back on track for possible recovery to pre-El Niño diversity.

Species-level Occupancy

To identify species that were particularly vulnerable or tolerant of the El Niño event, I highlighted species that went completely extinct from the region immediately with the El Niño disturbance and species that survived ("resilient" species). Species labeled as completely extinct never appeared at any site after 1981 throughout the study period. Resilient species were present in every year of the study. Using the null model of random extinction with species-level incidence matrices for 1981 and 1983, I set the species' occupancy as the dependent variable. I performed twenty simulations, six for the species that remained resilient and fourteen for the species that went extinct immediately after the severe El Niño disturbance. Of these 20 species that exhibit radical vulnerability or tolerance, my analyses pinpoint which species changes were statistically unlikely under random chance reflecting deterministic processes shaping community structure.

Family-level Occupancy

I applied the family-level incidence matrices to the null model to identify potential patterns in occupancy changes that could be more apparent at a broader level of taxonomic classification. Any family-level bias in species that are resilient or susceptible to either disturbance is likely indicative of phylogenetic nonindependence to the respective type of stress, an important indicator of deterministic processes in community restructuring after disturbance. I grouped the species present pre-disturbance into their nine respective families to create the family-level incidence matrices. For each comparison between two years I ran nine simulations, one for each family, designating the family occupancy as the dependent variable. Local extirpation rates were still

calculated per site, as they had been for the other null-model analyses, using family presence and absence data between pre-disturbance and post-disturbance years (1981 and 1983 for El Niño, 1985 and 1987 for unidentified stress). In 1987, two of the sites had more families present than in 1985. For the two sites showing recovery of family presence, I converted total number of families present in 1987 into a probability of each family being present. For example, if only four families were present in 1985 but six were present in 1987, each family has a 0.6 probability of being present. Instead of applying the extirpation rate into the null model for each species present, the probability of recovery is applied to all nine possible families regardless of their presence in the previous year to account for families that reappear.

I repeated the family-level null model to identify possible recovery by comparing expected and observed occupancies in 1985 and 1988 with pre-disturbance years of 1981 and 1985 respective to each disturbance. Similar to the recovery seen in the stress disturbance data between 1985-1987, in 1988 three sites had more families present in 1985. Probabilities of family presence based on the 1988 occupation were applied to all of the nine families. For the other seven sites, 1985 and 1988 had the same number of families present so no extirpation or recovery rates were applied. By performing the analyses to compare observed and expected occupancies 2-3 years post-disturbance, we can determine the extent that the family recovers and which families become more or less dominant.

RESULTS

EL NIÑO INDUCED TEMPERATURE CHANGE: 1981-1985

Immediate Decrease in Beta Diversity

Prior to the 1982-1983 El Niño disturbance, the study site was characterized by high local species richness with an average of 18 species per site (range 7-30 species; Table 2; high compared to alpha richness in Glynn et al. 2001). Regional species richness was also high (54 species). The difference between local and regional species richness indicates low community similarity, or high beta diversity (Figure 1). Of the species present in 1981, 18 (33%) were locally endemic, occupying only one of ten sites.

The severe disturbance event immediately altered coral community structure. During the 1983 sampling period, average local species richness had dropped to only 2.5 species per site (range 1-5 species; Table 2), and regional species richness dropped to 14 species total. The slope of the line from average local species richness to regional species richness decreased in 1983, indicating lower beta diversity reflecting the increased similarity amongst sites in the region (Figure 1, Figure 2a). The null model of random extinction predicted a regional species richness of 19 in 1983 given random extinction of the coral community in 1981 (Figure 2a). Compared with the observed species richness in 1983 (14), the difference between observed and expected was significant ($p=0.024$, 95% CI), suggesting that the severe decrease in species richness surrounding the 1982-1983 El Niño event was non-random.

Immediate Change in Community Structure

Prior to the severe El Niño disturbance, the occupancy distribution was biased towards a large number of endemics, with only a few very widespread species (Figure 3). After the

El Niño event, 14 of the 54 species were completely extirpated from all sites. Of the 54 species present in 1981, only six were completely resilient after the disturbance event, present in at least one site every year through the study period. Species that were extirpated or remained resilient post-disturbance came from a range of occupancies in 1981 (Figure 4). However, predictions from the null model show that of all the species to have gone extinct or remained resilient, *Pocillopora verrucosa* was the only species whose reaction to disturbance was unexpected under conditions of random extinction; *P. verrucosa* had an original occupancy of 6 sites, and in greater than 95% of simulations it does not go extinct (p=0.044).

The classification of each species' occupancy class in 1981 compared with 1983 showed that species in all occupancy categories were affected by the severe disturbance event, not solely endemic species (Figure 3). The majority of species in all occupancy categories went extinct or absent post-disturbance (Figure 5a).

Recovery in Beta Diversity

In 1985, two years recovery time after the severe El Niño disturbance, local and regional species richness were still lower than the pre-disturbance levels in 1981. Average local species richness was 8.9 species (range 4-15 species; Table 2). Regional species richness had increased from 1983 to 28 species total, however has still not recovered to the 1981 regional species richness of 54. The proportional difference between local and regional species richness (beta diversity), increased from 1983, but community similarity was still much higher than the 1981 state. The null model applied to recovery in 1985 resulted in

an expected species richness of 41, significantly higher than the observed value (p=0) (Figure 2b).

Recovery in Community Structure

I analyzed species occupations in 1985 to identify possible recovery from the severe disturbance event. Only two occupancy categories (rare and somewhat common) showed fifty percent or more species still absent that had been present in 1981. All other occupancy categories showed more species present than absent (Figure 4b).

Family-level Patterns

Immediately after the disturbance in 1983, three families went extinct . Two of those families were expected to go extinct randomly (*Helioporidae*: p=0.11, *Milleporidae*: 0.42, 95% CI), whereas a third family, *Pocilloporidae*, which initially occupied 100% of the sites, would not have been expected to disappear from the region (p=0.012, 95% CI) (Table 3a). In 1985, *Agariicidae* also became absent from the system, and this decline in occupancy was greater than expected by the null model (p=0.012, 95% CI) (Table 3b).

The null model at the family level also identified patterns of resilience. Immediately post-disturbance, *Fungiidae* remained at a stable occupancy from 1981 to 1983, although the null-expectation was that this family should have decreased in occupancy (p=0, 95% CI) (Table 3a). However, in 1985 *Fungiidae* did decline to the expected occupancy (Table 3b). In both 1983 and 1985 *Poritidae* remained significantly more common than expected by chance (p=0, 95% CI). *Acroporidae* and *Faviidae* experience similar patterns, both decreasing to their expected low occupancies in 1983

post-disturbance and rebounding immediately to very common values in 1985 (*Acroporidae*: p=0. *Faviidae*: p=0.016 95% CI) (Table 3).

GENERAL STRESS: 1985-1988

Immediate Decrease in Beta Diversity

Unknown stress had significant but milder homogenizing effect than El Nino (Figure 6). In 1985, prior to general stress, the coral community had an average local species richness of 8.9 (range 4-15 species; Table 4) and a regional species richness of 28. In 1987, average local species richness dropped to 6.1 (range 2-12 species, Table 4) with total regional richness of 17 species. The null model of random extinction calculated an expected regional species richness of 25 species; observed regional species richness was significantly lower than expected given random extinctions (p=0, 95% CI) (Figure 7a).

Immediate Change in Community Structure

Although local and regional diversity in 1985 had not completely recovered to 1981 levels, the coral community had recovered to a similar structure. The occupancy distribution reflects the structure of many endemic species, many intermediate occupants, and a few common species. In 1987, however, the distribution shows a bias towards somewhat rare species (Figure 8). With general stress, both endemic species and very common species either went absent or shifted to a mid-level occupancy (Figure 9a).

Recovery in Beta Diversity

Recovery process post-unknown stress was faster than any possible recovery observed post-El Niño. In 1988, one year of recovery post-stress, average local species richness

had increased slightly from 1987 to 6.9 species (range 4-13 species, Table 4) and regional richness increased to 23 species. Using observed extinction rates between 1985 and 1988, the null model predicted an expected regional species richness of 25 species (Figure 7b). This value was not statistically significant given the test statistic of observed regional species richness of 23 (p=0.034, 95% CI), suggesting that coral diversity in 1988 had effectively recovered to the 1985 pre-stress level.

Recovery in Community Structure

The occupancy distribution in 1988 reflects pre-stress occupancies, indicating recovery in community structure post-stress (Figure 8). Species that were rare, somewhat rare, or somewhat common in 1987 mostly remained stable or decreased slightly in occupancy, adding more endemic species to the community and removing the bias on mid-level occupancy species. Common and very common species were also present again by 1988 (Figure 9b).

Family-level Patterns

I identified significant patterns in family-level resilience and intolerance in response to unidentified stress. *Acroporidae* remained resilient through general stress, a non-random occurrence in 1987 however expected in 1988 (p=0.0014, 95% CI). *Oculinidae* increases in occupancy in 1987 when it was expected to remain stable and rare (p=0, 95% CI) (Table 5a, 5b) After decreasing expectedly in 1987, the continued decrease of *Faviidae* in 1988 is not expected in the null model (p=0, 95% CI). Although *Fungiidae* disappeared from the community in 1987, they reappeared with great recovery in 1988, both

unexpected results (1987: p=0, 1988: p=0 95% CI) (Table 5a, 5b). Reappearances of three families in 1987 and another family in 1988 were not significant in the null model and could have been due to random chance (*Agariicidae:* p=0.24; *Milleporidae*: p=0.25; *Pocilloporidae:* p=0.24, *Helioporidae*: p=0.50, 95% CI).

DISCUSSION

I found that disturbances from both El Niño temperature change and unidentified stress result in selective extinctions leading to changes in local and regional diversity and community structure. The severe El Niño event of 1982-1983 led to substantial coral extinctions resulting in biotic homogenization with much slower recovery in regional diversity than would be expected by random chance. General, unidentified stress inflicted on the already disturbed community greatly affected endemic species, however regional diversity effectively recovered to pre-stress conditions. I conclude that changes in sea surface temperature affect corals in a predictable, highly deterministic way and further stress in the system halts any possible recovery.

The severe El Niño event resulted in immediate biotic homogenization, decreasing beta diversity significantly as local coral communities became more similar across the region. Biotic homogenization is generally indicative of a loss of endemic species (Smith et al. 2009; Orme et al 2005). In this scenario, species of all occupancies go extinct or absent. Local extirpation of endemic species was expected by random chance due to their vulnerability from low abundance, however, extirpations in every occupancy category was unexpected. The fact that species from all occupancy categories were affected by temperature change is indicative that the El Niño disturbance acted as a

broad filter for intolerant species, as it is statistically unlikely that very common species would disappear completely immediately post-disturbance.

Extinction patterns at the family-level are further evidence of selective extinction. The null model shows that *Poritidae* and *Acroporidae* were unexpectedly resilient to temperature increase during each year, while other families such as *Pocilloporidae* and *Faviidae* are unexpectedly intolerant. Because all four of these families were very common prior to disturbance, these results show distinct patterns in resilience of some families and intolerance of others. Statistically significant extinction patterns at the family-level supported by the null model demonstrate further evidence that deterministic processes are impacting the coral community. It is likely that deterministic factors, possibly phylogeny, competition (Smith et al. 2009) or historical biogeography (Santini et al. 2002; Chase 2003; Chase 2010; Veron 1995), are influencing the differential susceptibility of coral taxa. Other studies of coral bleaching on Indo-Pacific reefs support our findings, reporting selective extinction of certain taxa biologically less susceptible to disturbance (Nystrom et al. 2000; Jokiel and Coles 1990).

By 1985 the community showed some recovery in regional species richness from 1983. However, the null model predicts that random extinctions between 1981 and 1985 would not have shown much species loss; therefore under random extinctions there should have been more recovery. I have already concluded that increased SST from the El Niño event immediately selectively filtered susceptible species in 1983. Species left behind were likely more tolerant, with a predisposition to spread, leading to the homogenized local-regional diversity structure by 1985. Other speculative explanations of the slow recovery could be the dominance of macroalgae (Bellwood et al. 2006) or the

success of a few, more stable host-symbiont combinations (Podesta and Glynn 2001; Buddemeier and Fautin 1993).

The period of general stress between 1986-1987 halted recovery from the El Niño disturbance. The community structure showed biotic homogenization through significant loss in regional diversity and a bias towards mid-level occupancies. Assuming uniform stress across the community, endemic species were disproportionately affected, presumably due to their low abundances. However, regional species richness was significantly lower than the expected value under random extinctions, indicating that selective extinctions were again impacting the community. Upon closer look at the occupation distribution, six out of fourteen species rare in 1985 increased in occupancy post-stress, while common species decreased significantly in occupancy. Both of these findings are statistically unlikely given random extinctions. Unidentified stress impacting the previously disturbed community again acted as a filter of intolerant species, allowing the remaining and presumably resilient species area to spread to explain the further biotic homogenization and decrease in regional species richness.

By 1988, regional species richness had effectively recovered to pre-stress levels, as the observed regional species richness in 1988 was not significantly different from that expected by random chance. Effective recovery is an important result in our study because it shows that within two years of a short period of stress regional diversity can recover back to pre-stress levels. However, the community is still threatened. The occupancy distribution in 1988 had not completely rebounded to that of 1985; there are still fewer rare and common species. Until there is a significantly larger number of endemic species compared with other occupancy categories, it is unlikely that the

regional diversity will completely return to pre-disturbance species richness due to a smaller regional species pool.

The fact that the stress in this study was unidentified makes it impossible to determine definite causes to the patterns I have seen. Stress could have been due to anthropogenic disturbances (pollution, abusive tourism, etc.) possibly intensified by an increased sensitivity in the community from prior exposure to stress (Wilson et al. 2006; Brook et al. 2008), or another temperature fluctuation, where the community could have experienced lower extinction rates from acclimation to the specific stress (West and Salm 2003; Jokiel and Coles 1990; Podesta and Glynn 2001). Because the community was previously disturbed by a severe temperature fluctuation, the effects from both disturbances become confounded and difficult to identify. Examples shown in this study are indicative of coral bleaching events worldwide, as coral bleaching is becoming more widespread and confounding many other types of stressors all acting as selective pressures in the ecosystem.

The results of our analysis from both the severe El Niño disturbance and unknown stress identify important information for coral reef conservation and management. Considering widespread human impacts and global climate change, ocean conditions and coral reef communities will undoubtedly be affected (Glynn et al. 2001; Podesta and Glynn 2001; Goreau and Hayes 1994). SST increase, such as those exhibited by El Niño, is a severe threat to coral community structure and diversity leading to selective extinctions and biotic homogenization. As shown in our study, the community needs more than two or three years for regional species richness and community structure to recover from severe temperature disturbance. With more widespread anthropogenic

impacts on coral reef communities, it is expected that in the same regions affected by SST increases there will be further stressors. Our study shows that other stressors halts any possible recovery from the severe temperature disturbance; however with a very short period of stress the community is able to recover to pre-stress conditions and hopefully continue to recover to pre-El Niño diversity levels. In this case, there were no more than the two disturbance incidences during the eight-year study period; unfortunately, in many coastal or tourism-heavy areas there may be more common and continuing disturbances. Considering confounding effects of multiple possible stressors, it is vital to understand patterns in selective extinctions and regional species richness recovery associated with specific types of disturbances to assess and identify endangered areas as threats become global.

By exploring extinction patterns surrounding temperature fluctuation and unidentified stress, I show that selective extinctions lead to biotic homogenization in coral communities, with potential for recovery under a conservative timeframe. The two types of disturbances and the potential processes and mechanisms discussed – deterministic factors for selective extinction and confounding disturbances relating to extinction severity – affect community disassembly and reassembly post-disturbance. Future studies incorporating multiple disturbances could disentangle potential processes leading to patterns I have discussed. Understanding coral community reactions to increasingly widespread threats would move conservation efforts toward a more useful and effective methodology for coral reef management strategy.

FIGURES AND TABLES

Table 1. Most of my analyses used the null model for random extinction, utilizing the time periods surrounding disturbances as the independent variables and species richness and occupancy as the dependent variables to answer my ecological questions. The occupancy distribution was also used to help identify and support patterns.

Methods Used	Time Periods for Analysis (Independent Variables)	Dependent Variables in Null Model
Null model for random extinction	Immediately Post-El Niño 1981-1983	Average Local Species Richness
Occupancy distribution	Post-post El Niño 1981-1985	Regional Species Richness
	Immediately Post-Unidentified Stress 1985-1987	Occupancy of Extinct Species
	Post-post Unidentified Stress 1985-1988	Occupancy of Resilient Species
		Occupancy of Families

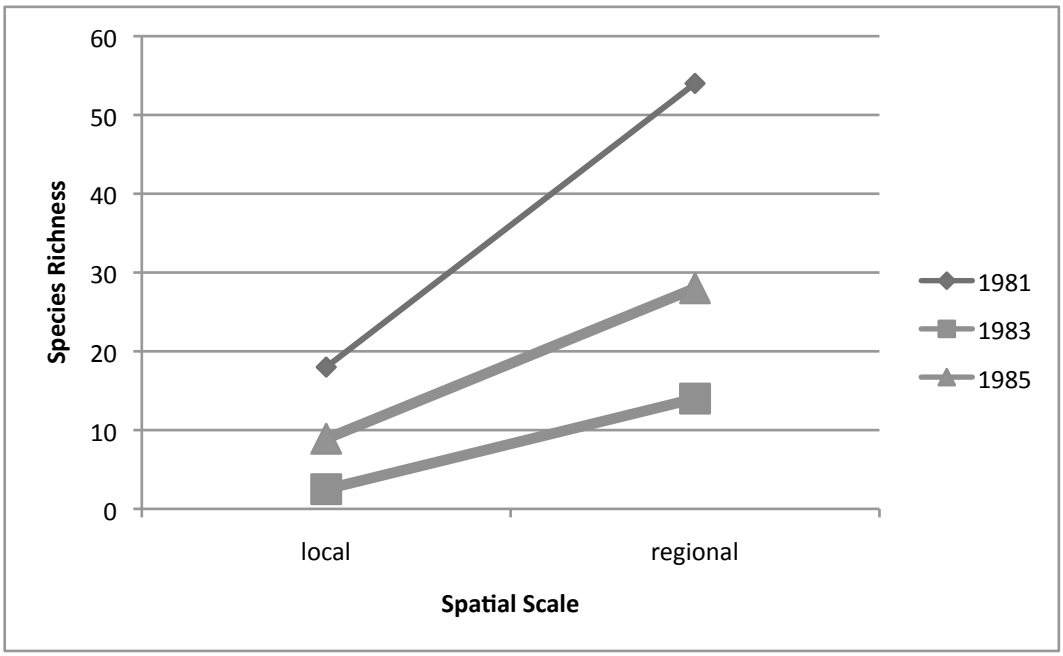
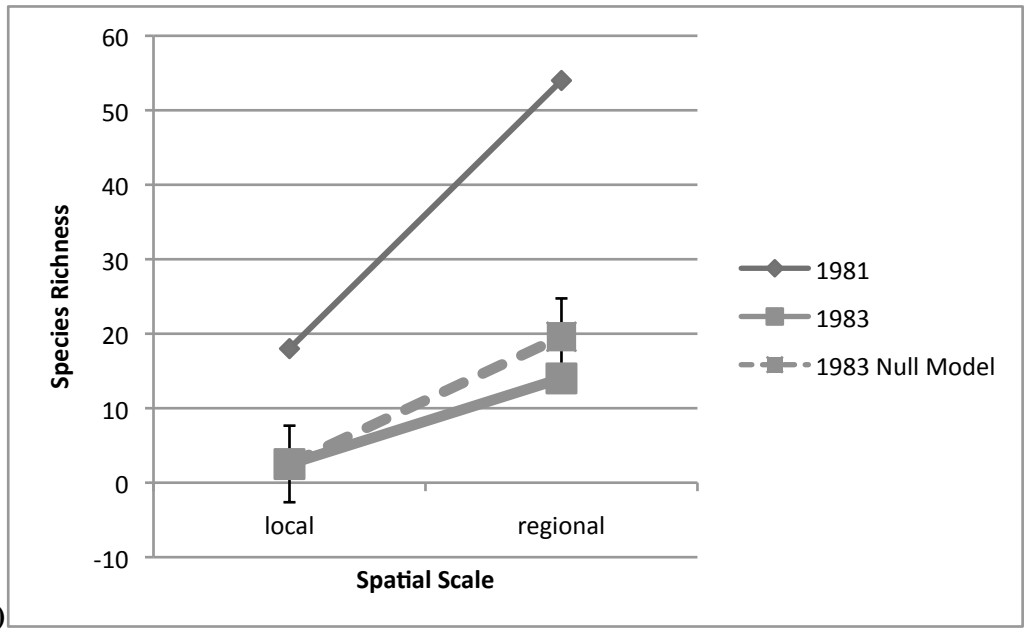


Figure 1. Raw data mapping the scaling of local and regional species richness in a coral community before (1981) and after (1983 and 1985) a severe El Niño disturbance. Local richness is the mean number of species per site and regional richness is the total number of species across all ten sites.

Table 2. Site locations and local coral species richness, 1981-1985.

Site	Pre-disturbance coral species richness	Post-Disturbance, 1983 coral species richness (% reduction)	Post-Disturbance, 1985 coral species richness (% reduction since 1981)
1	30	4 (-87)	15 (-50)
2	27	5 (-82)	12 (-56)
3	26	2 (-92)	14 (-46)
4	21	5 (-76)	11 (-48)
5	16	3 (-81)	9 (-44)
6	14	1 (-93)	7 (-50)
7	14	1 (-93)	6 (-57)
8	14	1 (-93)	6 (-57)
9	11	2 (-82)	5 (-55)
10	7	1 (-86)	4 (-43)
Total regional richness	54	14 (-74)	28 (-48)



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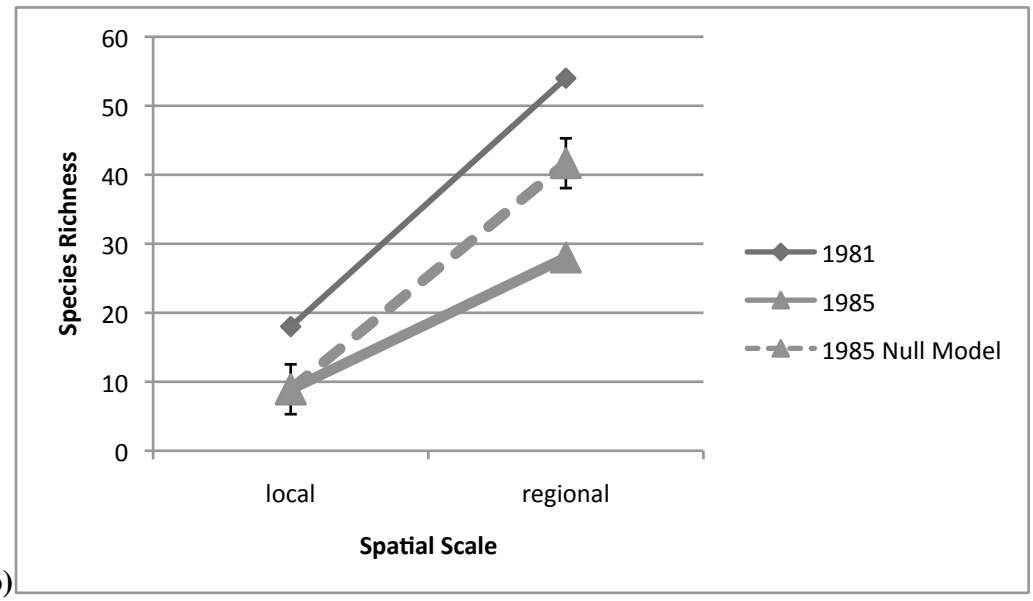


(b)

Figure 2. The scaling of local and regional richness in a coral community. Prior to the disturbance of a strong El Niño event in 1982-1983, beta diversity was high, showing the dissimilarity between species communities at local and regional scales. Vertical error bars show variance. (a) After the El Niño disturbance event, extinctions in the coral community were very high on local and regional scales (1983). Regional diversity loss was greater than would be expected if local extinctions were random (1983 Null Model) (permutation test based on null model, see Methods). (b) Observations of species richness in 1985 show higher local and regional diversity (1985) however significantly lower than would be expected if local extinctions were random (1985 Null Model) (permutation test based on null model, see Methods).

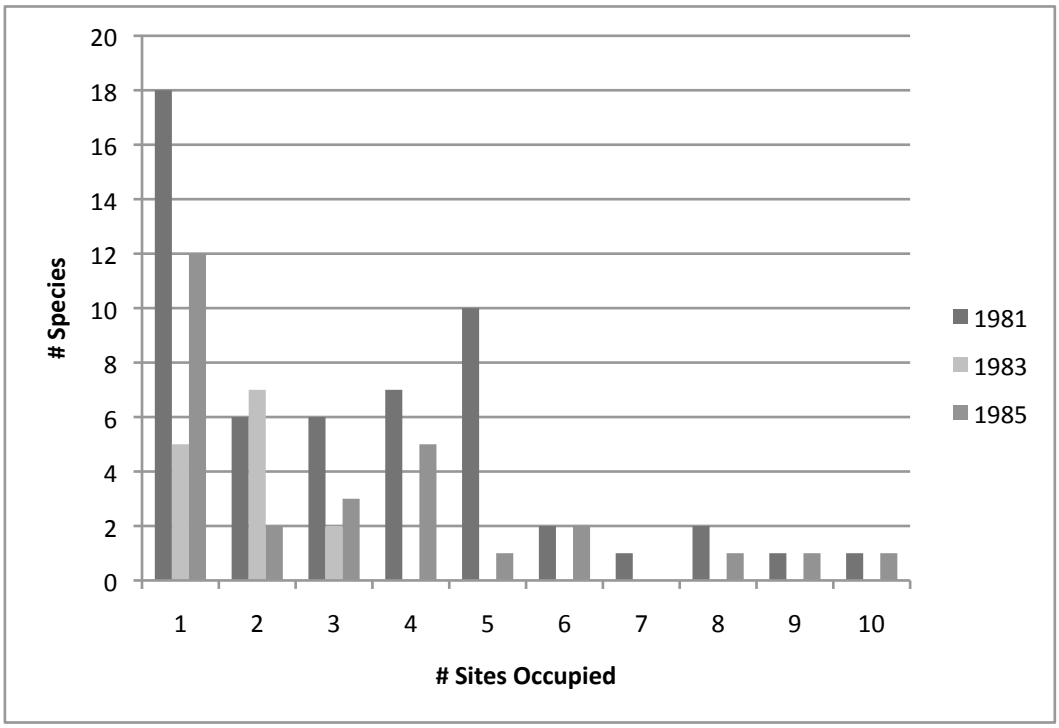


Figure 3. Occupancy distribution of species present between 1981-1985. In 1981, many species occupied an intermediate number of sites, while only a few species were very common. Post El Niño in 1983, only a few rare species remained. In 1985 some species became more common.

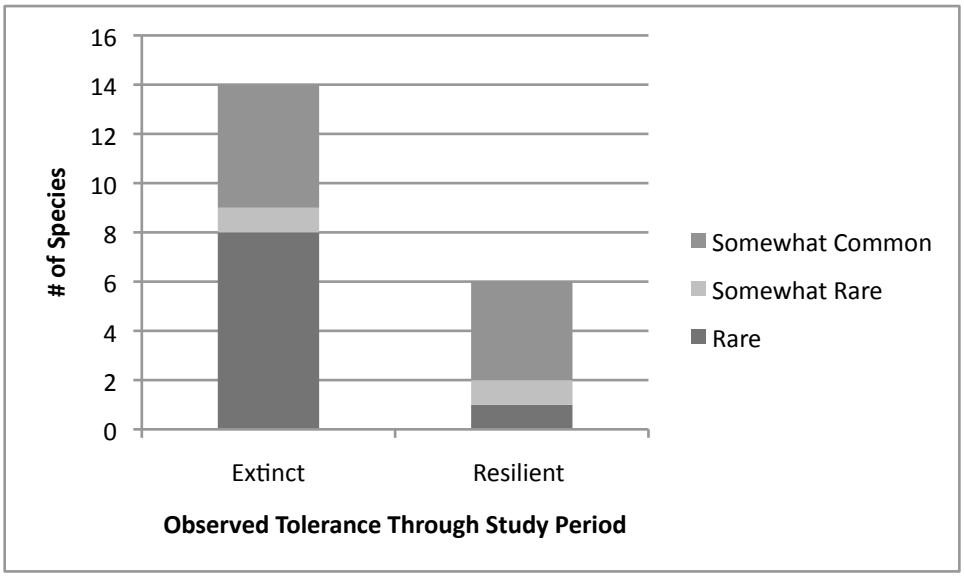
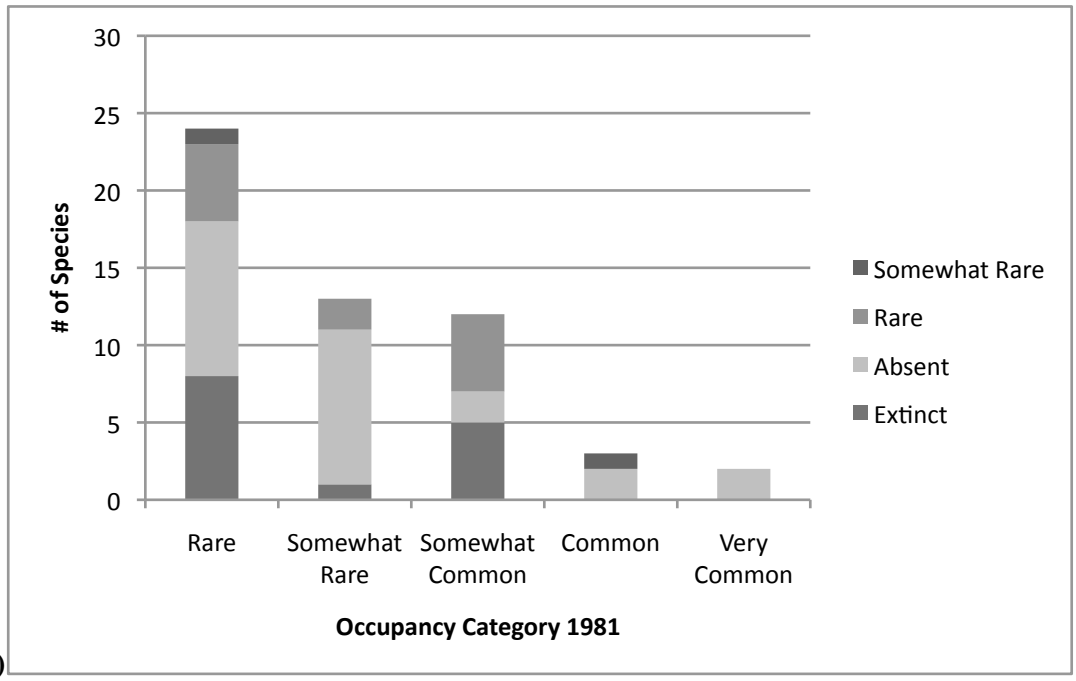
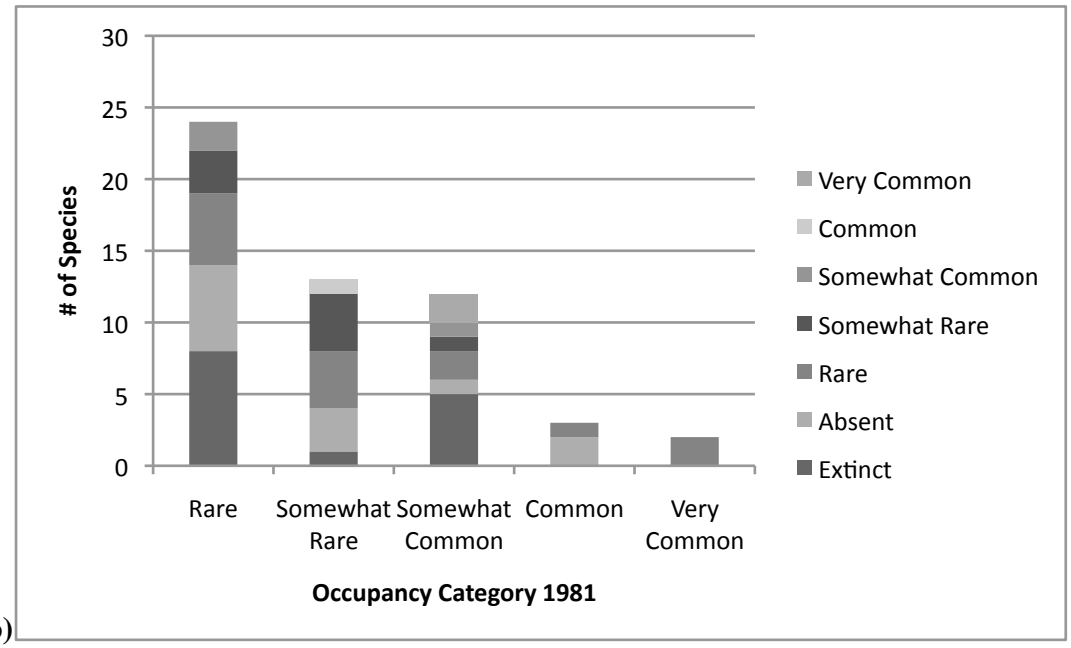


Figure 4. Pre-El Niño disturbance occupancies of species that go extinct or remain resilient throughout the study period. Extinct species were present in 1981 and never came back through the entire study period. Intolerant (resilient) species were present in 1981 and were present in every year throughout the study period. Pre-disturbance occupancies of both extinct and resilient species ranged from rare to somewhat common.



(a)



(b)

Figure 5. Changes in occupancy surrounding severe El Niño disturbance. Each species present in 1981 was assigned an occupancy category, from rare to very common. The x and y-axes identify the number of species at each occupancy level in 1981. The shades in the columns represent the occupancy in 1983 (a) and 1985 (b).

Table 3. Null model of random extinctions applied to family incidence. Expected occupations of each family with random extinctions calculated and compared with observed occupations. (a) In 1983, Fungiidae occupation remained stable while Poritidae was more abundant that expected. (b) In 1985, Acroporidae and Poritidae occupation remained very common and stable, which was significantly unexpected with random extinctions. Agariicidae and Pocilloporidae decreased from common occupancies to absent, which was also unexpected with random extinction. Faviidae remained relatively common post-disturbance, also calculated to have been unexpected given local extinction rates.

Family	Occupied 81	Occupied 83	Expected	p-value
Acroporidae	10	4	3.4281	0.2213
Agariicidae	6	3	2.1965	0.1176
Faviidae	10	3	3.8046	0.4239
Fungiidae	**3**	**3**	**1.178**	**0**
Helioporidae	4	0	1.6872	0.1062
Milleporidae	1	0	0.6719	0.4152
Oculinidae	5	1	1.8415	0.3767
Pocilloporidae	**10**	**0**	**3.3985**	**0.0118**
Poritidae	**10**	**7**	**3.927**	**0.0025**

(a)

Family	Occupied 81	Occupied 85	Expected	p-value
Acroporidae	**10**	**10**	**5.2462**	**0**
Agariicidae	**6**	**0**	**3.0762**	**0.0119**
Faviidae	**10**	**8**	**5.2743**	**0.0161**
Fungiidae	3	1	1.3029	0.5982
Helioporidae	4	0	1.8082	0.0909
Milleporidae	1	0	0.5058	0.2394
Oculinidae	5	1	2.308	0.2394
Pocilloporidae	**10**	**0**	**5.2702**	**0.0001**
Poritidae	**10**	**10**	**5.2743**	**0**

(b)

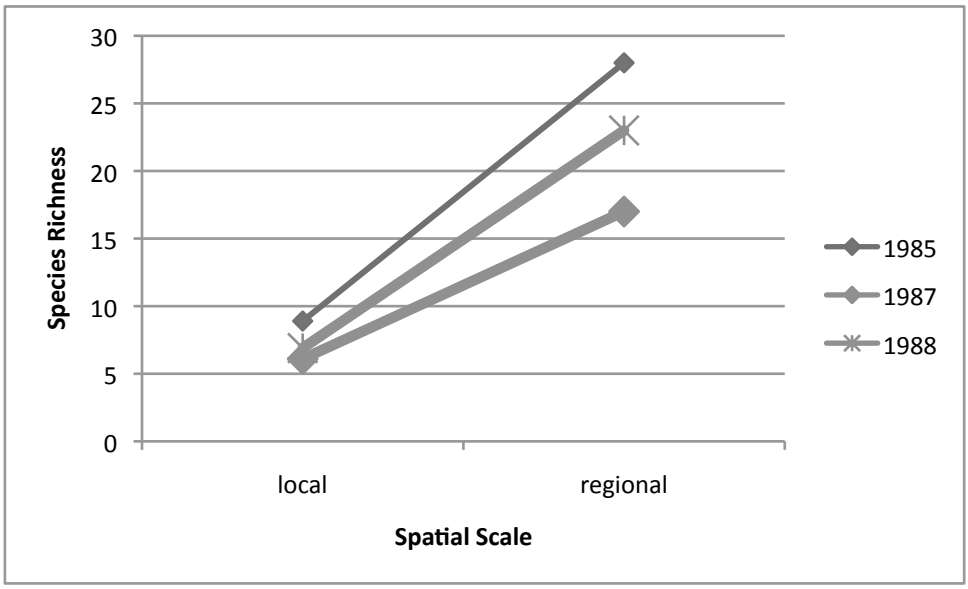
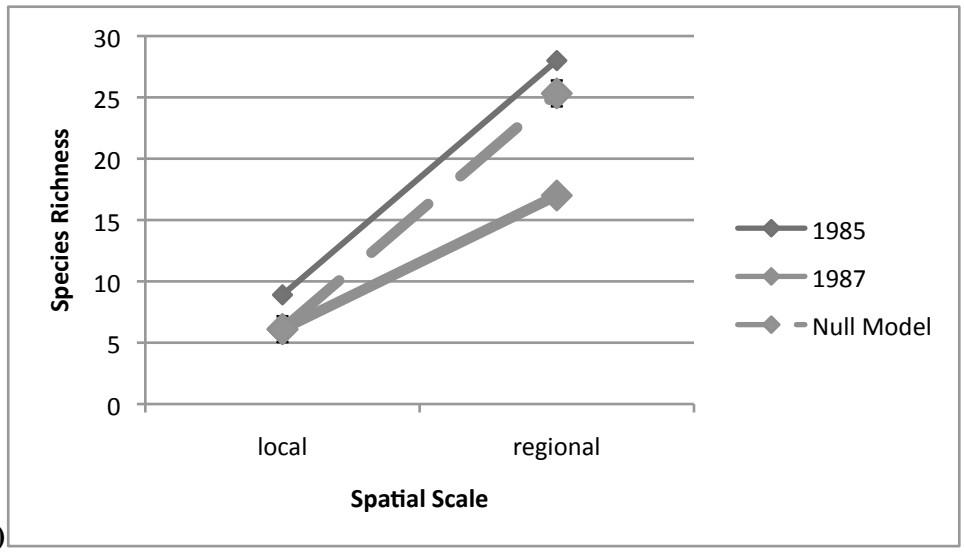


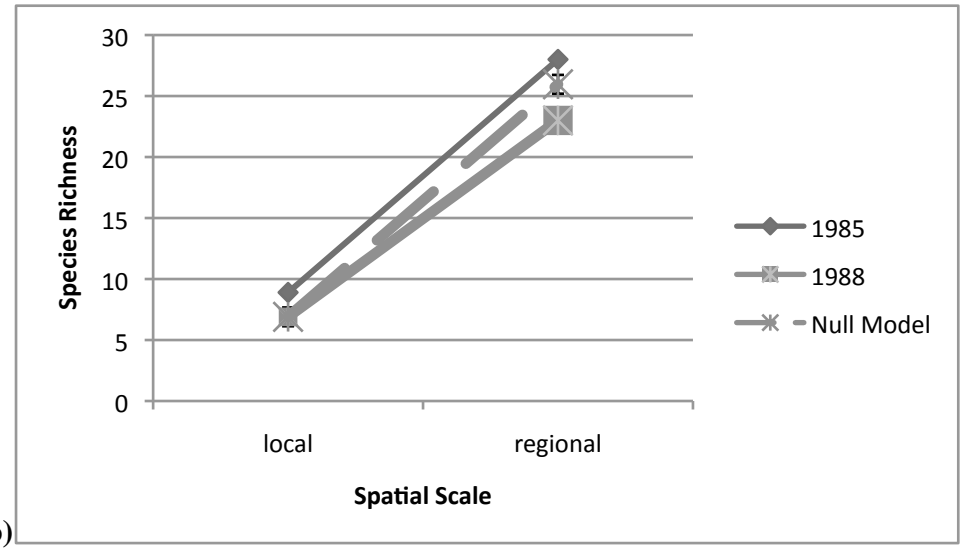
Figure 6. Raw data mapping the scaling of local and regional species richness in the coral community before and after a mild disturbance. Local richness is the mean number of species per site, and regional diversity is the total species richness over all ten sites.

Table 4. Site locations and local coral species richness, 1985-1988.

Site	Pre-stress coral species richness (% reduction)	Post-stress 1987 coral species richness (% reduction)	Post-stress 1988 coral species richness (% reduction since 1985)
1	15	11 (-27)	13 (-13)
2	12	12 (0)	11 (-8)
3	14	11 (-21)	12 (-14)
4	11	9 (-18)	5 (-55)
5	9	4 (-56)	5 (-44)
6	7	4 (-43)	5 (-29)
7	6	3 (-50)	5 (-17)
8	6	3 (-50)	4 (-33)
9	5	2 (-60)	5 (0)
10	4	2 (-50)	4 (0)
Total regional richness	28	17 (-39)	23 (-18)



(a)



(b)

Figure 7. The scaling of local and regional richness in a coral community. Prior to the disturbance of general stress in 1986-1987, beta diversity was relatively high, showing the dissimilarity between species communities at local and regional scales. (a) After the period of general stress, extinctions in the coral community were low on local scales but had a greater effect on regional diversity, declining beta diversity (1987). Regional diversity loss in 1987 was greater than would be expected if local extinctions were random (1987 Null Model) (permutation test based on null model, see Methods). (b) Observations of species richness in 1988 show higher local and regional diversity (1988) only slightly lower than would be expected if local extinctions were random (1988 Null Model) (permutation test based on null model, see Methods).

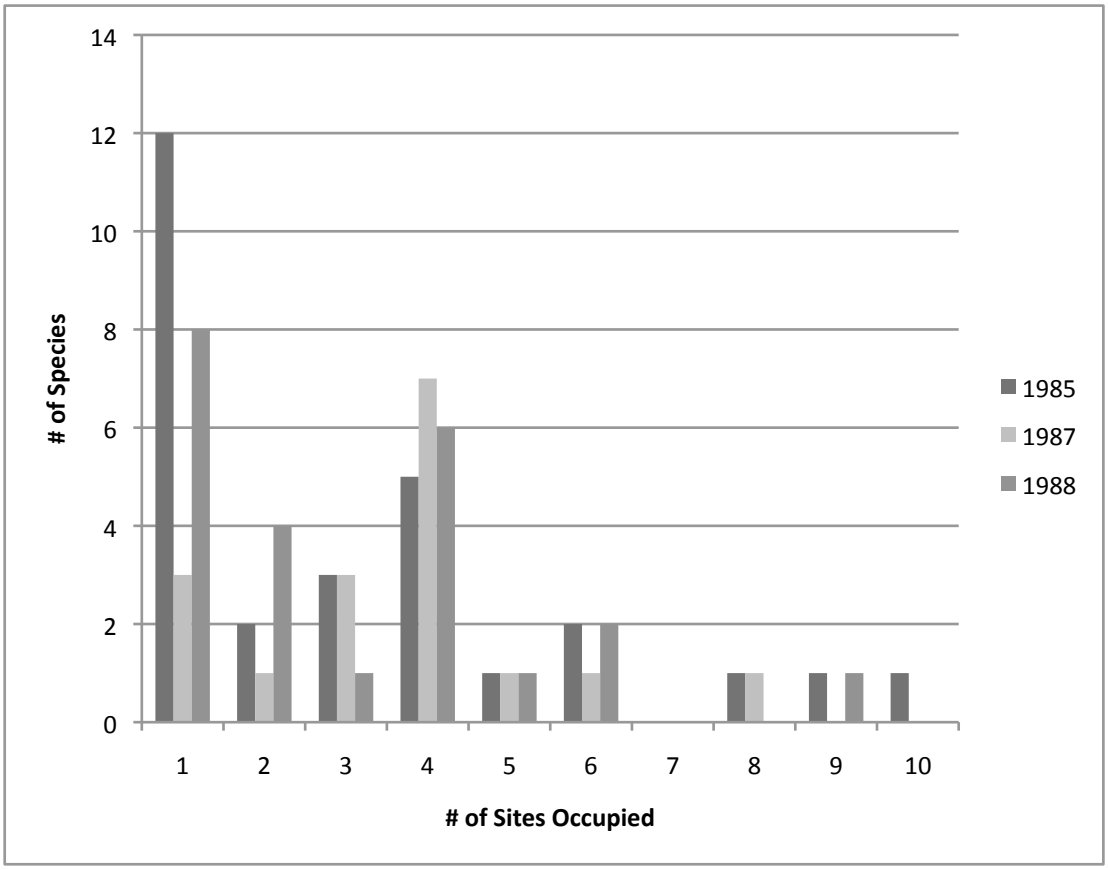
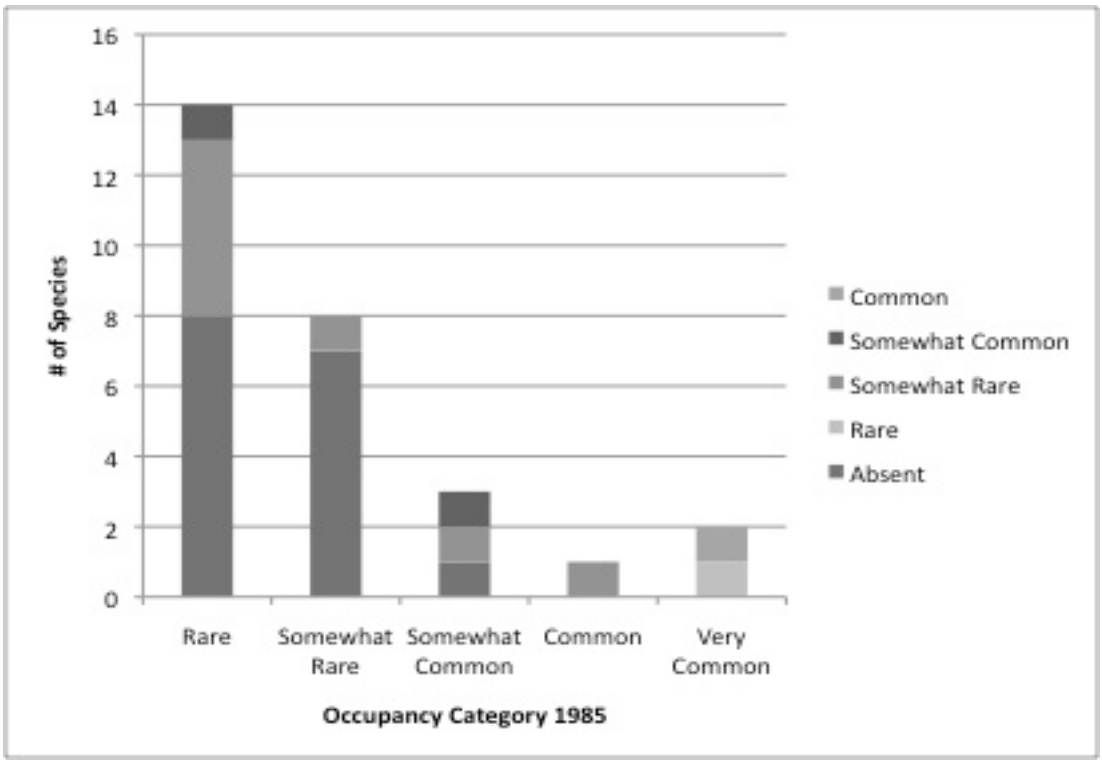
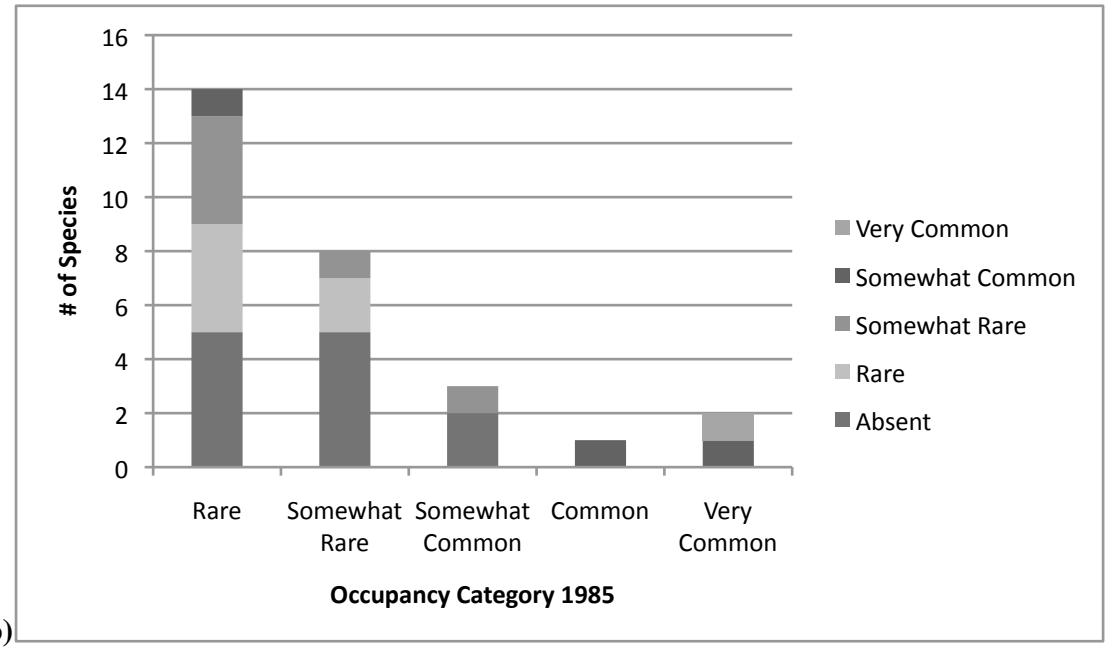


Figure 8. Occupancy distribution of species present between 1985-1988. In 1985, there were many rare species occupying only a few sites, fewer species occupying a medium number of sites, and few common species occupying many sites. After the mild disturbance, in 1987 more species occupied a medium number of sites while the rare and common species disappeared. By 1988 rare species returned, creating a distribution with many rare and intermediate species with few common.



(a)



(b)

Figure 9. Changes in occupancy from 1985 to 1987 and 1988. Species in 1985 were ranked by occupancy and placed into categories describing their level of occupancy, from absent to very common. The x and y-axes represent the number of species holding each occupancy in 1985. The colors of columns represent the number of species from 1985 that ended up in each occupancy category in 1987 (a) and 1988 (b).

Table 5. Null model of random extinctions applied to family incidence, reporting the expected occupations of each family simulating random extinctions and comparisons with observed occupations. (a) In 1987, Fungiidae occupation decreased, although it was expected to increase. Oculinidae was expected to remain the same, but instead increased in occupation. Acroporidae remained stable and very common, however it was expected to decrease significantly. (b) In 1988, Agariicidae and Fungiidae both increased in occupation far beyond expected, while Faviidae decreased in occupation much more than was expected given observed extinction and recovery rates.

Family	Occupancy 85	Occupancy 87	Expected	p-value
Acroporidae	**10**	**10**	**5.6732**	**0.0014**
Agariicidae	0	1	1.0046	0.2389
Faviidae	8	3	4.6768	0.1553
Fungiidae	**1**	**0**	**2.0118**	**0**
Helioporidae	0	0	1.0021	0.2378
Milleporidae	0	1	1.0128	0.2452
Oculinidae	**1**	**3**	**0.9973**	**0**
Pocilloporidae	0	1	0.9978	0.2391
Poritidae	10	5	5.6498	0.5388

(a) 1985-1987

Family	Occupancy 85	Occupancy 88	Expected	p-value
Acroporidae	10	10	8.4859	0.1216
Agariicidae	**0**	**3**	**1.4974**	**0**
Faviidae	**8**	**2**	**6.4874**	**0**
Fungiidae	**1**	**6**	**2.5001**	**0**
Helioporidae	0	1	1.5101	0.5031
Milleporidae	0	0	1.5017	0.1208
Oculinidae	1	1	1.488	0.5076
Pocilloporidae	0	2	1.507	0.1172
Poritidae	10	10	8.4906	0.1173

(b)1985-1988

APPENDIX

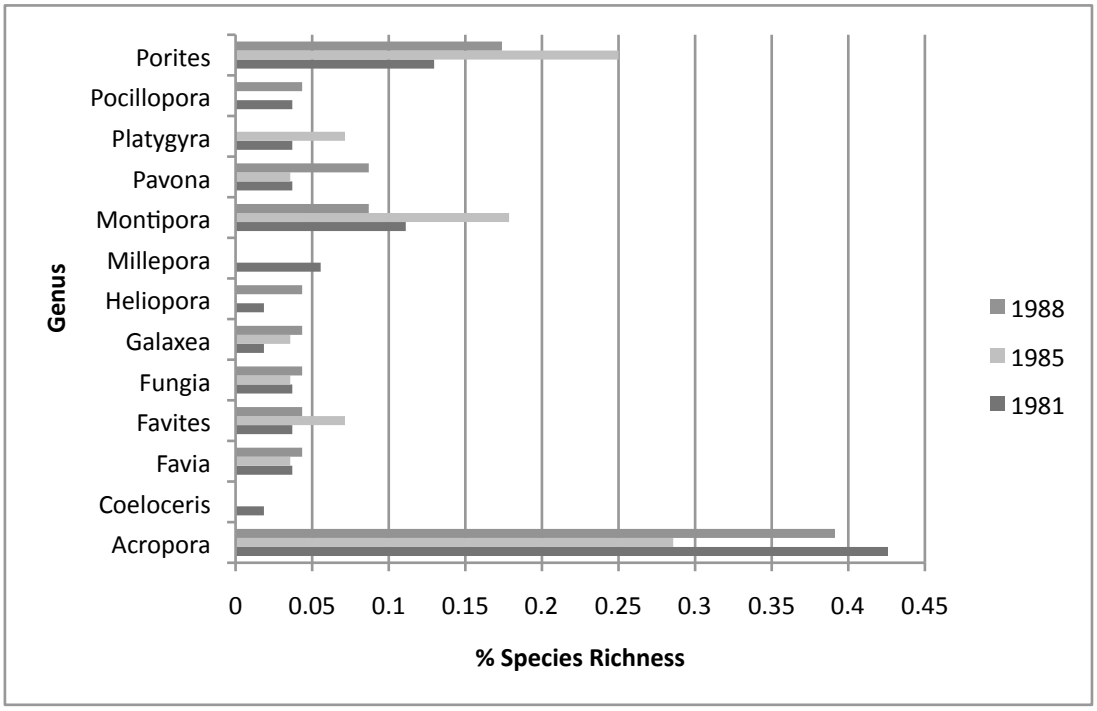


Figure 10. Percentage relative abundance of each genus present in the coral community.

Table 6. Changes in species occupancy categories between 1981 and 1983 (a) and 1985 (b).

	1983							
1981	Extinct	Absent	Rare	Somewhat Rare	Somewhat Common	Common	Very Common	Total (Occupancy 81)
Rare	8	10	5	1	0	0	0	24
Somewhat Rare	1	10	2	0	0	0	0	13
Somewhat Common	5	2	5	0	0	0	0	12
Common	0	2	0	1	0	0	0	3
Very Common	0	2	0	0	0	0	0	2
Total (Occupancy 83)	14	26	12	2	0	0	0	54

(a)

	1985							
1981	Extinct	Absent	Rare	Somewhat Rare	Somewhat Common	Common	Very Common	Total (Occupancy 81)
Rare	8	6	5	3	2	0	0	24
Somewhat Rare	1	3	4	4	0	1	0	13
Somewhat Common	5	1	2	1	1	0	2	12
Common	0	2	1	0	0	0	0	3
Very Common	0	0	2	0	0	0	0	2
Total (Occupancy 85)	14	12	14	8	3	1	2	54

(b)

Table 7. Changes in species occupancy categories between 1985 and 1987 (a) and 1988 (b)

	1987						
1985	Absent	Rare	Somewhat Rare	Somewhat Common	Common	Very Common	Total (Occupancy 85)
Rare	8	0	5	1	0	0	14
Somewhat Rare	7	0	1	0	0	0	8
Somewhat Common	1	0	1	1	0	0	3
Common	0	0	1	0	0	0	1
Very Common	0	1	0	0	1	0	2
Total (Occupancy 87)	16	1	8	2	1	0	28

(a)

	1988						
1985	Absent	Rare	Somewhat Rare	Somewhat Common	Common	Very Common	Total (Occupancy 85)
Rare	5	4	4	1	0	0	14
Somewhat Rare	5	2	1	0	0	0	8
Somewhat Common	2	0	1	0	0	0	3
Common	0	0	0	1	0	0	1
Very Common	0	0	0	1	0	1	2
Total (Occupancy 88)	12	6	6	3	0	1	28

(b)

BIBLIOGRAPHY

Anderson, Marti. J., CThomas O. Crist, Jonathan M. Chase, Mark Vellend, Brian D. Inouye, Amy L. Freestone, Nathan J. Sanders, Howard V. Cornell, Liza S. Comita, Kendi F. Davies. Susan P. Harrison, Nathan J.B. Kraft, James C. Stegen, and Nathan G. Swenson. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecology Letters:19-28.

Bellwood, D., T. Hughes, and A. Hoey. 2006. Sleeping functional group drives coral-reef recovery. Current Biology:2434-2439.

Brook, Barry W., Navjoy S. Sodhi, and Corey J.A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology and Evolution:453-460.

Brown, B. 1997. Coral bleaching: causes and consequences. Coral Reefs:S129-S138.

Brown, B. and Suharsono. 1990. Damage and Recovery of coral reefs affected by El-Niño related seawater warming in the Thousand Islands, Indonesia. Coral Reefs:163-170.

Buddemeier, R. and D. Fautin. 1993. Coral bleaching as an adaptive mechanism – a testable hypothesis. Bioscience:320-326.

Carilli JE, Norris RD, Black BA, Walsh SM, McField M, 2009 Local Stressors Reduce Coral Resilience to Bleaching. PLoS ONE 4(7): e6324. doi:10.1371/journal.pone.0006324

Chase, J. 2003. Community assembly: when should history matter? Oecologia:489-498.

Chase, J. 2010. Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. Science:1388-1391.

Chavez, F., P. Strutton, C. Friederich, R. Feely, G. Feldman, D. Foley, and M. McPhaden. 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997-98 El Nino. Science:2126-2131.

Condit, R., N. Pitman, E. Leigh, J. Chave, J. Terborgh, R. Foster, P. Nunez, S. Aguilar, R. Valencia, G. Villa, H. Muller-Landau, E. Losos, and S. Hubbell. 2002a. Beta-diversity in tropical forest trees. Science:666-669.

Cornell, H., R. Karlson, and T. Hughes. 2007. Scale-dependent variation in coral community similarity across sites, islands, and island groups. Ecology:1707-1715.

Cote, I. and E. Darling. 2010. Rethinking Ecosystem Resilience in the Face of Climate Change. Plos Biology:-.

Diamond, J.M. 1975. Assembly of species communities. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, Mass., pp 342 444

Gates, R., G. Baghdasarian, and L. Muscatine. 1992. Temperature stress causes host-cell detachment in symbiotic cnidarians – implications for coral bleaching. Biological Bulletin: 324-332.

Glynn, P. and L. D'Croz. 1990. Experimental-evidence for high-temperature stress as the cause of El-Niño-coincident coral mortality. Coral Reefs:181-191.

Glynn, P., J. Mate, A. Baker, and M. Calderon. 2001. Coral bleaching and mortality in panama and Ecuador during the 1997-1998 El Nino-Southern oscillation event: Spatial/temporal patterns and comparisons with the 1982-1983 event. Bulletin of Marine Science:79-109.

Goreau, T. and R. Hayes. 1994. Coral bleaching and ocean hot-spots. Ambio:176-180.

Harborne, A., P. Mumby, K. Zychaluk, J. Hedley, and P. Blackwell. 2006. Modeling the beta diversity of coral reefs. Ecology:2871-2881.

Jimenez, C., J. Cortes, A. Leon, and E. Ruiz. 2001. Coral bleaching and mortality associated with the 1997-98 El Nino in an upwelling environment in the Eastern Pacific (Gulf of Papagayo, Costa Rica). Bulletin of Marine Science:151-169.

Jokiel, P. and S. Coles. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated-temperature. Coral Reefs:155-162.

McKinney, M. 1987. Taxonomic selectivity and continuous variation in mass and background extinctions of marine taxa. Nature:143-145.

McKinney, Michael L. and Julie L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution:450-453.

Nystrom, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology & Evolution:413-417.

Orme, C., R. Davies, M. Burgess, F. Eigenbrod, N. Pickup, V. Olson, A. Webster, T. Ding, P. Rasmussen, R. Ridgely, A. Stattersfield, P. Bennett, T. Blackburn, K. Gaston, and I. Owens. 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature:1016-1019.

Podesta, G. and P. Glynn. 2001. The 1997-98 El Nino event in Panama and Galapagos: An update of thermal stress indices relative to coral bleaching. Bulletin of Marine Science:43-59.

Purvis, A., P. Agapow, J. Gittleman, and G. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. Science:328-330.

Reaka-Kudla, M. L. 1997. The Global Biodiversity of Coral Reefs: A Comparison With Rain Forests. Pages 81-85 *in* M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, editors. Biodiversity II: Understanding and Protecting our Biological Resources. National Academy of Science, United States of America.

Santini, F. and R. Winterbottom. 2002. Historical biogeography of Indo-western Pacific coral reef biota: is the Indonesian region a centre of origin? Journal of Biogeography:189-205.

Smith, K., K. Lips, and J. Chase. 2009. Selecting for extinction: nonrandom disease-associated extinction homogenizes amphibian biotas. Ecology Letters:1069-1078.

Veron, J. E. N. 1995. Corals in Space and Time: The Biogeography and Evolution of the Scleractinia. UNSW Press, Sydney.

Warwick, R., K. Clarke, and Suharsono. 1990. A statistical-analysis of coral community responses to the 1982-83 El-Niño in the Thousand Islands, Indonesia. Coral Reefs: 171-179.

West, J. and R. Salm. 2003. Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. Conservation Biology:956-967.

Wilkinson, C.R. and R.W. Buddemeier. 1994. *Global Climate Change and Coral Reefs: Implications for People and Reefs. Report of the UNEP-IOC-ASPEI-IUCN Global Task Team on the implications of climate change on coral reefs.* IUCN, Gland, Switzerland. x+124pp.

Wilson, Shaun K., Nicholas A.J. Graham, Morgan S. Pratchett, Geoffrey P. Jones, and Nicholas V.C. Polunin. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biology:2220-2234.