Population decline and the effects of disturbances on the structure and recovery of octocoral communities (Coelenterata: Octocorallia) in Pacific Panama

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Community structure, species composition, and changes over time after disturbances are frequently studied using common descriptors. We used rank abundance distribution plots (RADs), Rényi entropy plots, common theoretical community models, ordination analysis of similarities (ANOSIM and Clusters), and abundance spectra analyses to study the effects of a gradual natural population decline and an anthropogenic punctuated disturbance on the structure of octocoral communities in Panama, considered a hot spot area for octocoral diversity in the Tropical Eastern Pacific. Over a 17-month period, no significant change was found in community structure after a natural yearly population decline of 25.2%. After a disturbance, however, different recovery trajectories were observed in various coral communities. Possible physical and biological explanations for the observed differences include initial local species diversity and abundance, species life history patterns, colony morphology, and the geographical location of the community. Differences in community structure between study sites were best described using a combination of community descriptors, RADs, and abundance spectra. Rényi plots were useful in identifying changes in community structure, whereas the extent of the changes was best evaluated using ANOSIM and cluster analysis.

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INTRODUCTION

Octocorals (Coelenterata: Anthozoa: Octocorallia) are sessile colonial marine invertebrates that inhabit many diverse environments, including shallow and deep waters in tropical and subtropical regions (Bayer, 1981). They are a dominant part of their communities and provide living substrate to a variety of invertebrates (Cantera *et al.*, 1987). Octocorals are generally unevenly distributed in the eastern Pacific (Guzman *et al.*, 2004) and are poor dispersers compared to reef-building coral species (Concepcion *et al.*, 2010). In addition, they present a variety of growth forms, which increase the three-dimensionality and heterogeneity of the substrata, creating niche spaces for other taxa. Surprisingly, ecological and biological studies in the eastern Pacific are few (Abeytia *et al.*, 2013; Gomez *et al.*, 2014) and there is little understanding of community composition and the distribution of diversity and abundance in this region.

The distribution of abundance in octocoral communities is a topic of ongoing debate in ecology (McGill *et al.*, 2007). Different patterns have been detected, including the presentation of a few abundant species and large numbers of rare species as well as unimodal distributions with abundant intermediate species (McGill *et al.*, 2007). The distribution of species abundance has been studied graphically using species abundance distribution plots (SADs) (Preston, 1948), rank abundance distribution plots (RADs) (Macarthur, 1957), and more common diversity indices that include a spectrum of values with more or less weight given to species evenness, which can be summarized using Rényi (1961) plots.

Species abundance distribution plots and RADs are useful community composition descriptors (McGill *et al.*, 2007) and have been widely used because they require only basic information about the community (i.e. number of species and their abundance). However, there has been ongoing debate over whether these patterns are simply the result of different binning methods in Preston's plots (see Gray *et al.*, 2006) or the effect of a small sampling scale (McGill, 2003).

Diversity indices are also widely used to describe a sampled community. Common indices include species richness (S); Shannon diversity index (H') (Shannon & Weaver, 1949); Simpson concentration index (λ) (Simpson, 1949); and the dominance index (p_1) (Berger & Parker, 1970). All of these indices can be summarized on a Rényi entropy plot (Rényi, 1961), which provides a spectrum of species richness and evenness. In contrast to the diversity indices, Rényi entropy is a function, rather than a single index, which allows comparison of diversity between communities (Loreau, 2010).

Species abundance distribution plots, RADs, and Rényi plots use the same information to describe, in different ways, how communities are constituted and changed, and whether or not the original community composition pattern is restored after a recovery process. These plots can be used to compare a community to other communities and they can also be used to compare community composition before and after disturbance and recovery, including the impact that processes have on rare and common species. SADs, RADs, and Rényi plots, however, ignore species identity, so a possible species turnover process or reorganization of abundances will not be reflected in the three mechanisms proposed above (Mac Nally, 2007). The rate of change at which a species shifts from rare to common or vice-versa is highly variable (see Hanski, 1982; Hubbell, 2001; McGill *et al.*, 2007). Consequently, Murray *et al.* (1999) suggested that SADs should be used with the abundance spectrum introduced by Mac Nally (2007). In the abundance spectrum, the rank is species-specific and plotted against the relative abundance of the species either after a disturbance or compared to undisturbed reference communities. With this method, each species maintains its position in the rank, making it more clearly evident which species changed from rare to common. This method is ideal for habitat-specific analysis but is not as well suited to habitat comparisons, for which SADs and RADs are more useful.

The goals of this study were to: (i) describe the changes in species composition and structure of an octocoral community using RADs and Rényi entropy plots over time; (ii) determine if a naturally declining community maintains its distribution of species abundance and diversity profile; and (iii) determine if these patterns can be recovered after a punctuated anthropogenic disturbance. In addition, we used ordination analysis of similarities (ANOSIM) to measure differences in community composition and abundance spectra to illustrate species turnover.

MATERIALS AND METHODS

Study site

The study took place at Coiba National Park (CNP) located in the Gulf of Chiriquí, Pacific Panama. The CNP is the largest marine protected area in Panama and it was declared a UNESCO World Heritage site in 2005. CNP is located within the Eastern Tropical Pacific (ETP) biogeographical region, which ranges from the Sea of Cortez to the northern part of Peru (Robertson & Cramer, 2009). This biogeographical region hosts high levels of octocoral diversity, abundance, and endemism, with 11 genera in four families (Bayer, 1953; Guzman *et al.*, 2008).

The Gulf of Chiriquí presents special environmental characteristics that make it a biodiversity hot spot within the ETP with over 52 octocoral species in four genera (Guzman & Breedy, 2008a). The water column is highly stratified, with a shallow and strong thermocline (Fiedler & Talley, 2006). Coral reefs and coral communities in the area are affected by the El Niño Southern Oscillation every 2–7 years (Enfield, 2001). Between 1982 and 1983 this area suffered a major warming event in which water temperature rose above 29°C, killing 75% of hermatypic corals (Glynn, 1990). An event of such magnitude had not occurred for at least 200 years (Glynn, 1990). The Gulf of Chiriquí is not

exposed to the strong seasonal upwelling events that occur in the rest of Pacific Panama, but occasional shoaling of the thermocline increases nutrients in the upper layer and promotes phytoplankton growth near the surface (D'Croz & O'Dea, 2007).

The CNP encompasses ∼2024.63 km² of marine ecosystems, including 9 main islands, about 30 islets, and approximately 1700 ha of coral reefs and more diverse coral communities (Guzman *et al.*, 2004). The CNP is recognized as a diversity hotspot in the ETP, with over 35 reported octocoral species including some endemic species (Guzman *et al.*, 2004; Guzman & Breedy, 2008a; Breedy & Guzman, 2013). Octocoral communities in the CNP are not evenly distributed along the coast and sustain most of the observed diversity in high energy environments such as vertical rocky walls and underwater pinnacles or seamounts exposed to strong currents and swell (Guzman *et al.*, 2004). More than 84% of the islands are covered by primary forest, which gives immediate protection to marine ecosystems (Guzman *et al.*, 2004). However, marine communities in the north-eastern area of Coiba Island suffer from sedimentation due to drainage from at least eight main rivers in the basin (Cardiel *et al.*, 1997). In the CNP, octocorals share the basaltic rocky substrata with other sessile organisms such as scleractinian corals, sponges, macroalgae, tunicates and coralline algae (Gomez *et al.*, 2014).

Octocoral communities in four sites previously studied and described by Gomez *et al.* (2014) were used in the present study; they all had the similar depth (20 m) and water temperature (25.3–28.9°C) but different octocoral colony density and distance from shore and the deep water drop-off. All four communities were exposed to different levels of wave action, currents, and swell: (1) Frijoles islet (7°38′59.6″N 81°43′09.4″W), located in the northern leeward side of Coiba Island, is protected from strong currents and swell, 17 km away from the mainland and ∼30 km away from the 400 m deep water drop-off. It is located in a medium-high diversity area encompassing a species richness of 50–75% of the richness in the entire protected area (Guzman *et al.*, 2004) and an average octocoral density of 11.2 colonies/m² (Gomez *et al.*, 2014); (2) Roca Hacha (7°25′55.0″N 81°51′29.0″W) is a basaltic rocky outcrop located on the western seaward side of Coiba Island. It is exposed to swell and occasional sedimentation events due to the presence of rivers and natural mudslides. The outcrop is more than 50 km from the mainland and ∼5 km away from a 400 m deep drop-off. It is located in a medium-high diversity area (Guzman *et al.*, 2004) and has an average octocoral density of 77.6 colonies/m² (Gomez *et al.*, 2014); (3) Catedrales (7°13′33.7″N 81°49′45.4″W) is a pinnacle that lies 10 m below the sea surface in the southern region of the park and is exposed to strong currents. It is located more than 50 km away from the mainland and ∼3 km away from a 400 m deep drop-off. It is located in a high diversity area containing more than 75% of species found in the protected area (Guzman *et al.*, 2004) and has an average octocoral density of 44.3 colonies/m² (Gomez *et al.*, 2014); and (4) Jicarita (7°12′12.5″N 81°48′02.3″W), an island located in the southernmost seaward region of the park, more than 50 km away from the mainland and ∼3 km away from the 400 m deep drop-off. It has a vertical wall that drops down to deep water; it is exposed to strong swell and breaking waves and not exposed to river runoffs. This island is located in a high diversity area (Guzman *et al.*, 2004), has an average octocoral

density of 30.3 colonies/m² (Gomez *et al.*, 2014), and has the highest coral diversity in Pacific Panama (Guzman & Breedy, 2008b).

Experimental design

To describe the octocoral community composition and determine if this composition changed after a natural population decline, nine 1 m² fix plots (reference plots) were installed at 20 m depth at each of the four sites using SCUBA equipment. Plots were fixed by installing stainless steel square bars with underwater cement. Each colony present in the study plots was identified to the species level and a unique ID number was assigned. Colonies present in reference plots were previously identified by direct observation, photographic close-ups, and detailed morphological examination of sclerites in the laboratory (Gomez *et al.*, 2014) following major taxonomic reviews (Breedy & Guzman, 2002, 2007, 2009, 2011; Breedy *et al.*, 2009). Study plots were monitored every 4 months for a 17 month-period (1: 20 June 2009, 2: 20 October 2009, 3: 28 March 2010, 4: 21 July 2010 and 5: 30 November 2010). For logistical reasons, surveys three and four were 5 months apart. Plots were photo-monitored using a Nikon D-80 camera with a wide-angle lens inside an Ikelite underwater case and two external digital strobe flashes. The camera was attached to a custom-made stainless steel tripod in order to maintain a fixed object-to-lens distance (0.80 m) from the quadrat. In surveying each plot, an aluminium quadrant was divided into eight equal sections (0.42 × 0.30 m; equivalent to 1 m² plot) to improve resolution in digital photography, resulting in a total of eight pictures per fixed plot. The quality of the pictures was improved by using Nikon NX2 software. Species abundance data were obtained from the photographs for further analysis.

To evaluate the effect of a punctuated disturbance on the distribution of species abundance and determine whether the original distribution was recovered after a 17 month recovery period, three 1 m² plots at each site (disturbed plots), which were adjacent to the monitoring plots (or reference plots) described above, were completely cleaned with a wire brush of all sessile organisms, including octocorals, hard corals, sponges, and macroalgae, at the beginning of the study. This disturbance mimicked the effect of trawling, hurricanes, or significant mortality due to a drastic change in the physical properties of the water. Disturbed plots were monitored every 4 months using the protocol described above. The abundance and diversity of colonies recruiting in the empty space were quantified during each sampling period. Small recruits were quantified at first sight and identified when possible. Identification to the species level was then confirmed during the following surveys by visual observation, photographic close-ups and sclerite examination (*sensu* Gomez *et al.*, 2014).

Data analyses

RANK ABUNDANCE DISTRIBUTION PLOTS
The relative abundance of each species at each site during each sampling period was calculated and ranked from 1 to n, with 1 being the most common species. The relative abundance was plotted on a logarithmic scale against the species rank in abundance, creating a RAD. The same procedure was performed

for the colonies recruiting in the clean plots. The RAD curves, from both the monitored and cleaned plots, were plotted on the same graph.

RÉNYI DIVERSITY ENTROPY
Rényi plots were generated using the function >Rényi(x) in the Vegan 1.17-6 package (Oksanen *et al.*, 2011) of R64 software (R Development Core Team, 2010). This function calculates Rényi diversity of order a following equation (1). The following diversity indices can be found in a Rényi diversity profile: $H_0 = \log(S)$, $H_1 = H'$, H_2 $-\log(\Sigma p^2 i)$, and $H\infty = -\log(\max p_i)$. Equation (1) is written as:

$$H_a = \frac{1}{1-a} \log \sum_{i=1}^{S} p_i^a \qquad (1)$$

where p_i is the proportion of species i and S is the number of species.

BEST-FIT MODEL
By using the function >radfit in the Vegan Package (Oksanen *et al.*, 2011) in the R Software (R Development Core Team, 2010), count data for each site were compared with the most common rank abundance models using the maximum likelihood estimation. The following models were compared: broken-stick (null hypothesis), pre-emption, log-normal, Zipf, and Zipf–Mandelbrot. This function compared the models by alternately using Akaike's or Schwartz's Bayesian information criteria.

SIMILARITY ANALYSIS
Similarities in species abundance were analysed to test for a significant change in community assemblage after a population decline and a punctuated disturbance. These permutation/randomization tests operated on a Bray–Curtis coefficient resemblance matrix and were performed using PRIMER v.6 Software (Clarke & Gorley, 2006). Cluster analysis and the ANOSIM test (Clarke, 1993) were performed with standardized data and the maximum possible permutations. This test does not assume a balanced replication so cleaned plots (N = 3) could be compared with uncleaned reference plots (N = 9).

RESULTS

The initial total abundance at all sites was 1394 colonies representing 15 species (Table 1). Overall octocoral populations at the four study sites differed in diversity and abundance, and all showed a natural population decline of 25.2% during the 17 month study period. Roca Hacha had the highest species richness and abundance, with 14 species across 655 colonies; the yearly population decline at this site was 17%, while the site at Frijoles had the lowest species richness and abundance, with only five species across 56 colonies; it exhibited a large yearly population decline of 30%. The other two sites were intermediate in species and abundance, Jicarita with 268 colonies, 12 species and 24% yearly decline, and Catedrales with 350 colonies, 12 species, and 14% decline (Table 2).

Rank abundance distribution plots were compared by visual inspection. When comparing plots under a natural population decline (solid lines in Figure 1), a clear difference

Table 1. List of species in study plots.

Carijoa riisei Duchassaing & Michelotti, 1860
Heterogorgia verrucosa Verrill, 1868
Leptogorgia alba Duchassaing & Michelotti, 1864
Leptogorgia cofrini Breedy & Guzman, 2005
Leptogorgia taboguilla Hickson, 1928
Leptogorgia pumila Verrill, 1868
Leptogorgia rigida Verrill, 1864
Muricea austera Verrill, 1868
Pacifigorgia cairnsi Breedy & Guzman, 2003
Pacifigorgia rubicunda Breedy & Guzman, 2003
Pacifigorgia irene Bayer, 1951
Psamogorgia arbuscula Verrill, 1866
Pacifigorgia eximia Verrill, 1868
Pacifigorgia firma Breedy & Guzman, 2003
Pacifigorgia stenobrochis Valenciennes, 1846

between sampling periods was not evident. However, the RAD pattern did change for the recovery process after a punctuated disturbance (dotted lines in Figure 1). This change occurred differently in different sites. At Catedrales, disturbed plots increased in similarity with monitored reference plots from sampling period 2 to sampling period 5. By the end of the study, disturbed plots had recovered the RAD pattern of monitored reference plots, but with three species missing. In contrast, at Roca Hacha and Jicarita, RAD patterns did not change significantly between sampling periods 3, 4 and 5 and the community assemblage included more dominant species than in reference monitored plots. At Frijoles, no recovery occurred in the disturbed plots (Figure 1).

Visual inspection of the Rényi diversity profiles revealed differences in diversity between sites. Roca Hacha, Catedrales, and Jicarita demonstrated higher species richness and lower dominance compared to Frijoles, where species richness was lower and dominance was higher (Figure 2). Although an important population decline occurred at all sites, there was no notable change in the diversity profiles (i.e. overlapping black lines in Figure 2). The diversity profiles for recovering disturbed plots changed differently from site to site (Figure 2). Recovery at Roca Hacha occurred by increasing species richness and evenness simultaneously, while never reaching the diversity profiles of monitored reference plots. In contrast, the recovery at Catedrales moved from low richness and high evenness at sampling period 2 to high richness and low evenness at sampling period 5; thus the similarity of its diversity profile to that of the monitored reference plots increased over time. At Jicarita, species richness showed a relatively small increase whereas species evenness decreased over time. The data from Frijoles suggest that a small recovery took place after sampling period 4, as it showed a species evenness and lower species richness similar to data from the monitored reference plots.

Table 2. Baseline octocoral species richness and abundance and their population decline in 9 m^2 at 20 m depth during a 17 month study period at each study site in Coiba National Park, Panama.

Site	No. species	Initial abundance	Population decline (%)
Roca Hacha	14	678	17
Catedrales	12	350	14
Jicarita	12	268	24
Frijoles	5	98	30

Community structure at each site during each sampling period was compared using five different theoretical models: broken-stick (null hypothesis), pre-emption, log-normal, Zipf, and Zipf–Mandelbrot (Table 3). In the baseline community at sampling time 1, community structure at Catedrales, Jicarita, and Roca Hacha best fit the pre-emption model (Akaike's information criteria (AICs) = 64.9, 58.0, 84.4, respectively) and community structure at Frijoles best fit the Zipf model (AIC = 24.5). The best-fit model did not change after the population decline at Catedrales, Roca Hacha, and Frijoles, but it did change for Jicarita, where it shifted from the pre-emption to the log-normal model (AICs = 58.0 and 54.3, respectively). The best-fit model changed to the null model after the disturbance at Catedrales, representing the broken-stick theory (AIC = 31.51). At Jicarita, the Zipf model had the lowest AIC value (AIC = 23.84); however, the AIC value for the pre-emption model (24.47) was only slightly higher, and this was the one that best fit the baseline community. At Roca Hacha, the best-fit model did not change over the 17 month recovery process, implying that the community was similarly structured after disturbance. This analysis was not performed for disturbed plots at Frijoles due to the low population size (eight colonies).

The extent of the similarity in community structure between a reference baseline community and a community after population decline and recovery was analysed using the Bray–Curtis similarity matrix, tested with an ANOSIM, and plotted as a cluster figure. No significant dissimilarity in community structure was found between the baseline community and the community after the 17 month population decline at any of the study sites (Table 4). Jicarita had the lowest similarity after the population decline, at less than 80% (Figure 3). The least similarity was found in comparisons between disturbed and undisturbed plots. Community composition was only significantly different, however, at Jicarita (Table 5; Figure 4). The RAD plot for Frijoles suggested no recovery, with a substantial difference in community composition between disturbed and reference plots; however, the ANOSIM for this site showed the opposite pattern, with a non-significant difference between disturbed and reference plots (Table 5; Figure 4).

Abundance spectra were plotted to determine if species turnover occurred during the population decline or the recovery of disturbed plots. These spectra showed a similar species-specific composition after the population decline and, to a lesser extent, after the disturbance at Catedrales, Roca Hacha, and Frijoles. *Leptogorgia alba* was the most common species found at these three sites. This species did not lose its hierarchical rank after the population decline or after disturbance at Catedrales or Frijoles, and it became the second ranked species at Roca Hacha, where *Pacifigorgia rubicunda* became the first. At Catedrales, intermediate species changed in rank after disturbance and there was a significant increase of one rare species (*Leptogorgia rigida*). After the population decline in Jicarita, the more abundant species, *P. rubicunda*, further increased in abundance while the intermediate species, *C. riisei* became absent. Jicarita experienced species reorganization after disturbance. There, the most common species originally was *P. rubicunda*, which became rare after the disturbance. *Leptogorgia cofrini*, which was originally third in rank, became the first and dominant species after the disturbance (Figure 5). This reorganization of species abundance at Jicarita was identified but not described by the ANOSIM and cluster analysis.
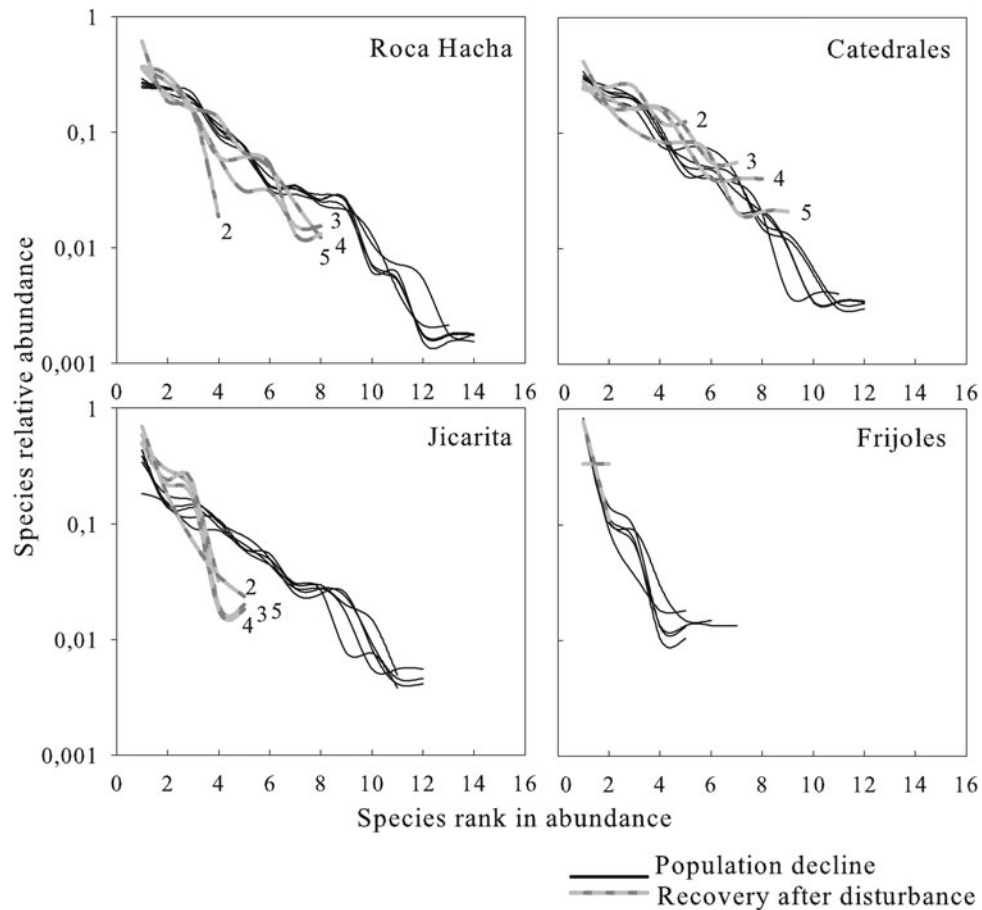
Fig. 1. Rank abundance distributions plots for each study site during five sampling periods. Black solid lines represent monitoring plots with a natural population decline (N = 9). Grey dotted lines represent plots in a recovery process after a punctuated disturbance (N = 3). Numbers indicate the sampling period, 2 = recovery after 4 months of disturbance, 3 = 9 months, 4 = 13 months and 5 = 17 months.

DISCUSSION

The baseline data from Catedrales, Jicarita, and Roca Hacha best fit the niche pre-emption model. This model describes low species evenness, as usually seen in communities that are highly dominated by few species, in resource poor environments, after an environmental disturbance, or in recently colonized environments (Giller, 1987; Fattorini, 2005). The RAD graphs and the Rényi plots showed a non-significant change in community composition at three of the sites, Roca Hacha, Catedrales, and Frijoles, after the population decline, and this result was confirmed by the ANOSIM and cluster analysis. There was no species turnover, as can be seen in the abundance spectrum. At Jicarita, the best-fit model switched from the pre-emption to the log-normal model, nonetheless, the log-normal model is related to the pre-emption model but with a greater number of rare species (Fattorini, 2005). This change was also indicated by the low similarity in the cluster analysis between sampling periods 1 and 5 relative to the other sites.

Analysing the effect of the disturbance on species diversity, abundance, and community composition was more complex. Disturbed plots did not regain the total number of species present in monitored reference plots. As predicted by Mac Nally (2007), rare species were lost in a greater proportion than common species, which also decreased in abundance. The octocoral community at Frijoles had the lowest initial population size and the highest population decline, which could be a factor that affected the recovery in cleaned plots shown by the RAD graphs. When the community structure of Frijoles was analysed with the ANOSIM, however, there was not a significant difference between disturbed and undisturbed plots, and this was reflected in the cluster graph. As in the other study sites, treated plots at Frijoles still had some species missing after the 17 month recovery process. The absence of these species had a larger effect on community recovery at Frijoles. One possible explanation is that initially there was low species richness and abundance and strong dominance by *L. alba* in both disturbed and undisturbed plots. In this case, the RAD was more sensitive to rare species than the ANOSIM permutation test, which gives more weight to the presence and hierarchy of the dominant species. This effect became clear in the abundance spectrum; the same dominant species was equally present in disturbed and undisturbed plots. In the case of Frijoles, the Rényi plot was a good community descriptor because it predicted the change in species richness and the non-significant change in species evenness after disturbance.

The RAD pattern of recovering plots at Jicarita did not change between sampling periods 3 and 5. This pattern did not resemble the pattern from reference plots, indicating that the community was assembling differently, with less species richness and less evenness, as reflected in the Rényi
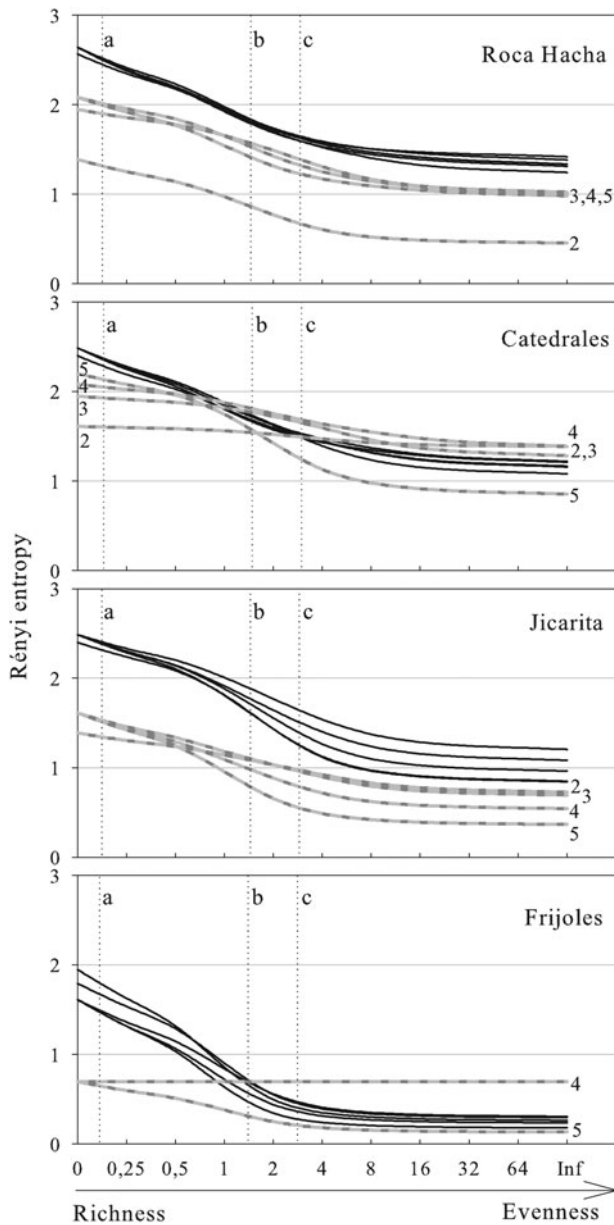
Fig. 2. Rényi diversity profiles for each study site during five sampling periods. Black solid lines, mostly overlapping, represent plots with a natural population decline (N = 9). Grey dotted lines represent plots in a recovery process after a punctuated disturbance (N = 3). Letters represent diversity indices: (A) Ln *S*, species richness; (B) *H*, Shannon–Weaver; (C) −ln λ, Simpson concentration.

entropy plot. The difference in community structure after disturbance was confirmed by the ANOSIM. The reason for this significant difference was evident in the abundance spectrum, which showed that Jicarita recovered with a different species composition: a non-dominant species (*L. cofrini*) became dominant after the disturbance and a previously common species (*P. rubicunda*) became rare. Jicarita was the site with the lowest similarity between the initial community and the community after the population decline (Figure 3), and it was the only site for which the best-fit model changed when comparing the effect of both population decline and disturbance. The fact that the similarity was lower after the population decline could indicate that the community structure at Jicarita is more vulnerable to disturbance than that of the communities found at the other study sites. The RADs and

Rényi plots showed that there was a change in the community structure at Jicarita, and the ANOSIM confirmed the extent of this change.

Although the ANOSIM did not show a significant difference between disturbed and monitored reference plots at Roca Hacha and Catedrales, meaning that the original community structure was recovered in the disturbed plots, the RAD, Rényi, and cluster plots reveal some interesting trends. Simple visual inspection of the RAD and Rényi plots shows that Catedrales had a better recovery process than Roca Hacha. However, the opposite trend was shown in the cluster analysis and by the best-fit model. Cluster analysis showed a higher similarity between disturbed and undisturbed plots at Roca Hacha (>80%) than at Catedrales (60%). In the same way, Roca Hacha fit the pre-emption model before and after the disturbance, as opposed to Catedrales, in which recovered disturbed plots fit the null hypothesis of the broken-stick model and the base line mature community best fit the pre-emption model. The results from Catedrales were not consistent with Fattorini's (2005) proposal that communities in early stages (of recovering after disturbance) best fit the niche pre-emption model, eventually shifting to the broken-stick model as they change (the mature base line community here).

The dominant species at Catedrales and Frijoles was *L. alba,* which is a fast-growing branched species with relatively high mortality and recruitment rates (Gomez *et al.*, 2014). This species was able to maintain its hierarchical rank even after the punctuated disturbance, which was also the case for the hard coral *Montastrea annularis* Ellis & Solander, 1786, in a coral reef community following hurricane Hugo in the Virgin Islands (Rogers, 1992). This was not the case, however, at Roca Hacha, where *L. alba* was dominant during the baseline survey, equally dominant with *P. rubicunda* after the population decline, and second in rank after the disturbance.

Physical, biological and ecological factors could explain the different recovery processes across the studied communities. Frijoles is located on the north-eastern part of Coiba Island. Due to its geographical location, it is less exposed to currents than the other three sites, which are located in the south-western seaward side of the marine protected area; these sites are farther away from mainland, closer to the 400 m deep drop-off, exposed to strong currents and swell, and potentially affected by local micro-upwelling (D'Croz & O'Dea, 2007). Currents, swell, and local upwelling could bring viable larvae to a suitable and stable substratum. Therefore, Frijoles may be less exposed to viable larvae. Moreover, the overall natural population decline and the lack of diversity recovery in disturbed plots could be due to environmental factors. The study period overlapped with El Niño and La Niña southern oscillation events (Gomez *et al.*, 2014). These temperature anomalies could have caused an overall decrease in recruitment in octocorals, as reported for hard coral species in the area (Glynn, 2000).

The temporal scale of the study may explain the lack of diversity recovery. The study duration may not have been long enough to quantify the recovery of slow-growing species with infrequent reproductive cycles, such as species in the genera *Pacifigorgia* and *Muricea* (Gomez *et al.*, 2014). In contrast, the weedy species *L. alba*, which is a fast grower with a relatively high recruitment rate (Gomez *et al.*, 2014), was able to cope with the population decline and was not as

Table 3. Best-fit model and Akaike's information criterion (AIC) value for each site and sampling period during a natural population decline (reference monitored plots) and after a 17 month recovery process from a disturbance (disturbed plots). n, abundance; S, species richness.

Site	Base line	Decline N = 9 m²				After disturbance N = 3 m²
		4 months	9 months	13 months	17 months	
Cat	Pree	Pree	Pree	Pree	Pree	Null
AIC	64.895	58.452	60.7042	61.858	55.5826	31.5158
n	333	199	291	285	247	47
S	12	12	12	12	11	9
Jic	Pree	Pree	Pree	Log-normal	Log-normal	Zipf
AIC	58.0438	56.1624	59.5042	54.046	54.329	23.84
						Pree
						24.47
n	260	242	217	202	180	85
S	12	12	12	11	12	5
Fri	Zipf	Pree	Zipf	Zipf	Zipf	–
AIC	24.4675	23.386	27.2561	25.8655	20.54132	–
		Zipf				
		24.209				
n	96	76	74	67	55	8
S	5	5	7	6	5	2
Roca	Pree	Pree	Pree	Pree	Pree	Pree
AIC	84.434	90.617	82.212	82.604	87.572	27.877
n	655	578	561	559	471	75
S	14	14	14	14	13	7

Pree, pre-emption; Cat, Catedrales; Jic, Jicarita; Fri, Frijoles; Roca, Roca Hacha.

Table 4. Analysis of similarity results comparing community composition between the baseline survey (June 2009) and after a 17 month population decline (November 2010). None of the results were significant.

Base line vs 17 month population decline	Catedrales	Frijoles	Jicarita	Roca Hacha
Sample statistics (Global R)	−0.003	−0.046	−0.023	−0.088
Significance level of sample statistics (%)	42.90	79.10	58.70	91.20
Number of permutations	999	999	999	999
Number of permuted statistics greater than or equal to Global R	428	428	586	911
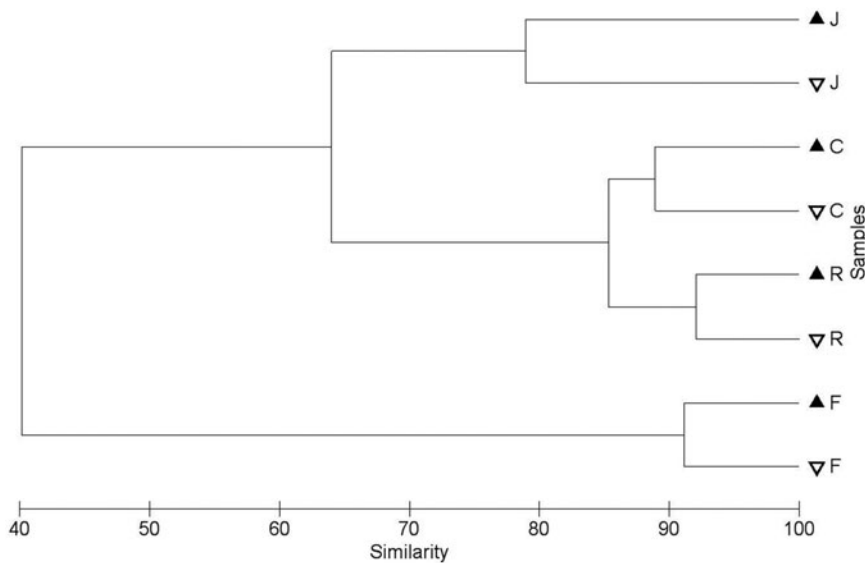
Fig. 3. Similarity cluster analysis comparing community structure during the baseline in June 2009 (filled triangles) and after 17 months of population decline in November 2010 (empty triangles). C, Catedrales; J, Jicarita; F, Frijoles; R, Roca Hacha.

Table 5. Analysis of similarity results comparing community composition between reference and disturbed plots. An asterisk indicates a significant difference. *, significance level is $P < 0.05$.

Reference vs disturbed plots	Catedrales	Frijoles	Jicarita*	Roca Hacha
Sample statistics (Global R)	0.324	0.358	0.903	0.172
Significance level of sample statistics (%)	10.90	10.5	0.50	19.50
Number of permutations	220	220	220	220
Number of permuted statistics ≥ Global R	24	23	1	43
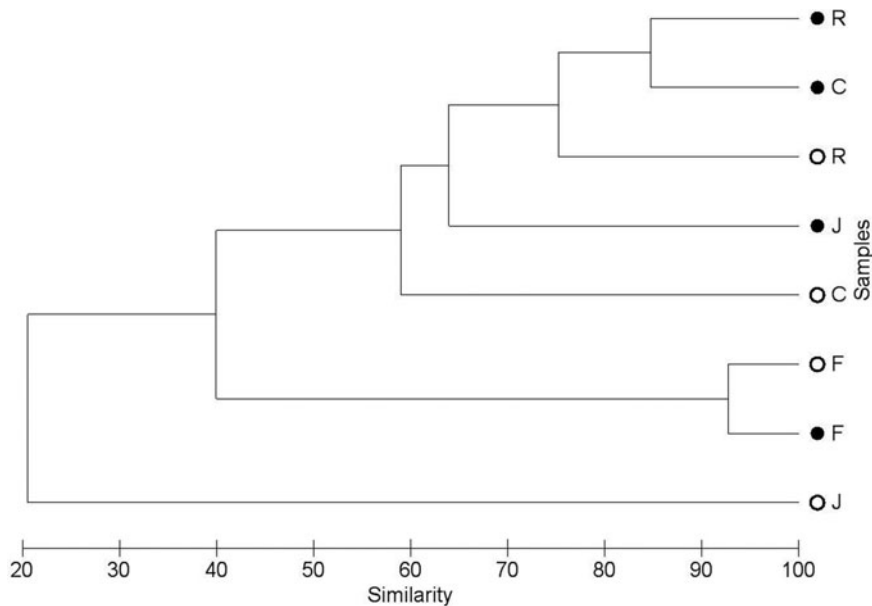
Fig. 4. Similarity cluster analysis comparing reference plots (filled circles) with disturbed plots (empty circles) after a 17 month recovery period. C, Catedrales; J, Jicarita; F, Frijoles; R, Roca Hacha.

severely affected by the disturbance as other species. Species within a genus can have different morphologies with more or less resistance to disturbance; this could be the case for *P. rubicunda*, which seemed to be physically more resistant to disturbance than *P. irene*, and for *L. alba* and *L. cofrini*, which were more common and occurred in patches compared to *L. rigida*. A factor that may have affected community recovery at Frijoles was the presence of the coral predator *Acanthaster planci* Linnaeus, 1758. This sea star was frequently seen among the study plots in Frijoles and never seen in the rest of the study sites. *Acanthaster planci* is known to prey on hard corals (Glynn, 1974), but it can also predate on octocorals and other taxa when hard corals are not abundant (Moran, 1990), which is the case in the study area. In this case it can be considered a predator of octocoral recruits and adult colonies.

The change in species composition that was observed in Jicarita may be the reason why this particular vertical wall is one of the most important hotspots in the region (Guzman & Breedy, 2008b). This wall, the southernmost point in the Panamanian Pacific shelf, faces the open ocean and drops down to >400 m where deep octocoral communities and mesophotic reefs are found (Breedy & Guzman, 2013). The wall is subject to strong currents from different directions and vertical surges during the tidal cycles. These conditions create a suitable heterogeneous habitat for larval settlement or detached colonies from deeper communities, which establish in shallower available substrata. Another factor is that

Jicarita's wall is far from the influence of any river or mud-slides, which increase sedimentation; therefore, a different environmental species sorting can take place here than at the other study sites.

The effect of scale needs to be considered when analysing the effect of the population decline and disturbance on community structure. This study was conducted at a relatively small spatial scale. Octocorals occur in a patchy distribution, making it difficult to study larger plots without affecting the entire local community. This is the primary justification for using nine undisturbed monitored plots to study the effect of a natural population decline and only three plots to study the effect of disturbance. Although the duration of the study was relatively short, it was long enough to see the immediate effect of disturbances and the beginning of the recovery process, which, interestingly, differed among sites. The effect of temporal scale can be species-specific (Hill & Hamer, 2004), so it will be interesting to observe the behaviour of the species present in the study site over a longer time in order to determine whether there are clear indicator species of disturbance.

Finally, we believe that the combination of methods used in this study were appropriate to quantify changes in octocoral community structure, and that this methodology can be easily extrapolated to other taxonomic groups. RADs, abundance spectra, and Rényi plots were useful for determining the changes, whereas their extent was best evaluated using
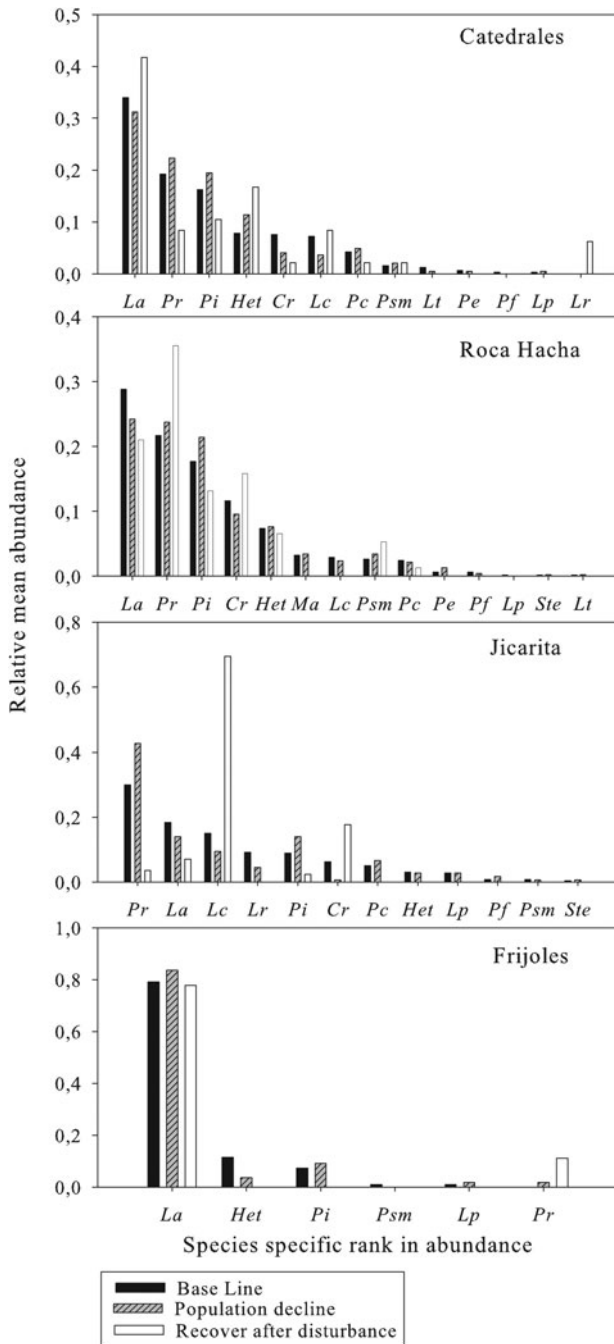
Fig. 5. Abundance spectra for octocoral communities at the four sites within Coiba National Park, Panama. Black: base line, community at time 1; grey: community after 17 months population decline; white: community after 17 months recovery process from a punctuated anthropogenic disturbance. Cr, *Carijoa riisei*; Het, *Heterogorgia* sp.; La, *Leptogorgia alba*; Lc, *Leptogorgia cofrini*; Lt, *Leptogorgia taboguilla*; Lp, *Leptogorgia pumilla*; Lr, *Leptogorgia rigida*; Ma, *Muricea austera*; Pc, *Pacifigorgia cairnsi*; Pr, *Pacifigorgia rubicunda*; Pi, *Pacifigorgia irene*; Psm, *Psamogorgia arbuscula*; Pe, *Pacifigorgia eximia*; Pf, *Pacifigorgia firma*; Ste, *Pacifigorgia stenobrochis*.

ANOSIM and cluster analysis. The lack of community recovery can be related to a low initial population size, the lack of current exposure, and the presence of the coral predator *Acanthaster planci*. On the other hand a change in community structure can be linked to exposure to the open-ocean and extreme currents, which brings available larvae to an empty substratum.

REFERENCES

Abeytia R., Guzman H.M. and Breedy O. (2013) Species composition and bathymetric distribution of gorgonians (Anthozoa: Octocorallia) on the southern Mexican Pacific coast. *Revista de Biología Tropical* 61, 1157–1166.

Bayer F.M. (1953) Zoogeography and evolution in the octocorallian family Gorgoniidae. *Bulletin of Marine Science* 3, 100–119.

Bayer F.M. (1981) *Status of knowledge of octocorals of world seas.* Rio de Janeiro: Academia Brasileira de Ciências.

Berger W.H. and Parker F.L. (1970) Diversity of planktonic foraminifera in deep-sea sediments. *Science* 168, 1345–1347.

Breedy O. and Guzman H.M. (2002) A revision of the genus *Pacifigorgia* (Coelenterata: Octocorallia: Gorgoniidae). *Proceedings of the Biological Society of Washington* 115, 782–839.

Breedy O. and Guzman H.M. (2007) A revision of the genus *Leptogorgia* Milne Edwards & Haime, 1857 (Coelenterata: Octocorallia: Gorgoniidae) in the eastern Pacific. *Zootaxa* 1419, 1–90.

Breedy O. and Guzman H.M. (2011) A revision of the genus *Heterogorgia* Verrill, 1868 (Anthozoa: Octocorallia: Plexauridae). *Zootaxa* 2995, 27–44.

Breedy O. and Guzman H.M. (2013) A new species of the genus *Eugorgia* (Cnidaria: Octocorallia: Gorgoniidae) from mesophotic reefs in the eastern Pacific. *Bulletin of Marine Science* 89, 735–743.

Breedy O., Guzman H.M. and Vargas S. (2009) A revision of the genus *Eugorgia* Verrill, 1868 (Coelenterata: Octocorallia: Gorgoniidae). *Zootaxa* 2151, 1–46.

Cantera J.R., von Prahl H. and Neira O.R. (1987) Moluscos, crustaceos y equinodermos asociados a la gorgonia *Lephogorgia alba* Duchassaing y Micheloti 1864, en la isla de Gorgona. *Colombia Boletin Ecotropica* 17, 3–23.

Cardiel J.M., Castroviejo S. and Velayos M. (1997) El Parque Nacional Coiba: El Medio Físico. In Castroviejo S. (ed.) *Flora y fauna del Parque Nacional de Coiba (Panama).* Madrid: Serviprint Press. pp. 11–30.

Clarke K. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117–143.

Clarke K. and Gorley R. (2006) *PRIMER v6: user manual/tutorial.* Plymouth: PRIMER-E.

Concepcion G.T., Kahng S.E., Crepeau M.W., Franklin E.C., Coles S.L. and Toonen R.J. (2010) Resolving natural ranges and marine invasions in a globally distributed octocoral (genus *Carijoa*). *Marine Ecology Progress Series* 401, 113–127.

D'Croz L. and O'Dea A. (2007) Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuarine, Coastal and Shelf Science* 73, 325–340.

Enfield D.B. (2001) Evolution and historical perspective of the 1997–1998 El Niño southern oscillation event. *Bulletin of Marine Science* 69, 7–25.

Fattorini S. (2005) A simple method to fit geometric series and broken stick models in community ecology and island biogeography. *Acta Oecologica* 28, 199–205.

Fiedler P.C. and Talley L.D. (2006) Hydrography of the eastern tropical Pacific: a review. *Progress in Oceanography* 69, 143–180.

Giller P.S. (1987) Community structure and the niche. *Folia Geobotanica* 22, 84–84.

Glynn P.W. (1974) The impact of *Acanthaster* on corals and coral reefs in the eastern Pacific. *Environmental Conservation* 1, 295–304.

Glynn P.W. (1990) Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. *Elsevier Oceanography Series* 52, 55–126.

Glynn P.W. (2000) *El Niño-Southern oscillation mass mortalities of reef corals: a model of high temperature marine extinctions? Volume 178.* London: Geological Society, Special Publications, pp. 117–133.

Gomez G.C., Guzman M.H., Gonzalez A. and Odalisca B. (2014) Survival, growth, and recruitment of octocoral species (Coelenterata: Octocorallia) in Coiba National Park, Pacific Panama. *Bulletin of Marine Science* 90, 623–650.

Gray J.S., Bjørgesæter A. and Ugland K.I. (2006) On plotting species abundance distributions. *Journal of Animal Ecology* 75, 752–756.

Guzman H.M. and Breedy O. (2008a) *Distribución de la diversidad y estado de conservación de los arrecifes coralinos y comunidades coralinas del Pacífico Occidental de Panamá (Punta Mal–Punta Burica).* Arlington, VA: The Nature Conservancy.

Guzman H.M. and Breedy O. (2008b) *Leptogorgia christiae* (Octocorallia: Gorgoniidae) a new shallow water gorgonian from Pacific Panama. *Journal of the Marine Biological Association of the United Kingdom* 88, 719–722.

Guzman H.M., Benfield S., Breedy O. and Mair J.M. (2008) Broadening reef protection across the marine conservation corridor of the eastern tropical Pacific: distribution and diversity of reefs in Las Perlas Archipelago, Panama. *Environmental Conservation* 35, 46–54.

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

Hanski I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38, 210–221.

Hill J.K. and Hamer K.C. (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology* 41, 744–754.

Hubbell S.P. (2001) *A unified theory of biodiversity and biogeography.* Princeton, NJ: Princeton University Press.

Loreau M. (2010) *The challenges of biodiversity science.* Oldendorf/Luhe: International Ecology Insititute.

Macarthur R.H. (1957) On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the United States of America* 43, 293–295.

Mac Nally R. (2007) Use of the abundance spectrum and relative abundance distributions to analyze assemblage change in massively altered landscapes. *American Naturalist* 170, 319–330.

McGill B.J. (2003) Does mother nature really prefer rare species or are log-left-skewed SADs a sampling artifact? *Ecology Letters* 6, 766–773.

McGill B.J., Etienne R.S., Gray J.S., Alonso D., Anderson M.J., Benecha H.K., Dornelas M., Enquist B.J., Green J.L., He F., Hurlbert A.H., Magurran A.E., Marquet P.A., Maurer B.A., Ostling A., Soykan C.U., Ugland K.I. and White E.P. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10, 995–1015.

Moran P.J. (1990) *Acanthaster planci* (L.): biographical data. *Coral Reefs* 9, 95–96.

Murray B.R., Rice B.L., Keith D.A., Myerscough P.J., Howell J., Floyd A.G., Mills K. and Westoby M. (1999) Species in the tail of rank-abundance curves. *Ecology* 80, 1806–1816.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H. and Wagner H. (2011) *Vegan: Community Ecology Package. R package version 1.17-6.* Available at: http://CRAN.R-project.org/package=vegan (accessed 19 June 2014).

Preston F.W. (1948) The commonness and rarity of species. *Ecology* 29, 254–283.

R Development Core Team. (2010) *R: a language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing.

Rényi A. (1961) On measurements of entropy and information. In Neyman J. (ed.) *Proceedings of the 4th Berkeley Symposium on Mathematical Statistics and Probability.* Berkeley, CA: University of California Press, pp. 547–561.

Robertson D.R. and Cramer K.L. (2009) Shore fishes and biogeographic subdivisions of the tropical eastern Pacific. *Marine Ecology Progress Series* 380, 1–17.

Rogers C.S. (1992) A matter of scale: damage from Hurricane Hugo (1989) to U.S. Virgin Islands reefs at the colony, community and whole reef level. In Richmond R.H. (ed.) *Proceedings of the 7th International Coral Reef Symposium, Guam. Volume 1.* UOG Station, Guam: University of Guam Press, pp. 127–133.

Shannon C.E. and Weaver W. (1949) *The mathematical theory of communication.* Urbana, IL: University of Illinois Press.

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Simpson E.H. (1949) Measurement of diversity. *Nature* 163, 688.

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