

The resilience of reef invertebrate biodiversity to coral mortality

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Abstract. Foundation species provide many important ecosystem functions including the provision of habitat for diverse communities, but their degradation and mortality has the potential to compromise these roles. Corals are widely recognized foundation species that create reef habitats that are hotspots for biodiversity. However, the impact of global reef degradation on overall patterns of biodiversity remains difficult to predict because of our limited knowledge of mechanistic relationships between reef structure and community composition. We examined the resilience of invertebrate abundance and biodiversity on reefs following a recent coral mass mortality event on the Caribbean coast of Panama. First, we surveyed mobile invertebrate communities at both healthy and degraded reef sites and found that dead coral habitats support invertebrate assemblages that can be more diverse and abundant than live coral habitats and that coral habitat (whether live or dead) in turn supports higher diversity and abundance than structurally simple sand areas without coral. Second, we experimentally tested mechanisms of reef habitat suitability for invertebrate colonization by manipulating coral mortality and structural complexity. We found that the abundance and species richness of mobile invertebrates were significantly affected by substrate complexity rather than whether coral was live or dead. However, we detected shifts in species identity between live and dead coral. Moreover, the sensitivity of the community to reef structural complexity indicates that the ability of degraded coral reefs to sustain invertebrate assemblages is unlikely to persist if declines in reef complexity outpace recovery of living corals to the reef. Our findings suggest that the biodiversity-sustaining function of reefs has the potential to persist following coral disturbance at the scale of entire reefs and that some metrics of community structure are therefore resilient to events of foundation species mortality.

Key words: biodiversity; coral reefs; ecosystem engineer; foundation species; habitat complexity; habitat degradation.

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INTRODUCTION

Foundation species (*sensu* Dayton 1972) create complex, biogenic habitats (i.e., kelp beds, coniferous forests, and coral reefs) that enhance local species richness through a variety of different

mechanisms, such as ameliorating environmental stress, creating refuges from predators and competitors, and increasing resource availability (Bruno and Bertness 2001, Ellison et al. 2005, Altieri and Van De Koppel 2013). The degradation of foundation species due to anthropogenic

impacts such as climate change, eutrophication, urban development, and the depletion of top predators is a widely recognized global problem (Ellison et al. 2005, Bracken et al. 2007, Polidoro et al. 2010, Altieri et al. 2012). In this era of unprecedented and rapid ecological change, it is necessary to consider how communities and ecosystems will respond as the ecosystem functions of foundation species are lost or modified.

Coral reefs are a representative and urgent example of this potential threat to biodiversity due to their function as foundation species and their vulnerability to global stressors. Although coral reefs cover less than 0.2% of the ocean floor, they harbor one-third of all described marine species (Reaka-Kudla 1997), making them one of the most concentrated centers of biodiversity on the planet. Despite recognition of this role, reef-building scleractinian corals, the foundation species of coral reefs, have been on a trajectory of decline due to human activities for at least a century (Pandolfi et al. 2003). With one-third of all corals facing extinction risk (Carpenter et al. 2008) and further degradation expected (Pandolfi et al. 2011), understanding the potential changes in reef biodiversity associated with the loss of live corals has become an increasingly significant concern.

More generally, the persistence of coral reef structure following the mortality of corals provides an opportunity to mechanistically understand the functional role of foundation species and their ability to sustain biodiversity by partitioning the physical structure from the biotic properties of the living corals. Corals can facilitate the presence of diverse communities of invertebrates through several different functional roles. By generating complex three-dimensional structures, they create habitats for the myriad species that dwell on and within their colonies (Idjadi and Edmunds 2006), offer refuges from predators and competitors (Almany 2004, Aguirre and McNaught 2013), and modify local hydrodynamic environments in ways that can enhance nutrient and zooplankton availability to their surrounding community (Atkinson and Bilger 1992). In addition, coral can supply food to their reef communities, through their microbial-enriched mucus (Gottfried and Roman 1983) or tissues (Rotjan and Lewis 2008). After a coral dies, the relic skeleton no longer fulfills some biological roles (e.g., food source) of the live coral colony, but it can

retain structural complexity with the potential to provide key physical functions (e.g., refuge from predation, modify local hydrodynamic environment) and continue to function as a habitat for associated organisms.

The degree to which coral reef communities are reliant on the physical, rather than biological, aspects of their coral framework is not well understood for two reasons. First, fishes historically have been used as surrogates of overall reef biodiversity in assessments because they are relatively large, conspicuous, taxonomically well defined, and easy to census (Bellwood and Hughes 2001). Fish are ecologically and economically important members of coral reef communities, but they represent only a fraction of reef-associated diversity, with estimates of noncoral invertebrate diversity being one to two orders of magnitude higher than fish (Stella et al. 2011). The response of fish to declining reef health may not be representative of the invertebrate community response because fish and invertebrates may differ in their relative reliance on the various functions of coral as a foundation species. Moreover, mobile invertebrates can differ from fish in their ecological roles on coral reefs, so understanding their response to reef degradation has implications for feedbacks into overall reef dynamics (Stella et al. 2011).

Second, few studies have experimentally tested the response of reef-associated invertebrates to the degradation of coral habitats. Surveys alone could confound the loss of live coral cover with the loss of structural complexity, as some degraded reefs suffer from both coral mortality and reduced structural complexity simultaneously (Bell and Galzin 1984). Without controlled experiments, it is difficult to isolate the effects of habitat structure from the environmental conditions driving coral mortality as factors that degrade corals (e.g., thermal stress, ocean acidification, pollution) could also affect associated invertebrates (Przeslawski et al. 2008). To our knowledge, only two studies have gone beyond observational surveys to experimentally test the role of coral habitat in shaping invertebrates communities, but neither incorporated degraded reef areas or were conducted in the Caribbean, and the first opted to not test specific mechanisms by which dead coral functions as a habitat (Enochs and Hockensmith 2008) and the second focused on a limited community of only eight species (Caley et al. 2001).

We utilized a recent coral mass mortality event on the Caribbean coast of Panama to better understand how the function of foundation species can persist following their mortality, and to explore the resilience of coral reef communities to degradation. First, we surveyed live coral, dead coral, and sand zones to quantify how patterns of mobile invertebrate abundance and diversity varied between these habitats within a given reef site, and how they varied between degraded and healthy reefs across the landscape. Second, we examined the mechanisms of habitat suitability associated with reef degradation by experimentally testing the relationship between invertebrate colonization and coral habitat quality including structural complexity and coral mortality status.

MATERIALS AND METHODS

Study system

We conducted our study on the shallow (6–9 m depth), sheltered fringing reefs of Almirante Bay, Bocas del Toro Archipelago, located on the northwestern Caribbean coast of Panama. Over the past century, some of these reefs have become increasingly turbid and nutrient-loaded due to a variety of large-scale anthropogenic disturbances, such as overfishing and land-clearing for intensive banana production in the archipelago (Cramer et al. 2012). As a consequence, reefs have transitioned to more stress tolerant and opportunistic species of *Agaricia* (Aronson et al. 2004), and Agariciidae is now the most abundant scleractinian coral family on mid-depth reefs in Almirante Bay (Seeman et al. 2013). Against this backdrop of degradation typical of many Caribbean reefs, coral cover in Almirante Bay remained relatively high for the region (Guzman 2003, Jackson et al. 2014) until a recent mortality event associated with hypoxia that killed some *Agaricia* reefs (<5% coral cover remaining) but left others relatively unscathed (>20% cover; A. Altieri, unpublished data).

Reef mobile invertebrate surveys

To examine the relationship between habitat (live coral, dead coral, sand) and invertebrate community composition, we surveyed the community of mobile invertebrates in July 2014 at six reef sites, which included three “healthy” (live coral cover 20–40%) and three “degraded”

(live coral cover <5%) sites. We haphazardly placed 0.25 × 0.25 m quadrats in patches of sand, dead *Agaricia* coral, and live *Agaricia* coral at each site ($n = 20$ per substrate type per site), and then, each quadrat was invasively sampled (i.e., coral was broken apart and examined piece by piece to investigate every surface) in situ by counting and identifying all mobile macroinvertebrates (>1 mm) to the lowest taxonomic level possible. Only the surface of the sand was surveyed. There were insufficient live coral at the three degraded sites, so surveys at these sites were conducted only in zones of sand and dead *Agaricia* coral. All *Agaricia* sampled was *Agaricia tenuifolia* or *A. lamarcki*, the two most abundant *Agaricia* species in the area (Guzman et al. 2005). While this sampling approach (in situ invasive sampling) allowed us to find small and/or cryptic taxa, it has the potential to underestimate the presence of some rapidly fleeing inhabitants such as crabs and shrimp. However, we minimized the likelihood of this loss by surrounding each plot with a dive team that approached while observing for movement, and we observed that most mobile organisms moved slowly, retreated into the reef matrix of the plot, and/or were readily apparent on the sand surface.

Habitat colonization experiment

To compare the potential of different habitats (live coral, dead coral, sand) to support invertebrate communities, we conducted an invertebrate colonization experiment in which we established plots with one of five habitat treatments: (1) sand, (2) live coral, (3) dead coral collected in situ (still encrusted with algae, sponges, etc.), (4) dead coral that had been killed and cleaned of epibionts (exposed to air and sun for two weeks prior to the experiment to kill and remove all sessile epibionts), and (5) control treatment (no handling of coral) within existing patches of dead coral ($n = 10$ plots per treatment per site). All sand, dead coral, and live coral were collected and deployed in situ at each site, with some additional live coral transplanted from healthy site to the degraded site. All coral treatments consisted of a mix of *Agaricia tenuifolia* and *Agaricia lamarcki*. Each plot was established within an open-top 30 × 30 × 15 cm mesh basket (plastic extruded mesh with mesh size of 13 mm) to maintain

a defined plot space, except for the control plots, which were marked with 2 mm diameter corner stakes. All baskets were filled with an approximately equal volume of habitat material for their respective treatment. Plots were cleaned of mobile invertebrates at the start of the experiment, and mobile invertebrates were observed to move freely over and through the mesh of the baskets during the course of the experiment. To determine whether the context of reef health affected the role of habitats in structuring reef communities, we conducted the same experiment at a representative healthy reef site and degraded reef site (Seagal and STRI Point, respectively). All experimental plots were established in July 2013 and invasively sampled in June 2014 for mobile invertebrate colonizers. All mobile macroinvertebrates (>1 mm) were counted and identified to the lowest taxonomic level possible.

Dead coral structural complexity experiment

To test the effect of reef structural complexity on colonization by mobile invertebrates, and to account for potential compositional differences between dead coral and sand, we conducted a second experiment at STRI Point in which we quantified mobile invertebrate colonization to plots in which we manipulated the size of dead coral pieces. We established plots in baskets as described above with one of four coral size treatments: (1) sand, (2) rubble, (3) whole colony, and (4) whole colony control ($n = 10$ plots per treatment). For all treatments, dead coral colonies (*Agaricia tenuifolia* and *Agaricia lamarcki*) were collected and exposed to air and sun for one week, and then broken or crushed to appropriate treatment sizes. Coral in the sand treatment passed through 7×7 mm mesh, rubble treatment passed through 27×35 mm mesh but retained by 13×13 mm mesh, and whole colonies had a maximum length >100 mm. The whole colony and whole colony control treatments were the same, except the control treatment plots did not have a basket and were marked with corner stakes. All baskets were filled with an approximately equal volume of habitat material for their respective treatment. Baskets were cleaned of mobile invertebrates at the start of the experiment. All experimental plots were established in June 2014, and

invasively sampled one month later for mobile invertebrate colonizers. All mobile macroinvertebrates (>1 mm) were counted and identified to the lowest taxonomic level possible.

Statistical analyses

We examined the role of habitat and reef health in determining the abundance and taxonomic richness of mobile invertebrates from the reef surveys with two different analyses. We included survey data from the live coral habitat (collected only at healthy sites) in the first analysis which allowed us to test for differences in the abundance and taxonomic richness of invertebrates between all habitat types (sand, dead coral, live coral). This analysis was conducted using a mixed-model ANOVA without interactions. Habitat (sand, dead, live) and reef health (degraded, healthy) were considered fixed factors, with site as a random factor nested within reef health. In the second analysis we excluded the live coral survey data and focused on dead coral and sand habitats which allowed us to test for interactions between all three factors (habitat, reef health, site). The second ANOVA model included the same factors as above, in addition to two interaction terms: (1) the interaction between habitat and reef health, and (2) the interaction between habitat and site.

For our habitat colonization experiment, we analyzed the effects of habitat on the abundance and taxonomic richness of mobile invertebrates at each site with a one-way ANOVA, with habitat as a fixed factor. For our structural complexity experiment, we analyzed the effects of dead coral fragment size on the abundance and taxonomic diversity of mobile invertebrates using a one-way ANOVA. Data were square-root-transformed where necessary to meet ANOVA assumptions. Post hoc analyses were performed with Tukey's HSD test ($\alpha = 0.05$). To examine potential differences in community composition with our survey data, we used a permutational multivariate analysis of variance (PERMANOVA). The dissimilarity matrix used in this analysis was constructed by first pooling the mobile invertebrate data by habitat (sand, dead, live coral) within each site, performing a Wisconsin-style double standardization, and then calculating the Bray-Curtis dissimilarity between all pairs. Differences in community composition

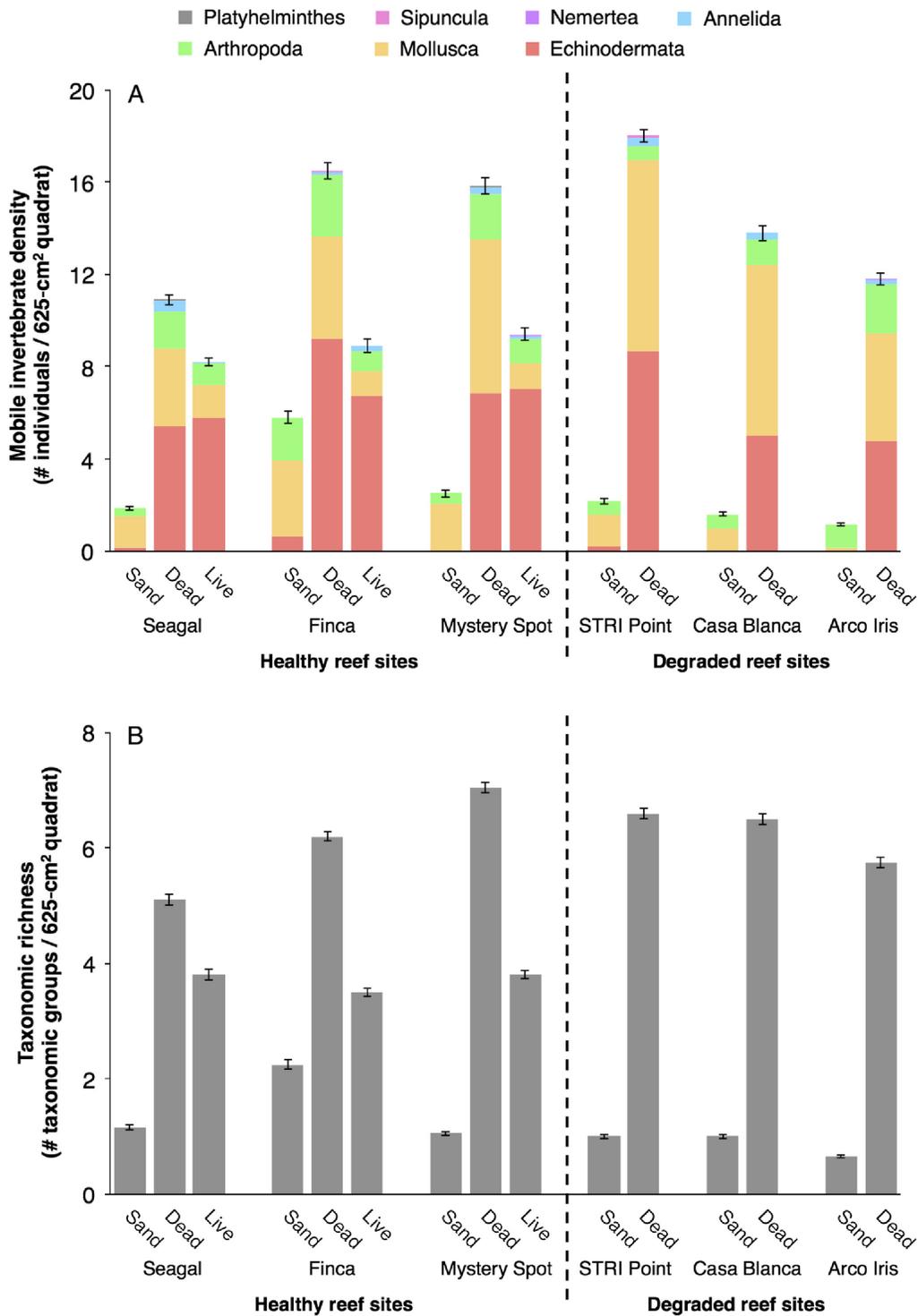


Fig. 1. Mean (\pm SE) abundance (A) and richness (B) of mobile invertebrates across different habitat substrates (sand, dead coral, live coral) in six reefs in Bocas del Toro Archipelago, Republic of Panama ($n = 20$), with the abundance bars divided by color to represent the relative abundance of dominant phyla.

between habitats were visualized using a multidimensional scaling (MDS) ordination, with similarity percentages (SIMPER) used to identify the taxonomic groups contributing the most toward dissimilarity among groups (Clarke 1993). All analyses of ANOVA models were carried out using JMP statistical software (version 11, 2013; SAS Institute, Cary, North Carolina, USA). The PERMANOVA, SIMPER, and MDS were all conducted using the open source software R 3.1.2 (R Development Core Team 2014), with the package *vegan* (Oksanen et al. 2009).

RESULTS

Reef mobile invertebrate surveys

Across the 300 quadrats sampled, we found 2568 mobile invertebrates, which were categorized into 40 taxonomic groups, representing seven phyla (Fig. 1A). Of the 2568 mobile invertebrate individuals surveyed, 26% were identified to the level of species, 18% to the genus level, 21% to the family level, 26% to the order level, and <10% to higher levels. The reef mobile invertebrate communities were numerically dominated by four taxonomic groups in particular: reef urchins (25%), brittle stars (22%), hermit crabs (12%), and *Cerithium* snails (11%), which collectively accounted for 70% of all of the individuals found during the surveys.

Surveys at the three healthy and three degraded reef sites yielded similar results in regards to habitat type. Mobile invertebrate abundance (Fig. 1A) and taxonomic richness (Fig. 1B) were significantly different between habitats ($F_{2, 292} = 74.303$, $P < 0.001$ and $F_{2, 292} = 96.849$, $P < 0.001$, respectively), with the highest abundance and taxonomic richness in dead coral, followed by live coral, and then sand. In all sites except Finca, the diversity and abundance of invertebrates in live and dead coral were at least double that found in sand.

There was no significant interaction between habitat type and reef health for mobile invertebrate abundance ($F_{1, 228} = 3.705$, $P = 0.127$) nor taxonomic richness ($F_{1, 228} = 3.046$, $P = 0.156$). Nor was there a main effect of reef health status for invertebrate abundance or taxonomic richness ($F_{1, 292} = 1.068$, $P = 0.356$ and $F_{1, 292} = 2.134$, $P = 0.207$, respectively). This indicates that at the landscape scale across all six survey sites, habitat

within a site had important effects on invertebrate abundance and diversity, but the overall status of a given site (healthy or degraded) was relatively unimportant as a predictor of invertebrate abundance and diversity.

There were significant differences in mobile invertebrate community composition between the live coral, dead coral, and sand habitats (PERMANOVA: $F_{2, 12} = 7.850$, $P < 0.001$; Fig. 2). However, SIMPER analyses revealed that the overall mobile invertebrate communities were 65% similar between live coral and dead coral and that no taxonomic group contributed more than 6% to the differences between the two habitats. These results indicate that there was significant overlap between community composition of live and dead coral habitats, with no single taxonomic group contributing strongly to the differences between the two communities. Sand communities were comprised of a small subset of the community typical of the coral habitats, with *Cerithium* snails and hermit crabs comprising on average 83–100% of the

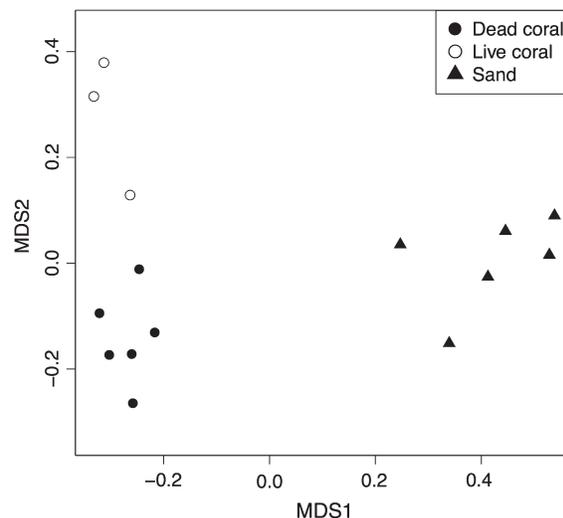


Fig. 2. A multidimensional scaling plot (MDS) showing the community composition of mobile invertebrates in sand, dead coral, and live coral habitats across six sites. There are no data for live coral habitat at the degraded sites because of insufficient live coral to sample invertebrate communities. Each point represents the mobile invertebrate community from a single habitat (pooled from twenty 0.25×0.25 m quadrats) at a single site.

mobile invertebrate communities found within sand at each site.

Of the 40 total taxonomic groups encountered during the reef surveys, 12 groups (30%) were associated exclusively with dead coral and four groups (10%) were associated exclusively with live coral. Five or fewer total individuals from each of these groups were encountered during

the surveys, so these groups may be exclusive to a habitat type, or the apparent exclusivity of these groups could be a sampling artifact associated with rare species. Twenty-seven of the 40 taxonomic groups (68%) were found only in the presence of coral (live and/or dead coral), and there were no taxonomic groups found exclusively in the sand habitat.

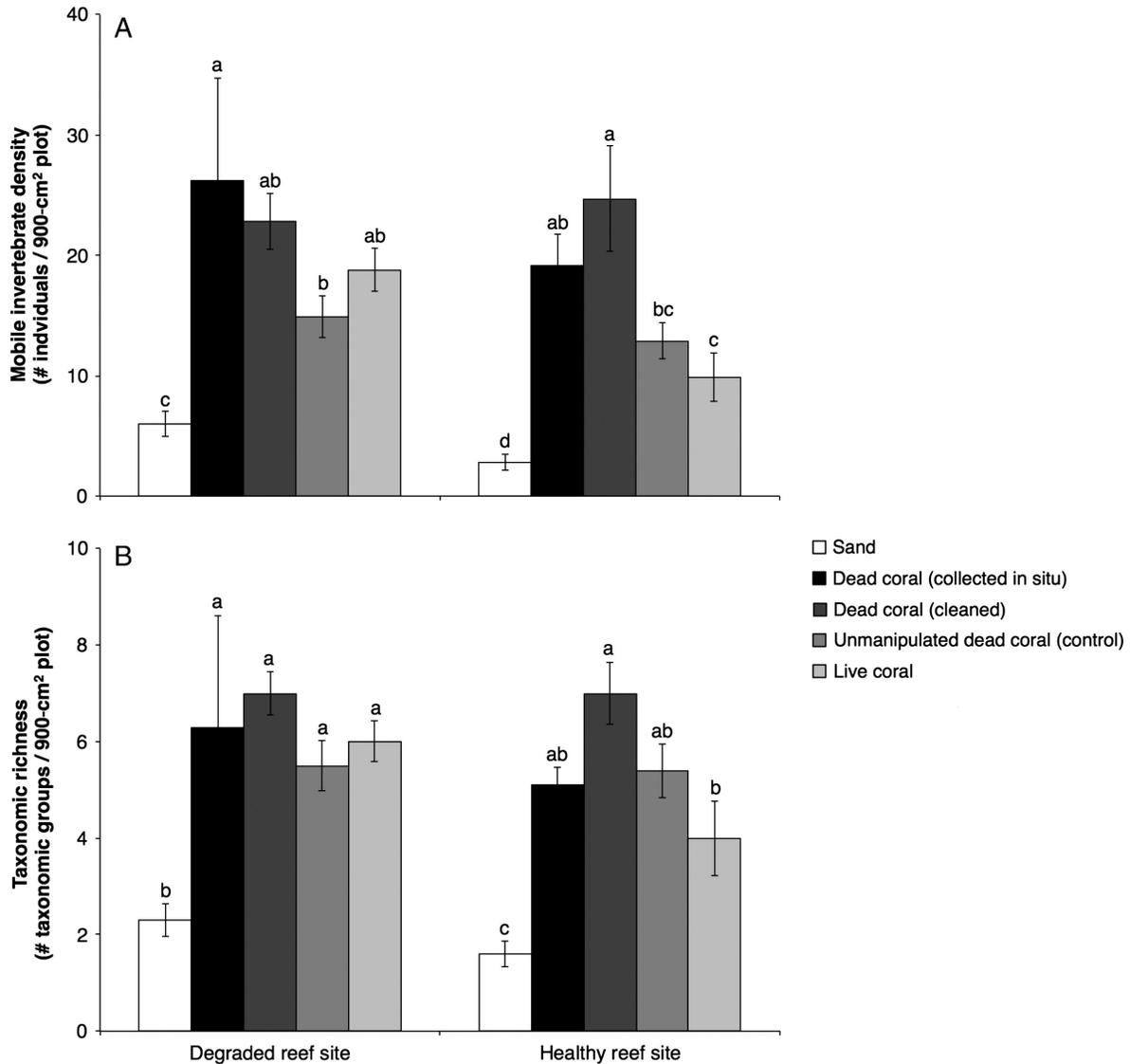


Fig. 3. Mean (\pm SE) abundance (A) and richness (B) of mobile invertebrates in experimental sand, dead coral collected in situ, dead coral cleaned of epibionts, unmanipulated dead coral control, and live coral plots ($n = 10$) at a representative healthy and degraded reef site. Plots in this habitat colonization experiment were sampled one year after they were initially established. Means that share a letter are not significantly different (Tukey's HSD test: $P < 0.05$).

Habitat colonization experiment

Habitat treatment had a significant effect on the abundance of mobile invertebrates at both the degraded ($F_{4, 45} = 15.265$, $P < 0.001$) and healthy ($F_{4, 45} = 17.048$, $P < 0.001$) reef sites (Fig. 3A). At both sites, the abundance of mobile invertebrates was significantly higher in coral habitats than sand habitats (Tukey's HSD: $P < 0.05$). At the healthy reef site, the abundance of mobile invertebrates was lower in live coral than dead coral (collected in situ; Tukey's HSD: $P < 0.05$),

reflecting the results of the reef surveys. However, at the degraded site, there were no significant differences in invertebrate abundance between the dead coral (collected in situ) and live coral habitats (Tukey's HSD: $P > 0.05$). There were no significant differences in mobile invertebrate abundance between dead coral collected in situ and dead coral that was cleaned of sessile epibionts at either site (Tukey's HSD: $P > 0.05$).

Habitat type had a significant effect on the taxonomic richness of mobile invertebrates at

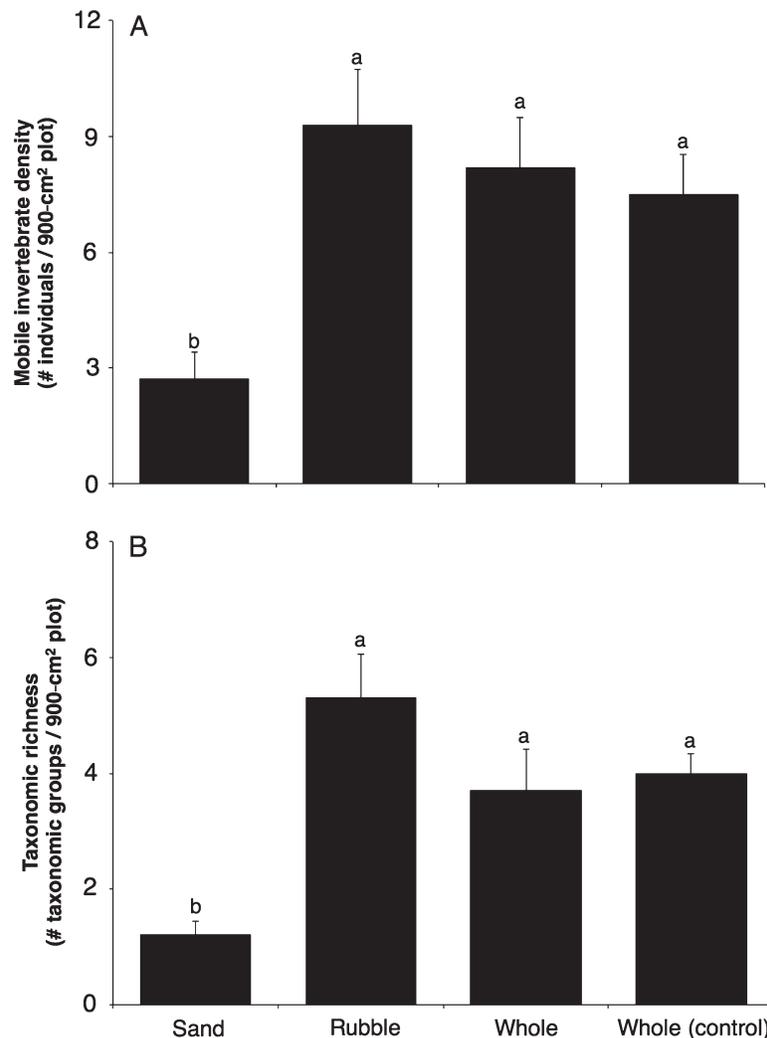


Fig. 4. Mean (\pm SE) abundance (A) and richness (B) of mobile invertebrates in experimental sand, rubble, whole, and whole (control) plots ($n = 10$) at a degraded reef site. Plots in this dead coral structural complexity experiment were sampled one month after they were initially established. Means that share a letter are not significantly different (Tukey's HSD test: $P < 0.05$).

both the degraded ($F_{4, 45} = 12.868$, $P < 0.001$) and healthy ($F_{4, 45} = 15.700$, $P < 0.001$) reef sites (Fig. 3B). At both sites, the taxonomic richness of mobile invertebrates was significantly higher in coral habitats than sand habitats (Tukey's HSD: $P < 0.05$). There was no significant differences in mobile invertebrate taxonomic richness between live coral and dead coral collected in situ, or between dead coral collected in situ and dead coral that was cleaned of all sessile epibionts, at either site (Tukey's HSD: $P > 0.05$).

Dead coral structural complexity experiment

Structural complexity, which was manipulated by the size of dead coral pieces, had a significant effect on both the abundance ($F_{3, 36} = 6.411$, $P = 0.001$; Fig. 4A) and taxonomic richness ($F_{3, 36} = 12.248$, $P < 0.001$; Fig. 4B) of mobile invertebrates. The abundance of mobile invertebrates was similar among rubble, whole colony, and whole colony control treatments, which in turn were threefold higher than in the sand treatment (Tukey's HSD: $P < 0.05$). The taxonomic richness of mobile invertebrates followed a similar pattern; rubble, whole colony, and whole colony control treatments were all similar to one another and threefold higher than the sand treatment (Tukey's HSD: $P < 0.05$).

DISCUSSION

Our reef surveys and habitat colonization experiments revealed that dead coral habitats support mobile invertebrate communities that are as diverse and abundant, or more so, than communities associated with live coral habitats. This similarity between live and dead coral habitats, and the relative paucity of the invertebrate community in simple sand habitats without coral structure, highlights the important role of structural complexity in the biodiversity enhancing function of coral reefs. While there were some differences in community composition between live coral and dead coral, few taxonomic groups were found exclusively in live coral, indicating significant overlap between the community composition of the two habitats.

Habitat characteristics of dead coral habitat

Our findings may appear somewhat surprising given that a number of fish and invertebrate

studies have identified correlations between the abundance and/or diversity of associated taxa and live coral cover (Jones and Syms 1998, Caley et al. 2001, Enochs 2012, Fabricius et al. 2014). Our results suggest that the total amount of coral habitat (including both live and dead coral), rather than the cover of live coral per se, is likely the best predictor of the mobile invertebrate community. This contribution of dead coral habitat to sustaining communities of invertebrates may explain why other studies have failed to find a relationship between live coral cover and the abundance and/or diversity of fish and invertebrates communities (Jones and Syms 1998, Vytopil and Willis 2001, Idjadi and Edmunds 2006).

The suitability of dead coral as a habitat, relative to live coral, may be explained by several complimentary characteristics of dead coral. First, high complexity of the skeletal structure remaining after coral death may be the most important factor in the suitability of dead coral as habitat for associated organisms. The correlation between habitat complexity and species diversity has been demonstrated in a wide range of communities, including mountain meadow complexity for fly diversity (Haslett 1997), tree canopy complexity for bird diversity (MacArthur and MacArthur 1961, Finch 1989), tropical rain forest complexity for small mammal diversity (Williams et al. 2002), and seagrass bed complexity for motile macroinvertebrates diversity (Heck and Westone 1977). Idjadi and Edmunds (2006) similarly demonstrated through surveys of reefs in the U.S. Virgin Islands that topographic complexity, rather than live coral cover, was correlated with invertebrate diversity. Structurally complex relic skeletons may enhance biodiversity by serving as sites for refuges, recruitment, feeding, mating and/or nesting for invertebrates. Also, the simple presence of structure (live or dead) modifies local hydrodynamic environments in ways that promote turbulent flow (Reidenback et al. 2006), which can enhance the delivery of larvae (Walters et al. 1997), planktonic prey (Shashar et al. 1996), and nutrients (Atkinson and Bilger 1992).

Second, the surface of the dead coral skeletons is often colonized by a variety of sessile epibionts including turf and macroalgae, sponges, bryozoans, and hydrozoans. The presence of these

epibionts on the surface of habitat-forming species such as corals, gorgonians, seagrasses has been associated with enhanced abundance and diversity of mobile invertebrates as they can further increase structural complexity (Martin-Smith 1993), provide additional food resources (Kitting et al. 1984), and generate settlement cues (Hadfield and Paul 2001). In our study, we found no difference in the diversity or abundance of mobile invertebrates between dead coral collected in situ and dead coral cleaned of all sessile epibionts, suggesting that mobile invertebrate communities are not linked to the presence of sessile epibionts. However, we sampled our experimental plots almost a year after they were established which may have allowed time for some epibionts to recolonize the coral skeletons.

Third, dead coral skeletons may be especially suitable as habitat for mobile invertebrates because they lack the defensive and feeding adaptations of live coral (e.g., sweeper tentacles and polyps, mesenterial filaments, mucus, and allelopathic chemicals) that can inhibit growth of macroalgae and colonial invertebrates (McCook et al. 2001). In addition, many species of corals are active heterotrophs and voracious predators of zooplankton (Houlbrequé and Ferrier-Pagès 2009), and so live corals may decrease local invertebrate diversity or abundances by feeding on their larval stages as predicted by the trophic amensalism hypothesis (Woodin 1976).

Fourth, there may be lower predation pressure associated with dead coral than live coral habitat. Some studies have found that the abundance and diversity of fishes are positively related to live coral cover (Jones and Syms 1998). Fewer fish, including invertivores, on dead reefs would release invertebrates from predation pressure typical of live reefs, while the structural complexity of the dead reef still offers a predation refuge by decreasing predator foraging efficiency as observed in bivalve reefs (Grabowski 2004).

Community composition of degraded reefs

Agreement between our small-scale experiments and large-scale surveys in the community associated with each habitat type suggest that mobile invertebrates either persisted through the disturbance event that killed the corals, or rapidly recolonized in the years since. While we found that the overall abundance and

diversity of mobile invertebrates did not differ between live and dead coral, we did find some differences in community composition between live coral, dead coral, and sand habitats, with the largest dissimilarity between live coral and dead coral communities (65% similar). Difference in community composition between habitats can be due to the presence/absence of certain species and/or differences in the relative abundance of the species present. SIMPER analyses revealed that no single taxonomic group contributed strongly (>6%) to the differences between live and dead coral communities. Furthermore, all of the taxa found exclusively within live or dead coral habitats were encountered five or fewer times during our surveys, indicating they were rare overall. These results suggest that differences in community composition between the live and dead coral communities resulted primarily from differences in the relative abundance of certain taxonomic groups rather than the presence/absence of certain taxa. For example, algal grazers and omnivorous scavengers occupied both live and dead coral, but dead coral hosted a larger proportion of chitons and *Modulus* snails, while live coral had a greater proportion of brittle stars and reef urchins. Our findings differ from observations in the Tropical Eastern Pacific in which species composition of cryptofauna differed considerably between live and dead coral colonies within a matrix of live coral (Enochs 2012). Where herbivores are present in sufficient abundance among dead coral, their grazing may help coral recruitment and recovery by preventing coral-algal phase shifts (Carpenter 1986, Hughes 1994, McManus and Polsenberg 2004).

Short- and long-term conservation implications of coral decline on reef biodiversity

Our study reveals that the presence of coral (live or dead) enhances biodiversity through the presence of structure and that function persists even after coral die-off at the scale of entire reefs. Several studies have suggested that rapidly declining live coral cover worldwide will cause precipitous drops in reef biodiversity (Jones et al. 2004, Munday 2004, Wilson et al. 2006). However, many of these predictions are based on the responses of reef fishes rather

than the overall community, or on correlations through space rather than actual trajectories established through time, and are potentially driven by corals and their associated organisms responding to some other environmental driver rather than one another. Although our sampling approach may have underestimated the presence of some fast-moving invertebrates and our results arose from a study system dominated by one family of coral, the ability of dead *Agaricia* coral to support mobile invertebrate communities that are just as abundant and diverse as communities supported by live coral suggests that dead coral may play an important role in the resilience (*sensu* Holling 1973) of coral reef communities. Dead coral may continue to function as a habitat for reef invertebrates while the corals themselves recover, particularly where herbivores are among the dead coral community, as we observed, leading to feedback between dead coral, herbivory, and enhanced coral recovery.

However, this potential for dead coral to sustain reef biodiversity may have some limitations. First, we found that the mobile invertebrate community composition differed between dead and live coral, with potential losses predicted for obligate coral associates if the coral disturbance is sufficiently extensive in spatial scale. Second, many of the anthropogenic stressors (*i.e.*, runoff, turbidity, ocean acidification) that are driving coral mortality also affect coral-associated invertebrates (Przeslawski *et al.* 2008); however, we did not find evidence for this in our study system. Third, the degradation and loss of live coral may have sublethal effects on associated organisms such as crabs that exhibit reduced reproductive activity and defensive behaviors when inhabiting dead coral (Glynn *et al.* 1985). Fourth, while coral reefs may maintain their function as a habitat for invertebrates following coral mortality, the loss of live coral will likely have consequences for other ecosystem functions including biogeochemical cycling and primary production (Harborne *et al.* 2006). Fifth, the effects of coral mortality on invertebrate community composition could vary depending on the dominant species of reef-building coral species and may differ depending the cause and pace of coral mortality.

The ability of dead coral to sustain invertebrate communities will not persist in the long term if

declines in reef complexity, due to mechanisms such as ocean acidification, storm damage, and bioerosion, outpace recovery of living corals on the reef. Regionwide analyses have revealed overall declines in structural complexity (“flattening”) of coral reefs throughout the Caribbean on a timeline associated with declines in live coral cover (Alvarez-Filip *et al.* 2009). In our experiments, we detected no significant difference in mobile invertebrate abundance or taxonomic richness between whole coral colonies and coral rubble, but significant drops in the abundance and diversity of invertebrates at the threshold in complexity between coral rubble and coral sand habitats. Our study experimentally substantiate claims made by previous observational studies that dead coral frameworks of intermediate degradation can support diverse associated assemblages, but further degradation can cause nonlinear declines in reef biodiversity (Bailey-Brock *et al.* 2007, Enochs 2012). Our results suggest that reef biodiversity is most threatened not by the direct effects of coral death, but the indirect effects of loss of habitat-forming functions associated with declines in reef complexity.

Diversity in light of foundation species decline

Although declines in habitat-modifying foundation species are often associated with dramatic losses in ecosystem function and stability (Ellison *et al.* 2005, Altieri and Witman 2006, Bracken *et al.* 2007, Polidoro *et al.* 2010), there is increasing evidence that some communities associated with dead foundation species can be just as diverse, if not more diverse, than those associated with live foundation species. This pattern has been documented in the mobile macroinvertebrates found in dead seagrass mattes (Borg *et al.* 2006), diatom assemblages on dead grass stems (Grimes *et al.* 1980), and beetle communities associated with dead pine trees (Klepzig *et al.* 2012).

The potential short-term preservation of diversity provided by dead foundation species has several important implications for management and conservation efforts. As dead foundation species can continue to sustain diverse and abundant invertebrate assemblages, the habitats they create may be worth protecting even if the majority of structure-forming species have died. Additionally, traditional biodiversity estimates (*e.g.*, species richness, diversity) may not always be

good indicators of ecosystem health because they might remain high long after the foundation species host dies, with the lag masking a trajectory of overall ecosystem decline. Finally, our study suggests that structurally complex artificial habitats (e.g., artificial reefs) may be successful in retaining some ecosystem diversity while foundation species recover.

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LITERATURE CITED

- Aguirre, J. D., and D. C. McNaught. 2013. Habitat complexity mediates predation of juvenile abalone by starfish. *Marine Ecology Progress Series* 487:101–111.
- Almany, G. R. 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106:275–284.
- Altieri, A. H., and J. Van De Koppel. 2013. Foundation species in marine ecosystems. Pages 37–56 in M. D. Bertness, J. F. Bruno, B. R. Silliman, and J. J. Stachowicz, editors. *Marine community ecology and conservation*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Altieri, A. H., and J. D. Witman. 2006. Local extinction of a foundation species in a hypoxic estuary: integrating individuals to ecosystem. *Ecology* 87:717–730.
- Altieri, A. H., M. D. Bertness, T. C. Coverdale, N. C. Herrmann, and C. Angelini. 2012. A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. *Ecology* 93:1402–1410.
- Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B* 276:3019–3025.
- Aronson, R. B., I. G. MacIntyre, C. M. Wapnick, and M. W. O'Neill. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology* 85:1876–1891.
- Atkinson, M. J., and R. W. Bilger. 1992. Effects of water velocity on phosphate uptake in coral reef-flat communities. *Limnology and Oceanography* 2:273–279.
- Bailey-Brock, J., R. Brock, A. Kam, A. Fukunaga, and H. Akiyama. 2007. Anthropogenic disturbance on shallow cryptofaunal communities in a marine life conservation district on Oahu, Hawaii. *International Review of Hydrobiology* 92:291–300.
- Bell, J. D., and R. Galzin. 1984. Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series* 15:265–274.
- Bellwood, D. R., and T. P. Hughes. 2001. Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292:1532–1534.
- Borg, J. A., A. A. Rowden, M. J. Attrill, P. J. Schembri, and M. B. Jones. 2006. Wanted dead or alive: high diversity of macroinvertebrates associated with living and 'dead' *Posidonia oceanica* matte. *Marine Biology* 149:667–677.
- Bracken, M. E. S., B. E. Bracken, and L. Rogers-Bennett. 2007. Species diversity and foundation species: potential indicators of fisheries yields and marine ecosystem functioning. *CalCOFI Report* 48:82–91.
- Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201–218 in M. D. Bertness, M. E. Hay, and S. D. Gaines, editors. *Marine community ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Caley, M. J., K. A. Buckley, and G. P. Jones. 2001. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology* 82:3435–3448.
- Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* 56:345–364.
- Carpenter, K. E., et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321:560–563.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Cramer, K. L., J. B. C. Jackson, C. V. Angioletti, J. Leonard-Pingel, and T. P. Guilderson. 2012. Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and bleaching. *Ecology Letters* 15:561–567.
- Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81–95 in B. C. Parker, editor. *Proceedings of the Colloquium on Conservation Problems in Antarctica*. Allen Press, Lawrence, Kansas, USA.
- Ellison, A. M., et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486.

- Enochs, I. C. 2012. Motile cryptozoa associated with live and dead coral substrates: implications for coral mortality and framework erosion. *Marine Biology* 159:709–722.
- Enochs, I. C., and G. Hockensmith. 2008. Effects of coral mortality on the community composition of cryptic metazoans associated with *Pocillopora*. *Proceedings of the 11th International Coral Reef Symposium* 2:1368–1372.
- Fabricius, K. E., G. De'ath, S. Noonan, and S. Utlicke. 2014. Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. *Proceedings of the Royal Society B* 281:20132497.
- Feary, D. A., G. R. Almany, M. I. McCormick, and G. P. Jones. 2007. Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia* 153:727–737.
- Finch, D. M. 1989. Habitat use and habitat overlap of riparian birds in three elevation zones. *Ecology* 70:866–880.
- Glynn, P. W., M. Perez, and S. L. Gilchrist. 1985. Lipid decline in stressed coral and their crustacean symbionts. *Biological Bulletin* 168:276–284.
- Gottfried, M., and M. R. Roman. 1983. Ingestion and incorporation of coral-mucus detritus by reef zooplankton. *Marine Biology* 72:211–218.
- Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004.
- Grimes, J. A., L. L. St. Clair, and S. R. Rushforth. 1980. A comparison of epiphytic diatom assemblages on living and dead stems of the common grass *Phragmites australis*. *Great Basin Naturalist* 40:223–228.
- Guzman, H. M. 2003. Caribbean coral reefs of Panama: present status and future perspectives. Pages 241–274 in J. Cortes, editor. *Latin American coral reefs*. Elsevier Science, Amsterdam, the Netherlands.
- Guzman, H. M., P. A. G. Barnes, C. E. Lovelock, and I. C. Feller. 2005. A site description of the CARI-COMP mangrove, seagrass, and coral reef sites in Bocas del Toro, Panama. *Caribbean Journal of Marine Science* 41:430–440.
- Hadfield, M. G., and V. J. Paul. 2001. Natural chemical cues for settlement and metamorphosis of marine invertebrate larvae. Pages 431–461 in J. B. McClintock and B. J. Baker, editors. *Marine chemical ecology*. CRC Press, Boca Raton, Florida, USA.
- Harborne, A. R., P. J. Mumby, F. Micheli, C. T. Perry, C. P. Dahlgren, K. E. Holmes, and D. R. Brumbaugh. 2006. The functional value of Caribbean coral reef, seagrass, and mangrove habitats to ecosystem processes. *Advances in Marine Biology* 50:57–189.
- Haslett, J. R. 1997. Insect communities and the spatial complexity of mountain habitats. *Global Ecology and Biogeography* 6:49–56.
- Heck, K. L., and G. S. Westone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* 4:135–142.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.
- Houlbreque, F., and C. Ferrier-Pagès. 2009. Heterotrophy in tropical scleractinian corals. *Biological Reviews* 84:1–17.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Idjadi, J. A., and P. J. Edmunds. 2006. Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. *Marine Ecology Progress Series* 319:117–127.
- Jackson, J. B. C., M. K. Donovan, K. L. Cramer, and W. Lam. 2014. Status and trends of Caribbean coral reefs: 1970–2012. *Global Coral Reef Monitoring Network*. IUCN, Gland, Switzerland.
- Jones, G. P., and C. Syms. 1998. Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology* 23:287–297.
- Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V. Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences USA* 101:8251–8253.
- Kitting, C. L., B. Fry, and M. D. Morgan. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia* 62:145–149.
- Klepzig, K. D., M. L. Ferro, M. D. Ulyshen, M. L. Gimbel, J. B. Mahfouz, A. E. Tiarks, and C. E. Carlton. 2012. Effects of small-scale dead wood additions on beetles in southeastern U.S. pine forests. *Forests* 3:632–652.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.
- Martin-Smith, K. M. 1993. Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology* 174:243–260.
- McCook, L. J., J. Jompa, and G. Diaz-Pulido. 2001. Competition between coral and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417.
- McManus, J. W., and J. F. Polsenberg. 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects. *Progress in Oceanography* 60: 263–279.
- Munday, P. L. 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology* 10:1642–1647.

- Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2009. *vegan*: community ecology package. <http://cran.r-project.org/package=vegan>
- Pandolfi, J. M., et al. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958.
- Pandolfi, J. M., S. R. Connolly, D. J. Marshall, and A. L. Cohen. 2011. Projecting coral reef futures under global warming and ocean acidification. *Science* 333:418–422.
- Polidoro, B. A., et al. 2010. The loss of species: mangrove extinction risk and geographic areas of global concern. *PLoS ONE* 5:e10095.
- Przeslawski, R., S. Ah Yong, M. Byrne, G. Wörheide, and P. Hutchings. 2008. Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biology* 14:2773–2795.
- R Development Core Team. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Reaka-Kudla, M. L. 1997. The global biodiversity of coral reefs: a comparison with rain forests. Pages 83–108 *in* M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, editors. *Biodiversity II: understanding and protecting our biological resources*. National Academies Press, Washington, D.C., USA.
- Reidenback, M. A., S. G. Monismith, J. R. Koseff, G. Yahel, and A. Genin. 2006. Boundary layer turbulence and flow structure over a fringing reef. *Limnology and Oceanography* 51:1956–1958.
- Rotjan, R. D., and S. M. Lewis. 2008. Impact of coral predators on tropical reefs. *Marine Ecology Progress Series* 367:73–91.
- Seeman, J., C. T. Gonzalez, R. Carballo-Bolanos, K. Berry, G. A. Heiss, U. Struck, and R. R. Leinfelder. 2013. Assessing the ecological effects of human impacts on coral reefs in Bocas del Toro, Panama. *Environmental Monitoring and Assessment* 186: 1747–1763.
- Shashar, N., S. Kinane, P. L. Jokiel, and M. R. Patterson. 1996. Hydromechanical boundary layers over a coral reef. *Journal of Experimental Marine Biology and Ecology* 199:17–28.
- Stella, J. S., M. S. Pratchett, P. A. Hutchings, and P. J. Geoffrey. 2011. Coral-associated invertebrates: diversity, ecological importance, and vulnerability to disturbance. *Oceanography and Marine Biology* 49:43–104.
- Vytopil, E., and B. L. Willis. 2001. Epifaunal community structure in *Acropora* spp. (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity. *Coral Reefs* 20:281–288.
- Walters, L. T., M. G. Hadfield, and K. A. del Carmen. 1997. The importance of larval choice and hydrodynamics in creating aggregations of *Hydroides elegans* (Polychaeta: Serpulidae). *Invertebrate Biology* 116:102–114.
- Williams, S. E., H. Marsh, and J. Winter. 2002. Spatial scales, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* 83:1317–1329.
- Wilson, S. K., N. A. Graham, M. S. Pratchett, G. P. Jones, and N. V. Polunin. 2006. Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Global Change Biology* 12:2220–2234.
- Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages; patterns of abundance. *Journal of Marine Research* 34:25–31.