

Phase shift facilitation following cyclone disturbance on coral reefs

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Abstract While positive interactions have been observed to influence patterns of recruitment and succession in marine and terrestrial plant communities, the role of facilitation in macroalgal phase shifts is relatively unknown. In December 2012, typhoon Bopha caused catastrophic losses of corals on the eastern reefs of Palau. Within weeks of the typhoon, an ephemeral bloom of monospecific macroalgae (*Liagora* sp.) was observed, reaching a peak of 38.6 % cover in February 2013. At this peak, we observed a proliferation of a second macroalgal species, *Lobophora variegata*. *Lobophora* was distributed non-randomly, with higher abundances occurring within the shelter of *Liagora* canopies than on exposed substrates. Bite rates of two common herbivorous fish (*Chlorurus sordidus* and *Ctenochaetus striatus*) were significantly higher outside canopies

(2.5- and sixfold, respectively), and cage exclusion resulted in a significant increase in *Lobophora* cover. Experimental removal of *Liagora* canopies resulted in a 53.1 % decline in the surface area of *Lobophora* after 12 days, compared to a 51.7 % increase within canopies. Collectively, these results indicate that *Liagora* canopies act as ecological facilitators, providing a ‘nursery’ exclusion zone from the impact of herbivorous fish, allowing for the establishment of understory *Lobophora*. While the ephemeral *Liagora* bloom had disappeared entirely 9 months post-typhoon, the facilitated shift to *Lobophora* has persisted for over 18 months, dominating ~40 % of the reef substrate. While acute disturbance events such as typhoons have been suggested as a mechanism to reverse algal phase shifts, our results suggest that typhoons may also trigger, rather than just reverse, phase shifts.

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Introduction

Positive interactions play an important role in controlling large-scale landscape processes, shaping assemblages and regulating population dynamics in physically stressful habitats (Bertness and Callaway 1994; Bertness and Leonard 1997; Bruno et al. 2003). Positive interactions (or ‘facilitations’) are defined as ‘encounters between organisms that benefit at least one of the participants and cause harm to neither’ (Bruno et al. 2003; Stachowicz 2001), and occur when one organism renders the local environment more favourable for another either directly [e.g. reducing thermal stress via shading (Baumeister and Callaway 2006)] or indirectly [e.g. predator removal (Duffy 2003)]. Facilitation

can play an important role across a range of ecological processes, influencing recruitment patterns, regulating species distributions, and facilitating succession in a broad range of communities (Atsatt and O'Dowd 1976; Bertness and Callaway 1994).

Plant communities have traditionally played an important role as a model system for exploring the role of positive interactions (e.g. Brooker et al. 2008; Callaway 1995). Positive interactions have been observed to drive patterns of recruitment in terrestrial plants, resulting in patterns of density-dependent recruitment survivorship (Callaway 1995). Such interactions may occur through habitat amelioration, such as overstory shading by conspecific tree canopies (e.g. Weltzin and McPherson 1999), and enhanced primary productivity (Callaway et al. 1991), or through provision of a nursery environment to protect against herbivory (Fuentes et al. 1986). Facilitation can also influence species distributions in marine ecosystems. For example, the abundance of a palatable species may be positively correlated with the abundance of another less palatable species in both macroalgae (Hay 1986; Pfister and Hay 1988) and sponges (Wulff 1997). Positive interactions are a driving factor in both primary and secondary succession in marine plant assemblages. For example, primary succession of the kelp *Macrocystis pyrifera* is facilitated by the removal of herbivorous urchins (Harris et al. 1984), and secondary succession of the seagrass *Syringodium* is facilitated by a rhizophytic algae that stabilises sandy substrates (Williams 1990).

Following major disturbance events on coral reefs (e.g. cyclones, coral bleaching), widespread coral mortality reduces coral cover, in turn opening up new substrate for recruitment (Connell et al. 1997). If levels of herbivory are sufficient, then increased colonisation of coralline algae can, in turn, promote coral recruitment (Edmunds and Carpenter 2001). If substrates are insufficiently grazed by herbivores, then macroalgae can establish and become dominant (e.g. Hughes et al. 2007), inhibiting coral recruitment (e.g. Dixon et al. 2014) and outcompeting smaller corals and other benthic organisms (e.g. Lobel and Ogden 1981). While facilitation can be important for the establishment of macroalgae in temperate systems (e.g. Harris et al. 1984; Pfister and Hay 1988; Wahl and Hay 1995), the emergence of macroalgae in coral reef ecosystems is usually studied as a direct effect of either nutrification and/or reduced herbivory (but see Littler et al. 1986). Here, we examine the role of positive interactions in facilitating phase shifts from coral- to algal-dominated states.

Following catastrophic damage to reefs of Palau (Micronesia) from super-typhoon Bopha in December 2012, we documented a near complete loss of coral cover, with monospecific blooms of the foliose macroalga *Liagora* sp. observed across the exposed eastern reefs in the weeks following the typhoon. Such a transition from one phase

(coral dominated) to another (coral depleted and/or algal dominated) in response to acute disturbance represents a phase shift (sensu Done 1992). Following establishment, *Liagora* blooms are able to proliferate and persist because of effective anti-herbivory defences, including the presence of secondary metabolites that actively deter herbivorous fish (Paul and Fenical 1980; Wylie and Paul 1988), and incorporation of calcium carbonate directly into their thalli which may act as a chemical defence against acid-mediated digestion for grazing herbivores (Hay et al. 1994). Consistent with previous studies of *Liagora* blooms in the Caribbean region (e.g. Hughes 1994; Woodley et al. 1981), the post-disturbance bloom was ephemeral, lasting ~6 months. At the peak of the bloom, we observed the proliferation of a second macroalgal species, *Lobophora variegata*, which was first observed in an encrusting growth form underneath the *Liagora* canopy. In contrast to the ephemeral foliose rhodophyte *Liagora*, *Lobophora* represents an entirely different functional group of algae (Steneck and Dethier 1994), being a perennial phaeophyte with a morphology that is less susceptible to most herbivores (Coen and Tanner 1989). Critically, *Lobophora* did not exhibit any such colonisation at sites that lacked the *Liagora* bloom. Such a significant expansion of *Lobophora* across forereef habitats in Palau is unprecedented in at least the past decade (Y. Golbuu, P. J Mumby, personal observation).

To determine the roles of positive and negative interactions in successional processes, we first tracked the temporal dynamics of the macroalgal assemblages in the months following typhoon Bopha. Secondly, we quantified recruitment processes of *Lobophora* by determining patterns of abundance inside and outside *Liagora* canopies. Third, to determine the potential for *Liagora* canopies to act as refugia, we quantified spatial patterns of grazing by two key herbivores (*Ctenochaetus striatus* and *Chlorurus sordidus*) inside and outside of canopies. Fourth, to test the effectiveness of herbivores in removing *Lobophora*, we experimentally removed *Liagora* canopies. Finally, to explore the role of herbivory in influencing *Lobophora* cover, we conducted caging experiments to exclude the effects of large herbivorous fish. Collectively, our results show that *Liagora* canopies provide an important ephemeral refuge to *Lobophora* recruits from herbivory, and indicate that such positive interactions can be critical in facilitating the establishment of a macroalgal phase shift in ecosystems characterised by high herbivory.

Materials and methods

Temporal trends in benthic cover

This study was conducted at three sites on the eastern side of Palau that experienced a pronounced *Liagora* bloom

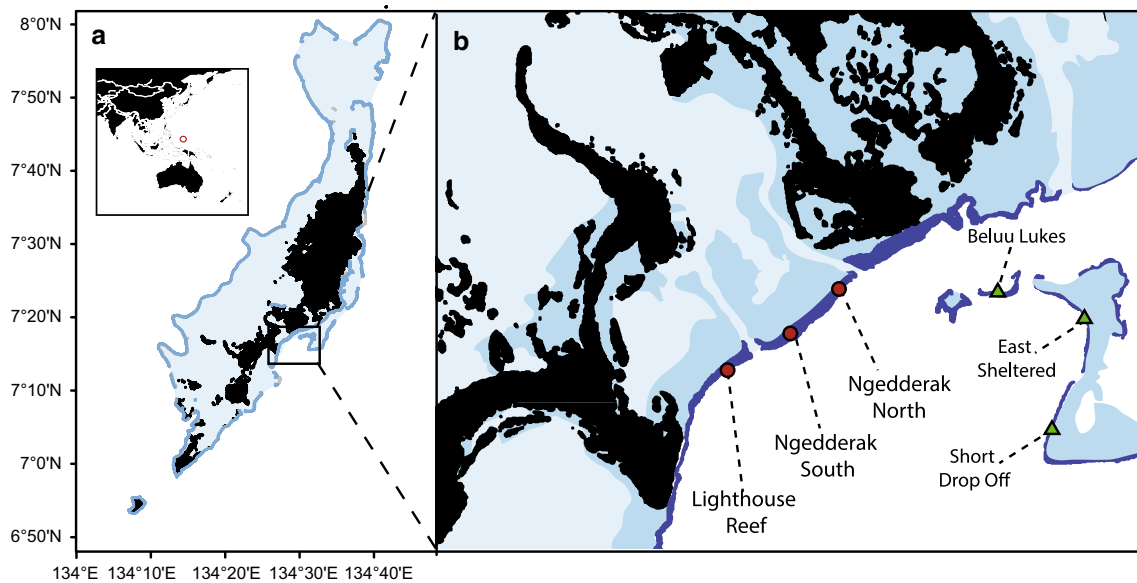


Fig. 1 **a** Map of Palau archipelago (dark blue reef crest, blue reef flat, pale blue lagoon, white open ocean), with inset world map with location of Palau in the western Pacific and **b** main study sites with *Liagora* blooms marked with red circles (Lighthouse North, Nged-

derak South and Ngedderak North) and adjacent study sites with no evidence of *Liagora* blooms marked with green triangles (Beluu Lukes, East Sheltered, Short Drop Off) (color figure online)

(Lighthouse North, Ngederrak South and Ngederrak North; Fig. 1). Surveys were conducted prior to typhoon Bopha in March 2012, and again following the typhoon in February, April, September and October 2013, and again in April and October 2014. Additional surveys (March 2012, February 2013, April 2014) were conducted at adjacent sites that showed no *Liagora* or *Lobophora* blooms (Table S1). At each site, three line-intercept transects (30-m length, $n = 3$) were conducted at 4–6-m depth parallel to the reef slope at each time period to quantify benthic cover. Line-intercept transects were haphazardly placed on hard substrata, separated by approximately 20-m distance, and placed in a similar location at each time point. Live coral (scleractinian coral), coralline algae, turf algae, encrusting and fleshy macroalgae, cyanobacteria, other invertebrates and non-living substrate (rubble, carbonate and sand) were identified to the lowest possible taxonomic resolution every centimetre along each transect. Percent cover for dominant groups was calculated as a mean from the three replicate transects.

Habitat availability beneath *Liagora* canopies and distribution of *Lobophora* on the reef

Individual *Liagora* were observed to sway with water motion from a single holdfast, creating a ‘swept’ zone underneath the canopy. As such, two possible substrate types were available for colonisation by *Lobophora*: areas free of *Liagora* and not swept by canopies (exposed substrate) and area that lay within the swept radius of *Liagora* canopies (swept substrate). To test whether the distribution

of *Lobophora* was non-random and significantly associated with swept substrates, we quantified: (1) the availability of exposed vs. swept substrates, and (2) the overall distribution of *Lobophora* across the reef including both categories of substrate.

To quantify the area of exposed vs. swept substrates, point-intercept transects (30-m length) were conducted at all sites in April 2013. At 20-cm intervals along each transect (total number of points per transect = 150), we quantified whether or not the transect tape was swept by *Liagora* canopies, and the proportion of each transect that was inside or outside of *Liagora* canopies was determined. To quantify the distribution of *Lobophora* among swept and exposed substrates, we selected 100 individual *Lobophora* by swimming a random number of fin kicks in a frequently changing direction at each site and quantified: (1) maximum diameter, (2) distance to the nearest *Liagora* holdfast, and (3) whether the *Lobophora* was swept by the *Liagora* canopy for each individual *Lobophora*. From this, the proportion of *Lobophora* inside or outside of *Liagora* canopies was determined. A χ^2 -test was used to determine whether the distribution of *Lobophora* was non-random and significantly associated with swept substrates at each site, where observed was the proportion of *Lobophora* inside and outside of *Liagora* canopies, and expected was the proportion of transect inside and outside of *Liagora* canopies. To test further for differences in the size structure of individuals of *Lobophora* between swept and exposed substrates, we used a Kolmogorov–Smirnov test in the stats package [R software (R Core Team 2014)].

Patterns of herbivore grazing on *Liagora* canopies

To quantify the capacity of *Liagora* canopies to act as a refuge from grazing herbivores, we collected observational data on fish grazing behaviour at Lighthouse North for two common and abundant herbivores: *Ctenochaetus striatus* ($n = 31$) and *Chlorurus sordidus* ($n = 27$). Individuals were observed for 5-min intervals, during which we recorded a visual estimate of total body length, and the number of bites inside and outside of *Liagora* canopies. To determine the feeding preference of the two herbivore species inside and outside of canopies, $(E_i = r_i - n_i/r_i + n_i)$, where r_i is the proportion of all bites that were taken on the i th substrate (i.e. inside and outside of canopies), and n_i is the proportional abundance of substrate (Ivlev 1961)]. Differences in bite rates (bites per min) and E_i inside and outside of *Liagora* canopies were compared using t -tests in the stats package [R software (R Core Team 2014)].

Experimental manipulation of *Liagora* canopy and herbivory on *Lobophora* cover

We identified 50 individuals of *Lobophora* within *Liagora* canopies at Lighthouse North in April–May 2013, and measured the canopy heights. We randomly selected half of the *Lobophora* individuals and removed the overstory canopy of *Liagora*, while the other half remained intact. Each individual of *Lobophora* was tagged, photographed and the surface area measured using Image-J software (US National Institutes of Health, Bethesda, MD), with two stainless steel nails on either side of each individual as reference points for size calibration. The surface area of each individual *Lobophora* was measured at 0-, 5- and 12-day intervals, and differences between treatments tested using a repeated-measures ANOVA in the stats package [R software (R Core Team 2014)].

Herbivore-exclusion experiments

To explore the role of herbivory in influencing *Lobophora* cover, we conducted additional caging experiments to exclude the effects of large herbivorous fish. Using a mould, we created tiles (10 × 10 cm) with equally spaced exposed and crevice surfaces (1-cm depth) to mimic small-scale micro-complexity observed on the reef (Fig. S1). Tiles were assigned to three treatments: caged, open, and partially caged, with replicate plots ($n = 5$ per treatment) separated by ≥ 1 m and interspersed along the benthos at a depth of ~ 7 m. The cages and partially closed cages measured 20 × 20 × 30 cm, and were constructed from PVC-coated galvanised steel, with a 2.5 × 2.5-cm mesh size. The partially closed cage had part of the roof and two sides removed to create large holes. Un-preconditioned tiles were deployed

facing upright ~ 5 cm above the benthos in April 2013, photographed in July 2013 (100 days following deployment), and percent cover of *Lobophora* quantified in the exposed and crevice microhabitats among treatments from the photographs. Significant differences in the percent cover of *Lobophora* among treatment and microhabitats (crevice vs. exposed surfaces) were tested using a two-way ANOVA, and significant differences among treatments tested using a Tukey's honest significant difference post hoc test using the stats package, R software [R software (R Core Team 2014)].

Results

Temporal trends in macroalgal cover

Baseline data recorded prior to typhoon Bopha in February 2012 indicated low macroalgal cover at all three sites ($< 2.3\%$), consisting entirely of *Halimeda* spp. within the understory of branching acroporid corals. Coral cover ranged from 64 % at Ngederrak South to 77 % at Lighthouse North (Fig. 2a). No *Lobophora* or *Liagora* were recorded at any of the three sites (Fig. 2b, c). Following Typhoon Bopha, which struck on 2 December 2012, our surveys revealed a near complete loss of coral at all sites (Fig. 3a). Blooms of *Liagora* were observed following the typhoon in late December 2012 (G. Mereb, Palau International Coral Reef Center, personal communication). By February 2013, *Liagora* was the dominant benthic cover, ranging between 7.4 and 38.6 % (Fig. 2b; Table S1). Subsequent surveys in April 2013 revealed a 62.4–95.9 % decline in *Liagora* cover as the bloom passed its peak (Fig. 2b), coinciding with the appearance of *Lobophora*, ranging between 3.9 and 10.9 % (Fig. 2c). By September, *Liagora* was completely absent (Fig. 2b), yet *Lobophora* continued to increase throughout September and October 2013 (Fig. 2c), reaching a maximum of 41.5 % by April 2014 (12 months after the first sighting). *Lobophora* persisted at the study sites until October 2014 at the last survey date, 18 months after it was first observed, and 22 months following the typhoon. Repeat surveys conducted at three additional adjacent sites (Fig. 1) that lacked *Liagora* indicated a complete absence of *Lobophora* throughout the study period (Table S1).

Habitat availability beneath *Liagora* canopies and distribution of *Lobophora* on the reef

The proportion of substrate within the 'swept' area of *Liagora* canopies varied from 59 % at Lighthouse North to 0.1 % at Ngederrak North (Fig. 4a). Despite such variability in *Liagora* canopies, the distribution of *Lobophora* was non-random at all sites, with higher abundance

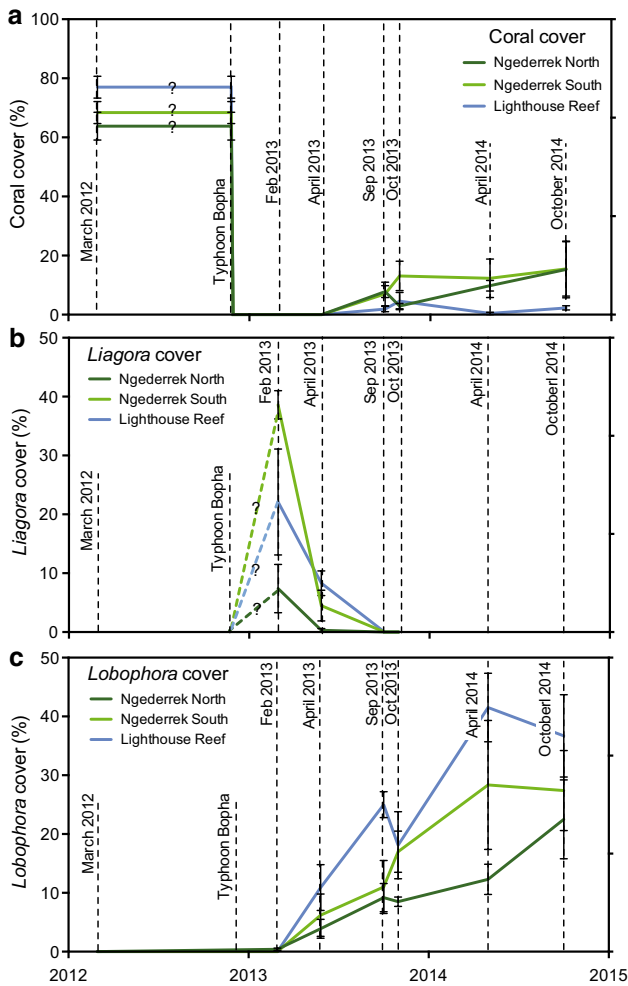


Fig. 2 Percent cover of **a** coral, **b** *Liagora*, **c** *Lobophora* at Lighthouse North, Ngederrek South and Ngederrek North between 2012 and 2014 (\pm SE). Question marks indicate presumed trajectories in the absence of survey data

of *Lobophora* occurring within canopies (Fig. 4a) than would have been expected by chance (Lighthouse North $\chi^2 = 48.2$, $z = 6.94$, $p < 0.001$; Ngederrak South $\chi^2 = 109.5$, $z = 10.47$, $p < 0.001$; Ngederrak North $\chi^2 = 8.3$, $z = 2.9$, $p < 0.01$). Measurements at Lighthouse North indicated an average sweep radius of 11.9 ± 0.9 cm per *Liagora* individual ($n = 181$). Most *Lobophora* were found close to the centre of canopies, with an average distance of 2.9 ± 0.8 cm from the holdfast ($n = 53$). Significant differences were observed in the size structure of *Lobophora* inside and outside of canopies (Fig. 4b; Kolmogorov–Smirnov test, $D = 0.39$, $p < 0.001$), in that a higher proportion of smaller individuals were recorded outside of *Liagora* canopies. Mean size of *Lobophora* inside of canopies ($n = 93$) was significantly higher than outside (19.3 ± 0.7 vs. 14.5 ± 0.8 mm, t -test = 4.16, $n = 101$, $p < 0.001$).

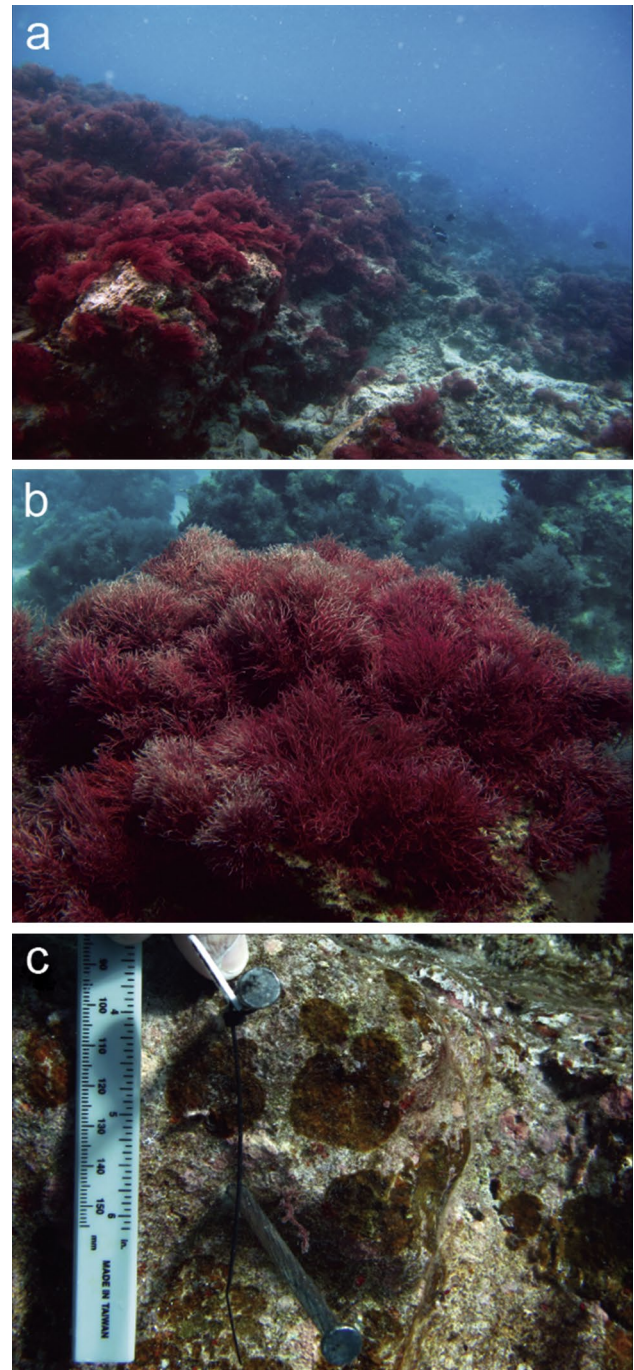
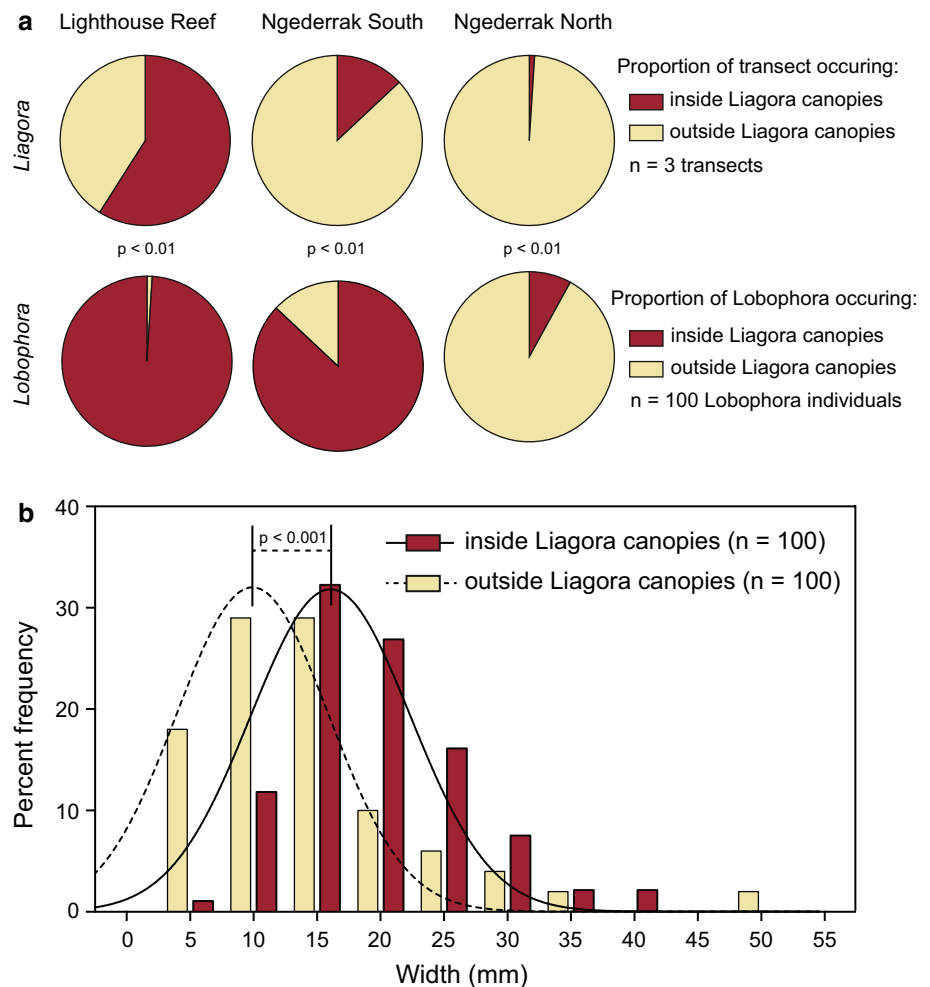


Fig. 3 **a** High cover of *Liagora* canopies following typhoon Bopha and subsequent loss of coral (February 2013), **b** canopies formed by individual *Liagora* plants attached by a single holdfast (February 2013) and **c** recruits of *Lobophora* visible following removal of *Liagora* canopies (April 2013)

Patterns of herbivore grazing on *Liagora* canopies

Bite rates of *C. striatus* were sixfold higher outside of canopies (21 ± 6.6 bites min^{-1} ; Fig. 5a) than within *Liagora* canopies (3.6 ± 2.5 bites min^{-1} , t -test = 12.72, $p < 0.001$).

Fig. 4 **a** Proportion of substrate within the ‘swept’ area of *Liagora* canopies vs. outside canopies ($n = 3$ transects) and the proportion of *Lobophora* occurring inside and outside of *Liagora* canopies ($n = 100$ individuals), and **b** size frequency distributions of *Lobophora* individuals inside and outside of *Liagora* canopies



Bite rates of *C. sordidus* were lower than that of *C. striatus* (Fig. 5b) yet were also significantly higher outside of *Liagora* canopies (4 ± 2.9 bites min^{-1}) than within canopies (1.6 ± 1.9 bites min^{-1} , t -test = 3.84, $p < 0.01$). *C. striatus* exhibited a clear avoidance of *Liagora* canopies compared with outside of *Liagora* canopies (Fig. 5c; t -test = 10.45, $p < 0.001$), and a similar pattern was observed with *C. sordidus* (Fig. 5d; t -test = 3.57, $p < 0.01$).

Grazing impact on *Lobophora* growth

Experimental removal of the *Liagora* canopy reversed the direction of *Lobophora* growth from positive to negative. *Lobophora* continued to grow under the *Liagora* canopy, with an average increase in surface area of 51.7 ± 8.7 % in 12 days (Fig. 6a). In contrast, *Lobophora* with the overstorey canopy removed were reduced to 53.1 % of their initial size within 12 days of the canopy removal (Fig. 6a), resulting in a clear and significant difference between treatments (repeated-measures ANOVA, $F_{2,98} = 33.42$, $p < 0.001$).

Of the 25 *Lobophora* individuals in the canopy-removal treatment, reductions of surface area were associated with evidence of continuous scrape marks associated with parrotfish feeding in all individuals (Fig. 6a). The remnant sections of *Lobophora* appeared visually unaffected, with no signs of pigment loss throughout repeated observations.

Herbivore-exclusion experiments

A significant difference was observed in the cover of *Lobophora* among herbivory treatments (two-way ANOVA, $F_{1,2} = 5.774$, $p < 0.001$), but no significant differences were observed among microhabitats (exposed or crevices) or herbivory \times microhabitat interactions (Fig. 6b). Post hoc tests revealed no significant difference in the cover of *Lobophora* among open and partially caged treatments, while a significant difference was observed between caged treatments and open ($p < 0.01$) and partially caged treatments ($p < 0.05$), indicating that the cover of *Lobophora* was higher when herbivores were excluded (Fig. 6b).

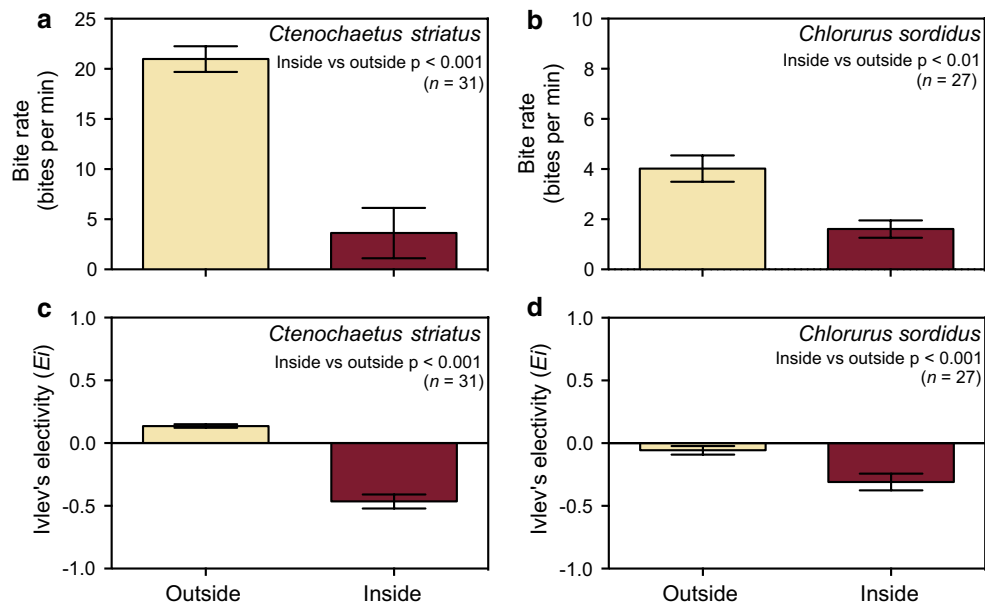


Fig. 5 Bite rates of **a** *Ctenochaetus striatus* ($n = 31$) and **b** *Chlorurus sordidus* ($n = 27$) inside and outside of *Liagora* canopies (\pm SE), and electivity (Ivlev's E_i) of **c** *C. striatus* and **d** *C. sordidus* inside and outside of *Liagora* canopies (\pm SE)

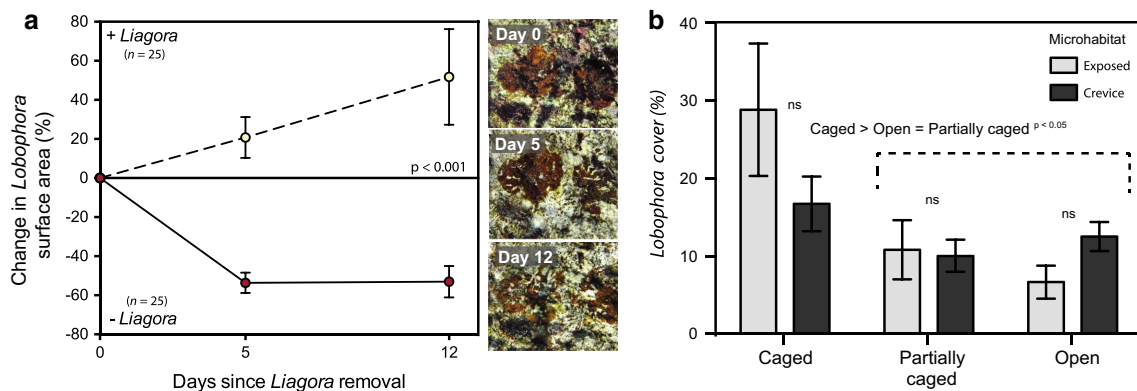


Fig. 6 **a** Change in surface area (percent cover) of *Lobophora* recruits ($n = 25$ per treatment) through time following experimental removal of *Liagora* canopies and controls (\pm SE) and time series (days 0–12) of an individual tagged *Lobophora* with parrotfish bite

marks following removal of *Liagora* canopy on day 0 and **b** percent cover of *Lobophora* after 100 days in exposed and crevice microhabitats of tiles deployed in caged, partially caged and open treatments (\pm SE, $n = 5$ per treatment)

Discussion

Temporary and persistent shifts from coral to macroalgal states have been observed following disturbance on coral reefs (e.g. Diaz-Pulido et al. 2009; Done 1992; Hughes 1994). Here, we define a phase shift as a marked change in the community structure of a coral reef as first defined by Done (1992). Importantly, the existence of a phase shift makes no assertion about stability or the presence of alternate attractors (Mumby et al. 2013b; Petraitis and Dudgeon 2004). The mechanisms influencing patterns of succession and persistence of coral—macroalgal phase shifts

are largely unknown. Here, we report a case of phase shift facilitation made possible by the response of *Liagora* to catastrophic typhoon disturbance that removed living coral. In the wake of typhoon Bopha in December 2012, coral cover on the eastern reefs of Palau declined from ~70 to <1 % cover. Consistent with previous studies in the Caribbean region (e.g. Hughes 1994; Woodley et al. 1981), blooms of *Liagora* were observed across impacted sites. By late February 2013, three months after typhoon Bopha, we documented a phase shift to monospecific canopies of *Liagora*, reaching a maximum of 38.6 % cover. The extent of the *Liagora* bloom was primarily determined by the degree of

wave exposure, in that highest *Liagora* cover was observed at highly exposed sites (G. Roff, unpublished data). By April 2013, the *Liagora* bloom had started to decline. However, a second and more persistent macroalga, *Lobophora variegata*, had established under the *Liagora* canopy and continued to increase throughout the study, reaching up to 41.5 % cover, and persisting for over 18 months following the first observations. Through a combination of observation and experiments we conclude that the secondary succession of *Lobophora* was facilitated by the *Liagora* canopy, which offered an ephemeral refuge to the understory brown alga from intense herbivory. Previous investigations of associational escapes in macroalgae have been studied on a scale of millimetres (i.e. epiphytic associations) or several centimetres (i.e. neighbouring associations), and focused on explaining patterns of distribution and maintenance of diversity within algal assemblages (e.g. Hay 1986; Littler et al. 1986; Pfister and Hay 1988). Here, we identify a novel associational escape that resulted in a larger community-scale phase shift to *Lobophora* dominance.

Several lines of evidence led us to conclude that *Liagora* canopies facilitated the secondary succession of *Lobophora*. First, the distribution of *Lobophora* was non-random, in that *Lobophora* occurred more frequently within than outside of *Liagora* canopies. Secondly, the size distribution of *Lobophora* within canopies was consistently larger than those outside of canopies. Thirdly, most *Lobophora* were found closer to the main holdfast rather than around peripheries of *Liagora* canopies, where they were more susceptible to herbivory. Fourth, direct measurements of bite rates of two common herbivores were higher outside than inside of canopies, and both actively avoided feeding within *Liagora* canopies. Fifth, *Lobophora* is seasonally abundant from November up to and including April in Micronesia (Tsuda 1972), making the timing of the *Lobophora* increase largely consistent with facilitation and inconsistent with seasonality (*Lobophora* would usually decrease from April to September). Sixth, removal of *Liagora* canopies resulted in a significant loss of *Lobophora* through herbivory whereas *Lobophora* continued to grow when the *Liagora* canopy remained intact. Seventh, and perhaps most conclusively, the cover of *Lobophora* was higher in tiles that were deployed in caged treatments than in open or partially caged treatments, indicating that while *Lobophora* was present in all treatments after 100 days, exclusion of herbivores resulted in a significantly higher cover of *Lobophora*. Finally, repeat surveys of exposed *Lobophora* revealed clear evidence of scrape marks associated with parrotfish feeding within days of removing *Liagora* canopies ($n = 25$ individuals). From this, we infer that grazing parrotfish were the primary cause of the reduction in *Lobophora* following canopy removal. While herbivory has been implicated in the removal of *Lobophora*, previous

studies have implicated browsing species (e.g. *Siganus doliatus* and *Kyphosus vaigiensis*) as primary consumers (Bennett et al. 2010). Our results provide an interesting example of grazing species influencing the distribution and abundance of a brown alga on Indo-Pacific reefs.

Importantly, the emergence of *Lobophora* is not simply a response to mass coral mortality because a previous mass bleaching event at our study sites (Golbuu et al. 2007), that resulted in a similar loss of coral but without a *Liagora* bloom, did not result in a rise of *Lobophora* (Y. Golbuu, personal observation). Moreover, only those storm-damaged sites that resulted in a *Liagora* bloom were found to undergo a phase shift towards *Lobophora*. Collectively, these results provide strong evidence that *Liagora* canopies provided a refuge from herbivory, driving patterns of recruit survival and growth in *Lobophora*. These results are consistent with associational plant refuges against herbivores previously documented in both temperate (Hay 1986; Pfister and Hay 1988; Turner 1983) and tropical environments (Littler et al. 1986).

Through selective herbivory on seedlings and saplings, herbivores are able to alter patterns of ecological succession (Huntly 1991). This influence on community development occurs through several mechanisms. Firstly, the spatial distribution of palatable and unpalatable plants can affect herbivore foraging behaviour, in turn affecting patterns of survival of mixed plant assemblages (e.g. Hay 1986; Hixon and Brostoff 1996; Pfister and Hay 1988). Secondly, plants can influence sapling survival through habitat amelioration from abiotic extremes, which ultimately influences the spatial distribution of communities (e.g. Gomez-Aparicio et al. 2008; Weltzin and McPherson 1999). Thirdly, the structure of plants can provide a physical refuge for new recruits from herbivory (e.g. Fuentes et al. 1986; Harris et al. 1984; Turner 1983). While all three processes could feasibly have contributed to facilitation in our study, our results indicate that physical refuge from herbivory was likely the primary mechanism involved in driving the secondary succession of *Lobophora*. Similar processes have been documented following storm disturbance in kelp forests, where early successional dominant turf algae provide refuge from herbivores for kelp sporophytes (Harris et al. 1984).

Previous studies of the dynamics of *Lobophora* on Indo-Pacific reefs have found it to be strongly limited in areas of high herbivory (Diaz-Pulido and McCook 2003; Verges et al. 2011). Indeed, previous surveys of our study sites and extensive surveys around Palau have not reported significant populations of *Lobophora* in this habitat (though it is found in shallow backreefs). Moreover, *Lobophora* did not bloom at sites that were unaffected by typhoon Bopha. This raises the question, how did the *Lobophora* canopy continue to expand even after the *Liagora* declined, particularly seeing as experimental manipulation of the canopy

led to a reduction in *Lobophora* size? We hypothesize a duality of explanation. First, the density of *Liagora* was high, reaching ~40 % cover, thereby providing a large, albeit ephemeral, refuge from herbivory. Second, while *Lobophora* can reproduce sexually and by fragmentation, colonisation tends to occur from vegetative growth along the marginal meristem from points of establishment, in that the rate of expansion increases with the patch size of *Lobophora* (van Steveninck and Breeman 1987). Thus, we hypothesize that local patches of *Lobophora* were able to become large enough in the presence of *Liagora* such that population growth could continue even when subjected to a moderately high herbivore regime once the *Liagora* died off. Such size-escape thresholds from herbivory have been previously documented in temperate and tropical macroalgae (e.g. Doropoulos et al. 2013; Lubchenco 1983), and both grazing and browsing herbivores avoid high-density patches of macroalgae (Hoey and Bellwood 2011). Had the *Liagora* bloom died back earlier, when *Lobophora* patches were smaller, the outcome may have been different as herbivory might plausibly have prevented a net increase in *Lobophora* population size.

The recovery of kelp forests after storm damage involves a facilitated primary succession (Harris et al. 1984), but to our knowledge, this is the first report of facilitated secondary succession towards a phase shift following acute disturbance. A phase shift in favour of *Lobophora* is a cause for concern. While *Liagora* is an ephemeral alga (Hughes 1994; e.g. Woodley et al. 1981), *Lobophora* is considered to be one of the strongest competitors for space on coral reefs (Nugues and Bak 2006), and is generally unpalatable to herbivores in decumbent growth form (Coen and Tanner 1989). The encrusting growth of *Lobophora* is competitively dominant (van Steveninck et al. 1988), and through allelopathic mechanisms (Rasher and Hay 2010), *Lobophora* is able to negatively impact upon multiple coral reef organisms, including corals (Diaz-Pulido et al. 2011; Lobel and Ogden 1981; Rasher and Hay 2010), sponges (Graham et al. 2013) and other macroalgal taxa (Brock 1979). While *Lobophora* is commonly found on forereefs in the Caribbean (e.g. Renken et al. 2010), blooms of it tend to be confined to inshore and somewhat eutrophic reefs in the Pacific (e.g. Diaz-Pulido et al. 2009). Palauan reefs tend to have relatively high herbivory (Mumby et al. 2013a) so the occurrence of *Lobophora* is unusual. That *Lobophora* has now persisted for over 18 months following the initial observations, and 22 months following the typhoon, raises questions as to the potential longer-term impacts of *Lobophora* in terms of competition with regenerating coral fragments that survived the initial typhoon disturbance, and potential effects on the recruitment of corals to the sites in successive recruitment events.

Many reefs have experienced algal phase shifts in the past few decades, raising questions over how to reverse such communities once established. While phase shifts on coral reefs might be difficult to reverse because of reinforcing biotic feedbacks (Mumby and Steneck 2008), a compelling argument has been made that acute disturbance events, such as typhoons, may lead to a reversal of phase shifts by removing macroalgal cover and promoting successful coral recruitment (Graham et al. 2013). Conversely, our results show that acute disturbance from typhoons may have the reverse effect, in becoming a mechanism by which persistent phase shifts are triggered, rather than reversed. While we do not suggest that this is a general phenomenon on coral reefs, the study of phase shift reversal should begin to consider the roles of algal facilitation.

Author contribution statement G. R., C. D., and P. J. M. conceived and designed the experiments. G. R., C. D., M. Z., A. R., R. S., Y. G. and P. J. M. performed the experiments. G. R., C. D., and M. Z. analysed the data. G. R. wrote the first draft of the manuscript; all authors provided editorial advice and contributed substantially to the final version of the manuscript.

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References

- Atsatt PR, O'Dowd DJ (1976) Plant defense guilds. *Science* 193:24–29
- Baumeister D, Callaway RM (2006) Facilitation by *Pinus flexilis* during succession: a hierarchy of mechanisms benefits other plant species. *Ecology* 87:1816–1830. doi:10.1890/0012-9658(2006)87[1816:Fbpfds]2.0.Co;2
- Bennett S, Verges A, Bellwood DR (2010) Branching coral as a macroalgal refuge in a marginal coral reef system. *Coral Reefs* 29:471–480
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193. doi:10.1016/0169-5347(94)90088-4
- Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976–1989 doi:10.1890/0012-9658(1997)078[1976:Tropii]2.0.Co;2
- Brock RE (1979) An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar Biol* 51:381–388
- Brooker RW et al (2008) Facilitation in plant communities: the past, the present, and the future. *J Ecol* 96:18–34. doi:10.1111/J.1365-2745.2007.01295.X
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119–125. doi:10.1016/S0169-5347(02)00045-9

- Callaway RM (1995) Positive interactions among plants. *Bot Rev* 61:306–349. doi:[10.1007/Bf02912621](https://doi.org/10.1007/Bf02912621)
- Callaway R, Nadkarni NM, Mahall BE (1991) Facilitation and interference of *Quercus douglash* on understory productivity in central California. *Ecology* 72:1484–1499
- Coen LD, Tanner CE (1989) Morphological variation and differential susceptibility to herbivory in the tropical brown alga *Lobophora variegata*. *Mar Ecol Prog Ser* 54:287–298
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- Diaz-Pulido G, McCook LJ (2003) Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. *Ecology* 84:2026–2033
- Diaz-Pulido G et al (2009) Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. *PLoS One* 4:e5239
- Diaz-Pulido G, Gouezo M, Tilbrook B, Dove S, Anthony KRN (2011) High CO₂ enhances the competitive strength of seaweeds over corals. *Ecol Lett* 14:156–162
- Dixon DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. *Science* 345:892–897
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132
- Doropoulos C, Hyndes G, Abecasis D, Verges A (2013) Herbivores strongly influences algal recruitment in both coral and algal dominated coral reef habitats. *Mar Ecol Prog Ser* 486:153–164
- Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecol Lett* 6:680–687. doi:[10.1046/J.1461-0248.2003.00494.X](https://doi.org/10.1046/J.1461-0248.2003.00494.X)
- Edmunds PJ, Carpenter RC (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proc Natl Acad Sci USA* 98:5067–5071
- Fuentes ER, Hoffman AJ, Poiana A, Alliende MC (1986) Vegetation change in large clearings: patterns in the Chilean matorral. *Oecologia* 68:358–366
- Golbuu Y et al (2007) Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. *Coral Reefs* 26:319–332. doi:[10.1007/s00338-007-0200-7](https://doi.org/10.1007/s00338-007-0200-7)
- Gomez-Aparicio L, Zamora R, Castro J, Hodar JA (2008) Facilitation of tree saplings by nurse plants: microhabitat amelioration or protection against herbivores? *J Veg Sci* 19:161–172. doi:[10.3170/2007-8-18347](https://doi.org/10.3170/2007-8-18347)
- Graham NAJ, Bellwood DR, Cinner JE, Hughes TP, Norstrom AV, Nystrom M (2013) Managing resilience to reverse phase shifts in coral reefs. *Front Ecol Environ* 11:541–548. doi:[10.1890/120305](https://doi.org/10.1890/120305)
- Harris LG, Ebeling AW, Laur DR, Rowley RJ (1984) Community recovery after storm damage—a case of facilitation in primary succession. *Science* 224:1336–1338. doi:[10.1126/Science.224.4655.1336](https://doi.org/10.1126/Science.224.4655.1336)
- Hay ME (1986) Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *Am Nat* 128:617–641
- Hay ME, Kappel QE, Fenical W (1994) Synergisms in plant defenses against herbivores: interactions of chemistry, calcification, and plant quality. *Ecology* 75:1714–1726
- Hixon MA, Brostoff WN (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecol Monogr* 66:67–90
- Hoey A, Bellwood D (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecol Lett* 14:267–273
- Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551
- Hughes TP et al (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17:360–365. doi:[10.1016/J.Cub.12.049](https://doi.org/10.1016/J.Cub.12.049)
- Huntly N (1991) Herbivores and the dynamics of communities and ecosystems. *Annu Rev Ecol Syst* 22:477–503. doi:[10.1146/Annurev.Ecolsys.22.1.477](https://doi.org/10.1146/Annurev.Ecolsys.22.1.477)
- Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New Haven
- Littler MM, Littler DS (1984) Models of tropical reef biogenesis: the contribution of algae. In: Round FE, Chapman DJ (eds) Progress in phycological research. Biopress, UK, pp 323–364
- Littler MM, Taylor PR, Littler DS (1986) Plant defense associations in the marine environment. *Coral Reefs* 5:63–71
- Lobel LMK, Ogden J (1981) Foraging by the herbivorous parrotfish *Sparisoma radians*. *Mar Biol* 64:173–183
- Lubchenco J (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64:1116–1123
- Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol Evol* 23:555–563. doi:[10.1016/j.tree.2008.06.011](https://doi.org/10.1016/j.tree.2008.06.011)
- Mumby PJ et al (2013a) Empirical relationships among resilience indicators on Micronesian coral reefs. *Coral Reefs* 32:213–226
- Mumby PJ, Steneck RS, Hastings A (2013b) Evidence for and against the existence of alternate attractors on coral reefs. *Oikos* 122:481–491
- Nugues MM, Bak RPM (2006) Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. *Mar Ecol Prog Ser* 315:75–86
- Paul VJ, Fenical W (1980) Toxic acetylene-containing lipids from the red marine alga *Liagora farinosa* Lamouroux. *Tetrahedron Lett* 21:3327–3330. doi:[10.1016/S0040-4039\(00\)78680-1](https://doi.org/10.1016/S0040-4039(00)78680-1)
- Petratits PS, Dudgeon SR (2004) Detection of alternative stable states in marine communities. *J Exp Mar Biol Ecol* 300:343–371. doi:[10.1016/j.jembe.2003.12.026](https://doi.org/10.1016/j.jembe.2003.12.026)
- Pfister CA, Hay ME (1988) Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia* 77:118–129
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rasher DB, Hay ME (2010) Chemically rich seaweeds poison corals when not controlled by herbivores. *Proc Natl Acad Sci USA* 107:9683–9688. doi:[10.1073/Pnas.0912095107](https://doi.org/10.1073/Pnas.0912095107)
- Renken H, Mumby PJ, Matsikis I, Edwards HJ (2010) Effects of physical environmental conditions on the patch dynamics of *Dictyota pulchella* and *Lobophora variegata* on Caribbean coral reefs. *Mar Ecol Prog Ser* 403:63–74. doi:[10.3354/Meps08441](https://doi.org/10.3354/Meps08441)
- Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities. *Bioscience* 51:235–246. doi:[10.1641/0006-3568\(2001\)051\[0235:Mfatso\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2001)051[0235:Mfatso]2.0.Co;2)
- Steneck RS, Dethier MN (1994) A functional-group approach to the structure of algal-dominated communities. *Oikos* 69:476–498
- Tsuda RT (1972) Marine benthic algae on Guam. 1. Phaeophyta *Micronesica* 8:87–115
- Turner T (1983) Facilitation as a successional mechanism in a rocky intertidal community. *Am Nat* 121:729–738
- van Steveninck EDD, Breeman AM (1987) Deep water vegetations of *Lobophora variegata* (Pheophyceae) in the coral reef of Curaçao—population dynamics in relation to the mass mortality of the sea urchin *Diadema antillarum*. *Mar Ecol Prog Ser* 36:81–90
- van Steveninck ED, Kamermans P, Breeman AM (1988) Importance of physical and biological processes in structuring tropical intertidal populations of *Lobophora variegata* (Phaeophyceae). *Mar Ecol Prog Ser* 44:77–84

- Verges A, Vanderklift MA, Doropoulos C, Hyndes GA (2011) Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. *Plos One* 6. doi:[10.1371/journal.pone.0017115](https://doi.org/10.1371/journal.pone.0017115)
- Wahl M, Hay ME (1995) Associational resistance and shared doom: effects of epibiosis on herbivory. *Oecologia* 102:329–340
- Weltzin JF, McPherson GR (1999) Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecol Monogr* 69:513–534. doi:[10.1890/0012-9615\(1999\)069\[0513:Focsra\]2.0.Co;2](https://doi.org/10.1890/0012-9615(1999)069[0513:Focsra]2.0.Co;2)
- Williams SL (1990) Experimental studies of Caribbean seagrass bed development. *Ecol Monogr* 60:449–469. doi:[10.2307/1943015](https://doi.org/10.2307/1943015)
- Woodley JD et al (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749–755
- Wulff JL (1997) Mutualisms among species of coral reef sponges. *Ecology* 78:146–159
- Wylie CR, Paul VJ (1988) Feeding preferences of the surgeonfish *Zebbrasoma flavescens* in relation to chemical defenses of tropical algae. *Mar Ecol Prog Ser* 45:23–32. doi:[10.3354/Meps045023](https://doi.org/10.3354/Meps045023)