Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs

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Ecosystem engineers that create habitats facilitate the coexistence of many interacting species. This biotic response to habitat engineering may result in non-intuitive cascading interactions, potentially including feedbacks to the engineer. Such feedback mechanisms, either positive or negative, may be especially important for the maintenance of biogenic habitats and their community-wide facilitation. Here, we describe the complex interactions and feedbacks that link marine habitat-forming engineers, the reef-building corals, and a group of herbivores, the parrotfishes; the latter preventing the overgrowth of macroalgae, a major competitor of corals. Using density data of eight parrotfish species on a Caribbean reef, we first describe the form of the response of parrotfish abundance to increasing topographic complexity generated by coral growth. Topographic complexity enhanced parrotfish abundance by promoting habitat suitability, but the shape (linear vs asymptotic) and strength of this response varied across species and size. Parrotfish grazing intensity, estimated from data on abundance and species-, size- and life phase-specific grazing rates also increased with topographic complexity despite an increase in the surface area over which parrotfish graze. Depending on fish species, this functional response was found to be linear or asymptotic. Using a simple analytical model we then explored the effects of topographic complexity and fishing pressure on coral-algal competition, with particular emphasis on the implications of non-linearities in the intensity of grazing. Simulations demonstrate that fishing and habitat degradation impair the performance of grazing, but that an asymptotic response of grazing intensity to topographic complexity increases the ecological resilience of coral reefs. Parrotfish and corals are mutually beneficial by creating a loop of positive, indirect feedbacks that maintain their own structure and function: coral growth promotes habitat suitability for parrotfish, concordantly enhancing grazing intensity, which in turn facilitates coral growth by reducing competitive exclusion by macroalgae. We conclude that the resilience of biogenic habitats is enhanced by non-linear biotic responses to engineering and by the emergence of reciprocal facilitation linking habitat engineering and response organisms.

Recent advances in ecology have emphasized the importance of positive interactions or facilitation in structuring biological communities (Bertness and Callaway 1994, Stachowicz 2001, Bruno et al. 2003). Facilitation occurs when one species makes local conditions more favorable for another species, either directly by reducing stress exposure, or indirectly through the mediation of predation risk, competitive interaction or resource availability for that species (Stachowicz 2001). One of the most striking examples of facilitation is the influence of organisms that create or modify habitats to the benefit of other species (Jones et al. 1997, Bruno and Bertness 2001). The community-wide facilitation of biogenic habitats (e.g. conifer forests, grasslands, coral reefs, mangroves, kelp forest) has long been recognized (MacArthur and MacArthur 1961, Whittaker 1975) but it is only recently that the concept of ecosystem engineering provided an appropriate framework for a more formal investigation (Jones et al. 2010).

Jones et al. (1994, 1997) define physical ecosystem engineering as the physical modification, maintenance or creation of habitats. An appealing aspect of this framework is that it explicitly recognizes the biotic outcomes of a change in physical conditions resulting from the activities of ecosystem engineers (Jones and Gutiérrez 2007, Jones et al. 2010). Physical engineering encompasses very different processes (Jones et al. 1994, Cuddington et al. 2007), the most obvious being the creation of habitat structure which controls the distribution and abundance of many species. Habitat-forming engineers create physical structures that enhance living space, resources and refuges from predators, thus facilitating coexistence and the emergence of biologically diverse, hierarchically organized communities (Stachowicz 2001, Bruno and Bertness 2001). Community-level facilitation by habitat engineering is likely to arise from the interplay of different processes, including the primary effects of the structural changes induced by the engineers, and consequent impacts on trophic and competitive interactions which cascade thorough the ecosystem, generating successive responses, such as secondary, tertiary, etc. (Jones et al. 1994, Jones and

Gutiérrez 2007, Thomsen et al. 2010). To date, however, most studies of habitat-forming engineers have taken a unidirectional approach, examining the primary effects of habitat engineering on response organisms, whereas only few works have examined more complex interaction pathways involving other organisms (Altieri et al. 2007, Thomsen et al. 2010). In particular, the importance of biotic feedbacks to ecosystem engineers and their consequences for engineering have received little attention (Jouquet et al. 2006, Cuddington et al. 2009).

Consideration of feedbacks is important because feedback loops, either positive or negative, favor the emergence of alternate community states (Scheffer and Carpenter 2003, Mumby and Steneck 2008). Biological feedbacks usually involve only a few species (Suding et al. 2004), but if they include habitat-forming engineers, any alteration of the interaction pathway may have important consequences for habitat structure with potential cascading impacts on many other biota. As ecosystem engineering is increasingly considered for the management of ecosystems (Byers et al. 2006, Hastings 2007), elucidating the pathways leading to feedbacks to habitat engineers is of particular importance for improved conservation and restoration of biogenic habitats. In addition, understanding the dynamics of the biotic response and consecutive impacts on habitat engineering is of primary importance for prioritizing management actions. Whereas many ecological interactions such as competition and predation are governed by non-linear, density-dependent processes (Turchin 2003), most studies examining the biotic effects of ecosystem engineers consider simplistic, linear relationships between the engineering activity and response organisms. As a result, little is known about the significance of non-linearity in facilitative interactions and their implications for engineering systems (Harley and O'Riley 2010).

Here, we investigate the complex dynamics that arise when ecosystem engineers and response organisms feedback on each other through non-linear, indirect facilitation. We explore these dynamics for a coral reef ecosystem and focus on the interactions between reef-building corals and herbivory, a critical ecosystem function maintaining coral reef resilience (Mumby et al. 2007, Mumby and Steneck 2008). Specifically, we explore the case of a consumer-mediated positive feedback (Lee 2006) for coral engineers, involving parrotfish (family: *Scaridae*), the dominant herbivores in many Caribbean reefs since the mass mortality of *Diadema* urchins (Carpenter 1986). Parrotfish play a crucial role in coral reef dynamics by maintaining macroalgae in a cropped state, thus facilitating coral growth and recruitment (Carpenter 1986, Diaz-Pulido and McCook 2004, Mumby and Steneck 2008). Grazer abundance generally increases with topographic complexity (Mumby and Wabnitz 2002, Howard et al. 2009, Harborne et al. 2011, Vergés et al. 2011) but the functional form of this relationship has received little attention despite being likely to vary with species, ontogeny, and the functional traits of the grazer. Because topographic complexity increases the three-dimensional surface area of a reef, an increase in complexity – for a given density of parrotfish – will tend to reduce the intensity of grazing (i.e. the grazing rate per unit area) because a given number of bites will be distributed over a larger area of reef. Thus, increasing topographic complexity exerts antagonistic forces on grazing intensity by simultaneously increasing the number of grazers (which increases grazing rate) while also mitigating the intensity of the grazing pressure. Given that the abundance of coral competitors (macroalgae) is determined by grazing intensity (Williams et al. 2001, Mumby 2006), it is difficult to predict, a priori, the directionality of a feedback caused by a simple change in reef structure; the outcome will depend on the relative importance of grazer abundance and grazing intensity. Moreover, the nature of the feedback might be expected to change with the functional form of the relationship between grazer abundance and topographic complexity.

Using a combination of empirical data and ecological models we explore the dynamics of feedbacks between coral engineers and herbivorous fish facilitators. We begin by examining the unidirectional response of parrotfishes to reef topographic complexity. We then explore the functional response of parrotfish grazing and the feedbacks that emerge through the action of the grazer assemblage on the coral ecosystem. We evaluate the overall ecosystem-level consequences of such feedbacks by modeling their effects on system resilience, and determine the significance of non-linearities in the maintenance of habitat engineering. Resilience is expressed in the context of important conservation issues; the harvesting of parrotfishes and deterioration of reef habitat quality (Hoegh-Guldberg et al. 2007, Wilson et al. 2008, Alvarez-Filip et al. 2009). Our results highlight the complex relationships between ecological feedbacks and acute and chronic disturbances experienced by biogenic habitats, and extend the conceptual framework of ecosystem engineers to include indirect, reciprocal positive interactions between engineers and non-engineer species.

Material and methods

Study site and data collection

We used field data gathered on the forereef of Glovers Atoll (16°44′N, 87°50′W) in Belize to investigate the response of both parrotfish abundance and grazing intensity to changes in reef topographic complexity. Fish surveys were conducted in April 2005 (Bejarano et al. 2011) at twenty five sites of comparable depth (~10 m) and >100 m distant from each other. The selected sites encompass reef habitats of variable topographic complexity, from structurally complex *Montastraea* reefs to flat hard-bottom dominated by gorgonians (Fig. 1). To avoid any confounding effects of fishing, all sites were located within a no-fishing reserve, which has been implemented since 1993 (Carter and Sedberry 1997). Moreover, the study sites include some of the highest grazing levels of the Caribbean (Mumby 2006). The abundance of parrotfish at each site was quantified using underwater visual census along 10–14 replicate belt transects, each measuring 30×4 m and placed >5 m apart. Total length was visually estimated to the nearest centimeter and life phase was recorded for each individual fish encountered. Individuals
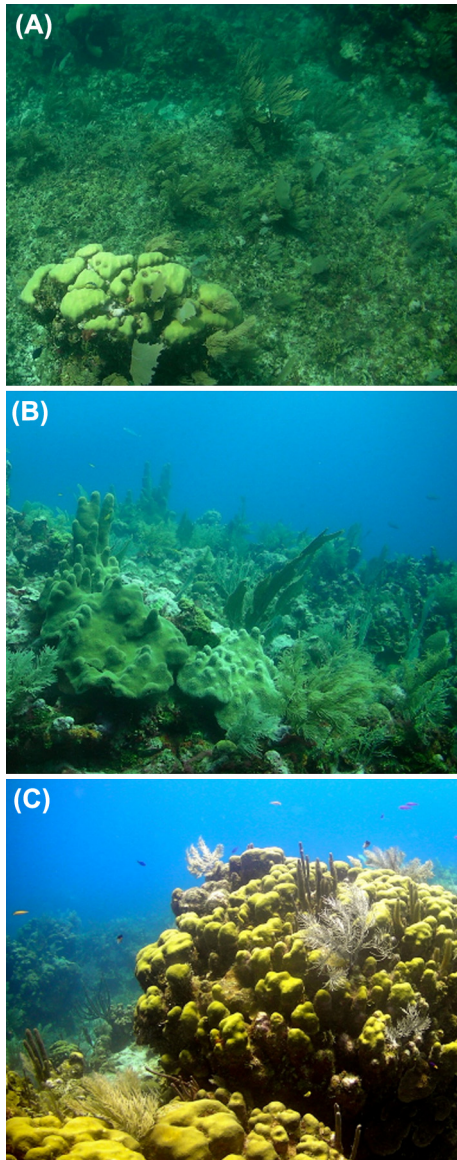
Figure 1. Typical seascapes of different topographic complexity on the forereef zone (depth ~ 10 m) of Glovers Reef Atoll. (A) Rubble flat non-consolidated reef (algal dominated); (B) medium-relief consolidated reef (mostly gorgonians and scattered coral colonies); (C) high-relief consolidated reef (*Montastraea* dominated reef with low macroalgal cover).

smaller than 4 cm were excluded from this analysis since very small fish are likely to be underestimated when using a 4-m width belt transect (Bozec et al. 2011). Restricting the analysis to parrotfish ≥ 4 cm also ensures that juveniles are effectively herbivores, since ontogenetic changes in the feeding mode occur in the early life stages of parrotfish (by 3.2 cm standard length for *Scarus* species, Bellwood 1988).

Reef topographic complexity was estimated at each site by assessing the rugosity (i.e. surface roughness) of the reef bottom using a modification of the 'chain and tape' method (Risk 1972). A chain of 4 m length was fitted to the contour of the substratum at randomly selected locations (n = 10 per site). Reef rugosity was calculated as the ratio of the length of the chain to the linear distance covered by the chain. As a result, the rugosity index increases

with topographic complexity, from 1 for a perfectly flat reef surface up to 3 for a highly rugose reef, higher rugosity values being rare on Caribbean reefs (Alvarez-Filip et al. 2009). Rugosity values in the 25 surveyed sites ranged from 1.05 to 2.15 with the complex reefs being dominated by massive colonies of *Montastraea annularis* although branching, pillar and encrusting corals also exist (Bejarano et al. 2011).

Response of parrotfish abundance to topographic complexity

Topographic complexity increases the surface area available for algal colonization, thus potentially enhancing food supply for herbivores. In addition, topographic complexity reduces the risk of predation for many fish by providing protective shelter (Hixon and Beets 1993, Beukers and Jones 1998). Hence, in more topographically complex reefs we expect the number of parrotfish to increase due to the combined effects of a reduced predation risk and higher levels of algal supply. We assumed that the response of parrotfish abundance to topographic complexity may follow two different models:

$$\text{model 1}: \ y = c_I + m(R - 1) \tag{1}$$

$$\text{model 2}: \ y = c_{II} + \frac{a(R - 1)}{1 + ab(R - 1)} \tag{2}$$

Model 1 is a simple linear model indicating that parrotfish abundance (y) increases with the rugosity index (R) defined on $[1, +\infty)$ at a constant rate (m) from an original abundance (c_I), a response assumed by coral reef studies that investigated fish-habitat relationships (Gratwicke and Speight 2005). Model 2 is a saturating function assuming that parrotfish abundance increases from an original abundance (c_{II}) at a decreasing rate to eventually asymptote at 1/b. The theoretical foundation of such a model is that fish abundance is unlikely to increase indefinitely at the same rate with reef rugosity due to density-dependent processes of competition for food and space, within or among parrotfish species.

We compared the likelihood of model 1 and 2 for describing the response of parrotfish abundance to reef rugosity. The two models were investigated for the overall abundance per site (i.e. for all parrotfish species combined) and for the two genera *Sparisoma* and *Scarus* separately. Since fish may respond differently to reef rugosity according to their body size, models were fitted by size classes for the most abundant species separately, and for the remaining species pooled together. For this purpose, four size classes were defined based on the size composition of parrotfish populations observed on the 25 sites (Supplementary material Appendix A1 Fig. A1): 4–7 cm, 8–12 cm, 13–20 cm and 21–40 cm. Models were fitted by non-linear parametric regression using the *nls* function of the R software (R Development Core Team). The *nls* function determines the least-squares estimates of the parameters of a model which provide the best fit to the observations (Ritz and Streibig 2008). For the two models, parameter means and

associated 95% percentile confidence intervals were determined by non-parametric bootstrapping (n = 999 bootstrap simulations). Response variables (i.e. abundance data) were square-root transformed to minimize departures from the assumptions of normality and variance homogeneity. The square-root transformation was also applied to the right-hand side of model 1 and 2 equations to preserve the shape (i.e. linear vs asymptotic) of the original relationship between fish abundance and rugosity. Fitted values were back-transformed for the graphical representations of model fits. Variance homogeneity and normality of residuals were evaluated for each model by means of graphical procedures (i.e. residuals vs fitted values plots and QQ plots of the standardized residuals).

The goodness of fit of the two competing models was assessed using a likelihood ratio test defined by:

$$Q = -2\left(\log L_{M0} - \log L_{Mi}\right)$$

where $\log L_{M0}$ and $\log L_{Mi}$ are the respective values of the maximized log-likelihood over the unknown parameters of a null model M_0 (with the mean as the prediction) and the model of interest M_i, given the data (Ritz and Streibig 2008). Q follows approximately a chi-square distribution with $df_{M0} - df_{Mi}$ degrees of freedom, where df_{M0} and df_{Mi} are the respective degrees of freedom of the null model and the model of interest. A fit was considered appropriate for $p < 0.001$. When both fits were supported by the data, higher support was afforded to the most parsimonious model using Akaike information criterion (AIC, Burnham and Anderson 2002), model 2 being penalized for using one parameter more than model 1. Since model 2 tends to be linear when parameter b tends to 0, AIC values were mostly used to decide if model 2 provided a significant improvement of linear fits. According to the rule-of-thumb of Burnham and Anderson (2002), model 2 was considered relevant if its AIC value was lower than that of model 1 with a difference greater than 2.

Functional response of parrotfish grazing intensity to topographic complexity

Parrotfishes comprise species-rich and functionally diverse assemblages (Bellwood and Choat 1990). In the Caribbean, some species, such as those in the genus *Scarus*, mostly graze diminutive algal turfs and crustose coralline algae. Algal turfs, which are a highly diverse functional group of filamentous algae and cyanobacteria (Steneck and Dethier 1994), require frequent grazing for their maintenance, as do crustose corallines. Other parrotfish species, particularly those in the genus *Sparisoma*, have a more varied diet and also consume substantial amounts of fleshy macroalgae such as *Dictyota* (Bruggemann et al. 1994). The grazing behavior of some Caribbean parrotfishes was initially modeled by Bruggemann (1995) and extended by Mumby (2006) to multiple species based on parrotfish feeding observations from Belize, Honduras and the Bahamas. This empirical model is based on species- and life phase-specific allometric relationships linking parrotfish body length to both bite rate (per hour) and mouth size (cm^2), and allows estimation of the grazing rate for each

individual (cm^2 h^{-1}). For n individuals of a particular species detected on a given transect, the overall grazing intensity (G) of that species is estimated by:

$$G = 100\% \; \frac{\sum_{i=1}^{n} g_i}{10^4 \times S \times R} \tag{3}$$

where g_i is the per capita grazing rate (cm^2 h^{-1}) of individual i, S is the planar surface area (m^2) covered by the transect (in our case, 120 m^2) and R the rugosity index estimated for the entire site. Note that $S \times R$ is the actual three-dimensional surface area of the belt transect used for the fish survey. As such, grazing intensity is scaled to the grazable area of the reef bottom, i.e. the actual surface area that can be colonized by algae. Grazing intensity is then expressed as a percentage of the actual surface area of a reef that is grazed per hour (% area h^{-1}). In a manner similar to parrotfish abundance, model 1 and 2 were fitted to the estimates of grazing intensity versus rugosity, 1) for the whole assemblage and 2) separately for the genera *Sparisoma* and *Scarus*.

Theoretical impacts of topographic complexity and fishing on coral–algal competition

Mumby et al. (2007) have previously described a set of ordinary differential equations that simulate the continuous competition for space between macroalgae (M) and coral (C), where algal turfs (T) are assumed to constitute the default seascape cover. Turf subsumes both algal turfs and crustose corallines, which essentially represents those algal functional groups that require frequent grazing. For a given reef area at any time, $M + C + T = 1$ so that only two equations are actually needed to represent the dynamics of the system:

$$\frac{dM}{dt} = aMC - \frac{gM}{M+T} + \gamma MT \tag{4}$$

$$\frac{dC}{dt} = rTC - dC - aMC \tag{5}$$

The model assumes that macroalgae overgrow coral and spread vegetatively over algal turfs at the respective rates a and γ. Fish herbivores graze macroalgae and turf without discrimination at a rate g, so that $gM/(M + T)$ is the proportion of grazing that affects macroalgae. Algal turfs are considered an early successional state of macroalgae and therefore algal turfs give rise to macroalgae if they are not grazed whereas grazing of macroalgae reverts the algal assemblage back to turfs. Corals recruit to and overgrow turf at a combined rate r and die with a natural mortality rate d. Space freed by coral mortality is recolonized by turf. The system can be used to describe how coral and macroalgal populations change over time for a given initial cover and grazing intensity (Mumby et al. 2007, Blackwood et al. 2011). When grazing is high, the system can be attracted towards two stable equilibrium states (coral or macroalgal dominated), depending on the initial conditions. At low

grazing levels, however, the system tends to be attracted by a single stable equilibrium (macroalgal dominated).

Blackwood et al. (2011) extended this model by describing the dynamics of parrotfish populations responding to habitat quality and fishing. In the present paper, we allow for greater flexibility and detail in the parameters governing grazing intensity by considering 1) different grazing behaviors of parrotfish, 2) different functional responses of grazing to topographic complexity and 3) fishing practices that target different parrotfish species.

Considering that *Scarus* spp. preferentially graze upon turf and that *Sparisoma* spp. graze upon both turf and macroalgae (Bruggemann et al. 1994, Mumby 2006, Burkepile and Hay 2008), the proportion of grazing that affects macroalgae and algal turf can be explicitly modeled as follows:

$$\frac{dM}{dt} = aMC - \frac{G_{spar}M}{M+T} + \left[\gamma - G_{scar} - \frac{G_{spar}T}{M+T}\right]MT \qquad (6)$$
$$- hurr\left(z_M M\right)$$

$$\frac{dC}{dt} = rTC - dC - aMC - hurr\left(z_C C\right) \qquad (7)$$

where G_{spar} and G_{scar} are the respective grazing intensities of parrotfish for the genera *Scarus* and *Sparisoma*. Similar to the original model, the first grazer–algae interaction term, i.e. $G_{spar}M/(M+T)$ represents the grazing intensity directly applied to macroalgae, but is now exclusively due to *Sparisoma*. The second interaction term, which must be greater than zero, represents the effect of both *Sparisoma* and *Scarus* grazing on turf, so that grazing slows the rate at which macroalgae emerge from algal turfs. In this way, G_{spar} represents the total grazing of *Sparisoma* partitioned across both macroalgae and algal turfs, according to their relative cover. In addition, the function 'hurr' was introduced to perturb the system by removing a proportion z_C and z_M of corals and macroalgae. A hurricane occurs in a given year when $U < 0.1$, where U is a random number sampled uniformly from the interval [0, 1]. Therefore, hurricanes with decadal return times stochastically perturb both coral and macroalgal populations, but are assumed not to affect reef rugosity when the reef is dominated by coral of massive morphology (Mumby et al. 2005), as is the case in the system modeled here.

To investigate the indirect effects of fishing and habitat engineering on coral–algal dynamics, grazing intensity for each genus (G_{gen}) was designed as a function of fishing rate (F) and rugosity (R) based on the two alternative model 1 and 2, given support from Glovers Atoll data:

$$G_{I,gen} = \left(1 - F_{gen}\right) \times \left[c_{I,gen} + m_{gen}\left(R - 1\right)\right] \qquad (8)$$

$$G_{II,gen} = \left(1 - F_{gen}\right) \times \left[c_{II,gen} + \frac{a_{gen}\left(R - 1\right)}{1 + a_{gen}b_{gen}\left(R - 1\right)}\right] \qquad (9)$$

with the parameters of model 1 (c_I and m) and model 2 (c_{II}, a and b) as estimated for the two genera from the

empirical data. F_{gen} allows for both genera to be fished at differing rates. Two types of fishing practice were considered: one that discriminates specific target species, which might represent spear-fishing, and a second, indiscriminate fishing that takes either species and better represents trapping (Hawkins and Roberts 2004).

Time simulations were undertaken across a full range of rugosity values and fishing rates for both fishing practices to determine the importance of the functional response of grazing intensity to reef rugosity on system resilience. For this purpose, scenarios of fishing/rugosity changes were tested for different grazing responses to rugosity following the significance of empirical relationships supported by Glovers Atoll data for *Sparisoma* and *Scarus*. Simulations were initiated from a coral-dominated state (specifically, with $C(0) = 0.1$ and $M(0) = 0.01$) and ran for 20 years with a 6-month time step. In the absence of disturbance (fishing and hurricanes), simulations invariably result in coral increasing to its non-zero equilibrial value (Mumby et al. 2007). Under disturbance regimes, an alternative scenario can arise: macroalgal cover may increase to its non-zero equilibrial value leading to a phase-shift from a coral-dominated to a macroalgal-dominated state. For every pair of fishing rate and rugosity values, one hundred simulations were performed to calculate the probability of a phase shift towards a macroalgal-dominated state under a decadal regime of hurricane disturbance (on average, once every 10 years). For each scenario, the probability of phase shift was estimated from the number of final states dominated by macroalgae. A 20-year time period was selected because realistically tracking changes in rugosity at low coral cover is difficult (Blackwood et al. 2011); reef structure will degrade slowly once corals cease to build skeleton but the actual rate of this process is unknown (Wilson et al. 2008). Parameterization for coral-macroalgal competition was taken from Mumby et al. (2007) which fitted the analytic solution to the equilibria of a more complex, field-tested simulation model. Symbols, definitions and values of the simulation model parameters are described in Supplementary material Appendix A2 Table A2.

Results

Numerical response of parrotfishes

Eight parrotfish species were sighted on a total of 258 transects. The parrotfish assemblage was dominated by *Scarus iserti* (4.28 ± 0.38 ind./120 m², mean ± SE), *Sparisoma aurofrenatum* (2.41 ± 0.16 ind/120 m²), and *Sparisoma viride* (1.12 ± 0.09 ind./120 m²), with the remaining five species occurring in smaller numbers (0.55 ind./120 m² in total, see details in Supplementary material Appendix A1 Table A1). The relationship between the overall abundance of parrotfish and reef rugosity was approximately linear (Fig. 2A) with a similar fit for model 1 and 2 but greater support for model 1 due to a lower AIC (Table 1A). However, relationships demonstrated different trends when analyzed separately for each genus. Whereas model 1 was clearly supported by the abundance of *Scarus* spp. (Fig. 2B, Table 1B), model 2 provided a better fit for
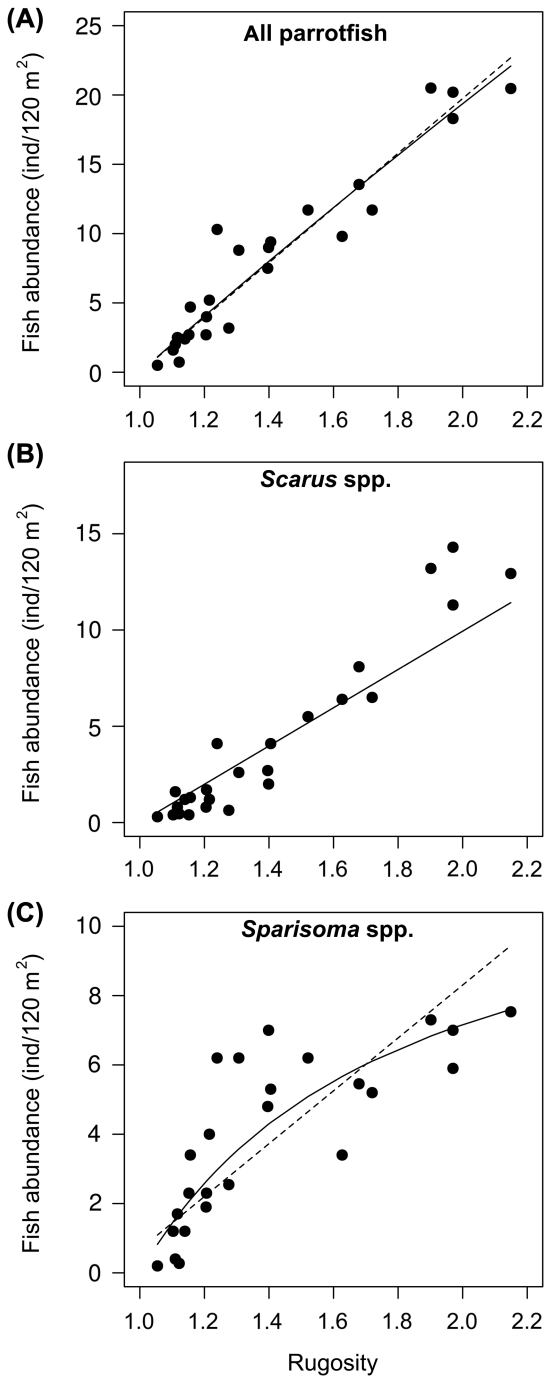
Figure 2. Relationship between reef rugosity and the abundance per site of (A) all parrotfish species combined, (B) *Scarus* spp. and (C) *Sparisoma* spp. Model 1 (dashed line) and model 2 (solid line) are represented when they provide an acceptable fit (p < 0.001, see Table 1).

Table 1. Statistics and parameter estimates of models 1 and 2 fitted to the response of parrotfish abundance to reef rugosity for (A) all parrotfish species combined, (B) *Scarus* spp. and (C) *Sparisoma* spp. For each case, the selected model is denoted by an asterisk.

	p[†]	AIC	Parameters	95% CI[‡]
(A) all species				
model 1*	< 0.001	25.74	$c_I = 0.00$	(0.00, 0.98)
			$m = 19.74$	(17.17, 21.59)
model 2	< 0.001	27.61	$c_{II} = 0.00$	(0.00, 0.87)
			$a = 20.46$	(17.30, 25.00)
			$b = 0.00$	(0.00, 0.01)
(B) *Scarus* spp.				
model 1*	< 0.001	29.52	$c_I = 0.00$	(0.00, 0.71)
			$m = 9.94$	(7.90, 11.27)
model 2	< 0.001	31.52	$c_{II} = 0.00$	(0.00, 0.55)
			$a = 9.94$	(8.19, 13.01)
			$b = 0.06$	(0.00, 0.04)
(C) *Sparisoma* spp.				
model 1	< 0.001	34.98	$c_I = 0.68$	(0.00, 1.50)
			$m = 7.63$	(5.46, 10.05
model 2*	< 0.001	29.74	$c_{II} = 0.00$	(0.00, 1.42)
			$a = 16.14$	(6.08, 23.60)
			$b = 0.08$	(0.00, 0.013)

[†]p-value of the likelihood ratio test with DF = 2 and DF = 3 for model 1 and 2 respectively.
[‡]95% percentile confidence interval determined by non-parametric bootstrapping.

was supported by *S. iserti* abundance, across the three size classes available for this species (Fig. 3A). The relationship was stronger for the abundance of the smallest individuals (4–7 cm) and decreased markedly as body length increased. In contrast, the relationship between rugosity and abundance of *S. aurofrenatum* (Fig. 3B) and *S. viride* (Fig. 3C) was stronger for the largest individuals (21–40 cm) with a greater support of model 1 for both *Sparisoma* species. Relationships with rugosity were weak for most of the other size classes, with inconsistent discrimination between model 1 and 2. The two competing models did not demonstrate acceptable fits for the abundance of the five other parrotfish species when combined together (Fig. 3D).

Response of grazing intensity

Mean grazing intensity at Glovers Atoll was $0.30 \pm 0.02\%$ area h^{-1} (mean ± SE) with *Sparisoma* spp. being the main contributor to the grazing process (70% of total) despite its lower abundance compared to *Scarus* spp. Both model 1 and 2 provided acceptable fits to the relationship between rugosity and the overall grazing intensity of parrotfish (Fig. 4A). Model 2, however, was better supported due to a lower AIC (Table 2A). Grazing intensity appeared linearly related to rugosity for *Scarus* spp. (Fig. 4B, Table 2B) but was clearly asymptotic for *Sparisoma* spp. (Fig. 4C, Table 2C) with a marked inflexion at intermediate levels of rugosity (around R = 1.5), thus disqualifying model 1 (p = 0.006).

Non-linear impacts of grazing on coral persistence

Time simulations of coral and macroalgal covers were performed according to two alternative fishing scenarios. In the first scenario, fishing did not discriminate between the

Sparisoma spp. (Fig. 2C, Table 1C). The selected models did not demonstrate clear departures from variance homogeneity and normality of residuals (Supplementary material Appendix A3 Fig. A3).

Further exploration of the relationship between rugosity and abundance, this time disaggregated among parrotfish species and size classes, revealed marked variability (Fig. 3, Supplementary material Appendix A4 Table A4). Model 1

Figure 3. Relationship between reef rugosity and the abundance per site for different size classes of (A) *Scarus iserti*, (B) *Sparisoma aurofrenatum*, (C) *Sparisoma viride* and (D) all other parrotfish species combined. See Fig. 2 legend and Supplementary material Appendix A4 Table A4 for fitness statistics.

two parrotfish genera, and in the second, fishing exclusively targeted *Sparisoma* which is the larger-bodied group and more commercially desirable. The two fishing scenarios were first compared (Fig. 5) for systems in which grazing intensity of *Sparisoma* and *Scarus*, respectively, responds asymptotically (Eq. 9) and linearly (Eq. 8) to rugosity,

according to the best-fit empirical models from Glovers Atoll. To highlight the importance of non-linearity for coral persistence, those scenarios were contrasted with systems in which grazing intensity of both genera responds linearly to rugosity (Fig. 6). For all scenarios, Eq. 8–9 were parameterized using the regression parameters estimated from

Figure 4. Relationship between reef rugosity and the grazing intensity per site estimated for (A) all parrotfish species combined, (B) *Scarus* species and (C) *Sparisoma* species. See Fig. 2 legend and Table 2 for fitness statistics.
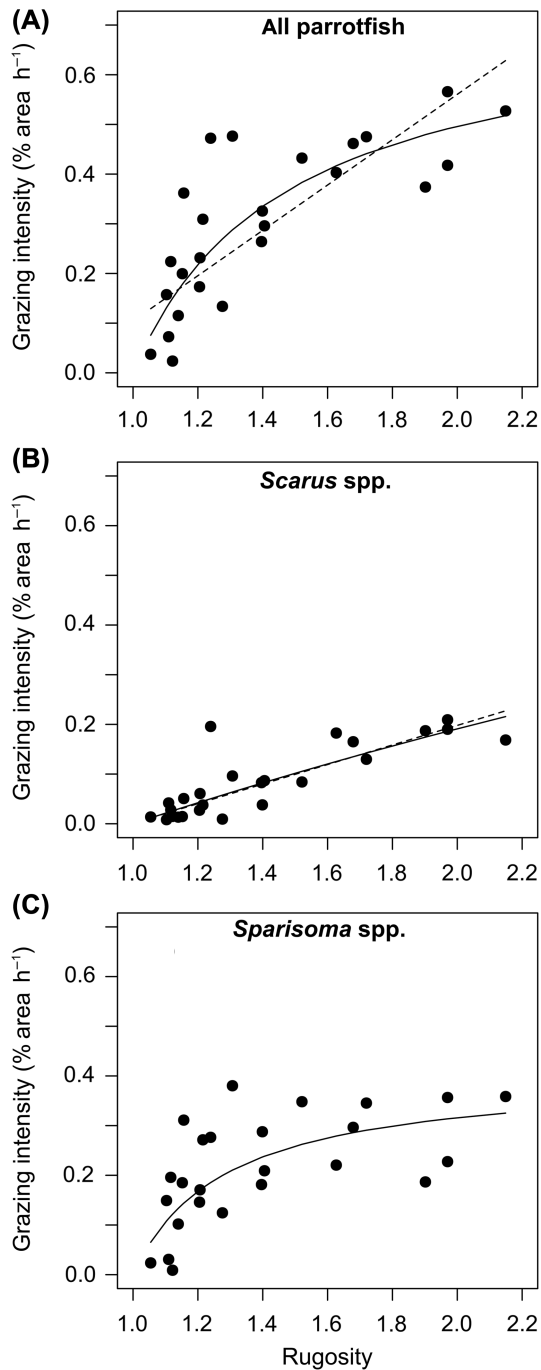
Table 2. Statistics and parameter estimates of model 1 and 2 fitted to the response of parrotfish grazing intensity to reef rugosity for (A) all parrotfish species combined, (B) *Scarus* spp. and (C) *Sparisoma* spp. For each case, the selected model is denoted by an asterisk.

	$p^{†}$	AIC	Parameters	95% CI‡
(A) all species				
model 1	<0.001	-33.80	$c_I = 0.10$	(0.04, 0.18)
			$m = 0.45$	(0.29, 0.64)
model 2*	<0.001	-38.20	$c_{II} = 0.00$	(0.00, 0.13)
			$a = 1.55$	(0.42, 2.15)
			$b = 1.37$	(0.00, 1.95)
(B) *Scarus* spp.				
model 1*	<0.001	-58.03	$c_I = 0.00$	(0.00, 0.02)
			$m = 0.20$	(0.15, 0.24)
model 2	<0.001	-56.22	$c_{II} = 0.00$	(0.00, 0.02)
			$a = 0.22$	(0.15, 0.31)
			$b = 0.62$	(0.00, 2.83)
C) *Sparisoma* spp.				
model 1	0.006	-32.16	$c_I = 0.10$	(0.05, 0.16)
			$m = 0.25$	(0.12, 0.38)
model 2*	<0.001	-36.34	$c_{II} = 0.00$	(0.00, 0.13)
			$a = 1.43$	(0.23, 2.49)
			$b = 2.47$	(0.00, 3.76)

†p-value of the likelihood ratio test with DF = 2 and DF = 3 for model 1 and 2 respectively.
‡95% percentile confidence interval determined by non-parametric bootstrapping.

the empirical data set (Table 2B–C, Supplementary material Appendix A2 Table A2).

Invariably, phase shifts towards macroalgal-dominated states occurred more readily at low levels of rugosity, and when there was greater fishing pressure. Systems in which the fishing pressure was distributed evenly over both genera (indiscriminate fishing practices, Fig. 5A and 6A) were more resilient than systems where fishing focused solely on *Sparisoma* (discriminate fishing practices, Fig. 5B and 6B).

Figure 5. Fishing effects and non-linear impacts of changing rugosity on coral persistence. Indiscriminate fishing (A) is compared to the scenario whereby *Sparisoma* is fished exclusively (B), for systems in which *Sparisoma* grazing intensity has an asymptotic relationship with rugosity (Eq. 9). Panels display contour maps of the probability (see key) of phase shift from a coral-dominated (circled C) to a macroalgal-dominated (circled M) state as estimated by 100 simulations for different values of rugosity (horizontal axis) and fishing pressure (vertical axis) over a twenty-years timeframe.

(A) Indiscriminate fishing (*Scarus + Sparisoma*)
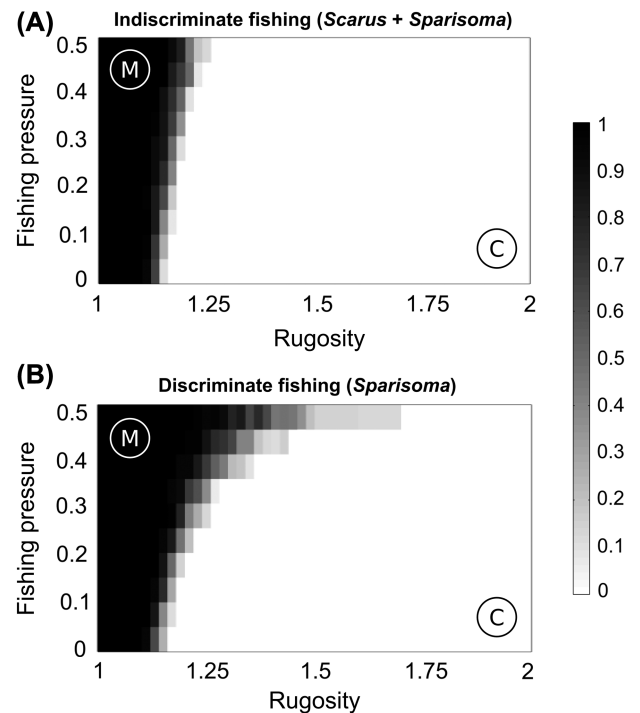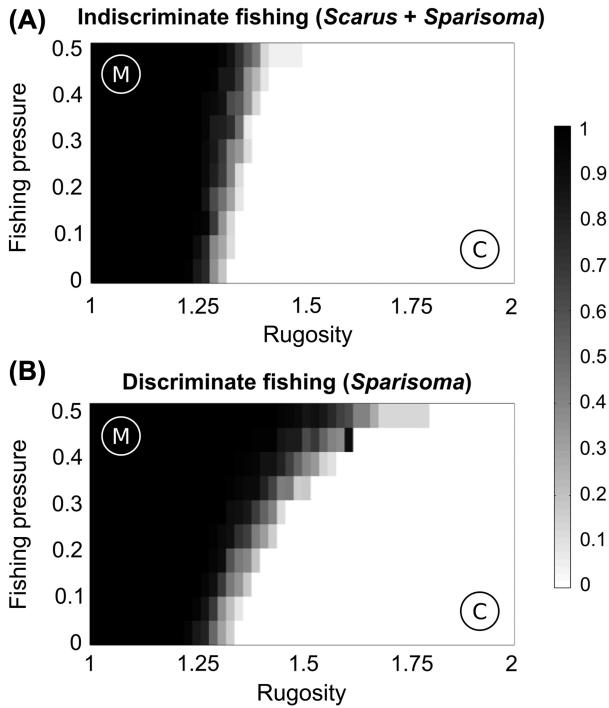
(B) Discriminate fishing (*Sparisoma*)

Figure 6. Fishing effects and linear impacts of changing rugosity on coral persistence. Indiscriminate fishing (A) is compared to the scenario whereby *Sparisoma* is fished exclusively (B), for systems in which *Sparisoma* grazing intensity has a linear relationship with rugosity (Eq. 8). See Fig. 5 legend.

For similar levels of rugosity and fishing pressure, systems in which *Sparisoma* abundance had an asymptotic relationship with rugosity were more resilient for both fishing scenarios, as indicated by a lower probability of phase shift (Fig. 5A–B) compared to a linear response to rugosity (Fig. 6A–B). In all scenarios, phase shifts were highly sensitive to rugosity levels, with transitions between high probability of coral dominance and macroalgal dominance occurring over a narrow range of rugosity.

Discussion

Understanding the biotic consequences of ecosystem engineering and how, in turn, the biotic response affects the engineering activity requires consideration of key interactions, whether they are positive or negative, direct or indirect, linear or non-linear, and the potential for feedbacks to the habitat engineers. Using empirical data to inform the construction of mathematical models, we have shown that complex interactions and feedbacks drive the functional relationships between habitat-forming engineers (reef-building corals) and key response organisms (parrotfish), and that non-linearities in their functional relationships (between rugosity and grazing intensity) influence the resilience of the system.

Feedbacks are important mechanisms that can force a system into divergent basins of attraction and contribute to its stability (Scheffer and Carpenter 2003, Mumby and Steneck 2008). A number of feedbacks tend to attract reef systems toward either coral-dominated or algal-dominated

equilibria, although such equilibria are rarely realized because of frequent disturbance events. For example, high macroalgal levels limit coral recruitment (Diaz-Pulido and McCook 2004) thus facilitating macroalgal expansion when coral cover declines (Mumby et al. 2007). Our results support the view that feedbacks involving habitat structure and herbivory play an important role in the stability of alternate states on reefs (Lee 2006, Mumby and Steneck 2008, Hoey and Bellwood 2011). Coral growth produces topographic complexity which promotes habitat suitability for parrotfish populations. Larger parrotfish populations enhance grazing intensity, facilitating coral growth and thereby further enhancing habitat structure. As a result, parrotfish and coral are mutually beneficial by creating a loop of positive feedbacks that maintains their structure and function (Fig. 7A). This loop of facilitative processes may lead to the self-reinforcement of a coral-dominated state, thus increasing the ecological resilience of the system (Levin and Lubchenco 2008) by keeping the reef in a coral-rich basin of attraction.

Our results demonstrate that the form (e.g. linear vs non-linear) of feedback interactions strongly influences the emergent behavior of the system. On Glovers Atoll, the abundance of *Scarus iserti*, the dominant species, increased linearly with reef rugosity. The numerical response of the two main *Sparisoma* species, *S. aurofrenatum* and *S. viride*, was less obvious, except for the largest size class (21–40 cm). However, when abundance of those two species were pooled together, the numerical response of *Sparisoma* appeared asymptotic. The mechanisms driving the different responses of each species to topographic complexity are unclear at this stage but likely involve relative risk of predation and competition for refuges. A non-linear response of parrotfish abundance indicates density-dependence in habitat use, and this density-dependence may arise from a limiting capacity of the reef substrate to supply refuges from predation.

Taking into account fish size, life phase composition, and the relative abundance of parrotfish species, total grazing intensity had an asymptotic relationship with topographic complexity despite *Scarus* dominating parrotfish abundance. The reason is that *Sparisoma* contributed more to grazing intensity because it comprised larger individuals. This underlines the importance of using species-size specific grazing rates when estimating parrotfish grazing intensity. In the present study, the grazing rate of each individual was estimated from an empirical model based on feeding observations of different species, body sizes and life phases (Bruggemann 1995, Mumby 2006). This model implicitly assumes that rugosity has no direct impact on grazing behavior, thus ignoring potential effects of topographic complexity on foraging activity (e.g. time dedicated to feeding) and efficiency (e.g. ability to pick/excavate algae). At present the magnitude of such effects remain largely enigmatic and warrant further empirical research. Moreover, with such a radical (20-fold) increase in parrotfish density from low to high rugosity reefs, it seems unlikely that changes in feeding behavior would affect the trend observed on grazing intensity in Glovers Atoll.

When a non-linear response of grazing intensity was incorporated into an ecosystem model we found that they

Figure 7. (A) Conceptual diagram of reciprocal facilitation between corals and parrotfish. The structure of these two functional groups benefit from each other through positive indirect feedbacks: coral growth generates hard limestone structures enhancing rugosity; rugosity reduces predation risk for parrotfish, thus indirectly promoting parrotfish abundance; grazer abundance enhance grazing rate which is dampened by the extension of the substrate, yet the net outcome for grazing intensity is positive; grazing intensity reduces macroalgal cover thus indirectly benefits to corals. (B) Impact on coral reef resilience of a non-linear response of grazing intensity to rugosity based on model simulations. Compared to a linear response, an asymptotic response provides greater persistence of a coral-dominated state to disturbances (left plot: decreasing rugosity for $F = 0.5$; right plot: increasing fishing pressure with for $R = 1.3$). Coral persistence, illustrated by the probability of a coral-to-macroalgal phase shift, is estimated from model scenarios where *Sparisoma* is exclusively fished and where *Sparisoma* grazing intensity responds asymptotically (Fig. 5B) or linearly (Fig. 6B) to rugosity.

reduced the probability of a phase-shift toward macroalgal dominance, thereby increasing system resilience (Fig. 7B). This is because grazing intensity was consistently higher under the non-linear function throughout much of the range of rugosity. Essentially, non-linearity increases the robustness of grazing intensity against habitat degradation, which means that high levels of grazing intensity can be maintained even if reef structure declines because of damage and erosion.

Another key aspect of the non-linear functional relationship is that grazing intensity increased rapidly at low levels of rugosity. Such high sensitivity to a small increase in reef structure has important implications for ecosystem recovery after an acute disturbance that removes much of the coral (e.g. a ship grounding). If the grazer community can

respond rapidly to an increase in reef structure, then the strength of the feedback between the habitat engineers and the habitat facilitator is increased, thereby building greater system resilience much faster.

Our study has several implications for the management of coral reefs. First, although reef rugosity has contrasting impacts on grazing – a positive impact on fish abundance but negative impact on the intensity of grazing because of increased surface area – the net outcome appears to be positive for all the herbivores studied. High rugosity favors, rather than impedes, the overall grazing intensity of herbivores by enhancing fish abundance to levels that offset the potentially deleterious effect of increasing actual surface area. Therefore, as a general principle, coral resilience – which is strongly tied to grazing intensity in the Caribbean

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(Mumby et al. 2007) – should relate positively with the rugosity of a site. Second, as some Caribbean fisheries are selective for large parrotfish (Rakitin and Kramer 1996, Hawkins and Roberts 2004), which tend to exhibit asymptotic scaling between grazing intensity and rugosity, fishing is expected to result in an increasingly linear functional response between overall grazing intensity and reef topographic complexity. Because linear responses are associated with lower reef resilience, fishing appears to be eroding an important, and hitherto under-appreciated, source of reef resilience.

Ecosystem engineers that create large physical structures have clear, primary effects on many organisms (Jones et al. 1994, 1997). However, engineers also have cascading impacts on many other biota by facilitating or disrupting competitive or trophic processes (Altieri et al. 2007, Thomsen et al. 2010). These cascading effects are sometimes nonintuitive and might involve the emergence of feedbacks to the engineer. The positive feedback loop reported here is an example of a habitat cascade (sensu Thomsen et al. 2010) in which some habitat-users exert an indirect positive control on the habitat-formers through the trophic mediation of a competitive process. We refine the nature of this positive feedback loop further by describing it as reciprocal facilitation, in which the habitat-formers and habitat-users benefit mutually through indirect, positive interactions (Fig. 7A). The term reciprocal facilitation has been previously used for describing feedback loops of positive interactions in plant communities (Rousset and Lepart 2000, Frérot et al. 2006, Zhang et al. 2011). It has been also employed as a synonym of facultative mutualism (Milbrink 1993, Thieltges and Buschbaum 2007) but mutualism may be less appropriate for qualifying the mutual benefits arising from indirect, community-wide interactions, especially when the organisms concerned are multi-species functional groups (such as coral engineers and fish herbivores) rather than single species. We stress that loops of reciprocal facilitation may be essential for the maintenance of biogenic habitats sustained by engineers with low intrinsic competitive abilities. Many marine sessile competitors benefit from the consumption of their superior counterpart by a keystone consumer (Paine 1966, 1974, Menge 1995). In rocky intertidal assemblages, seastars prevent sessile organisms such as barnacles being outcompeted by mussels, a dominant competitor (Paine 1966). Such a consumer-mediated control of mussels can also lead to the emergence of alternative community states (Bertness et al. 2004, Paine and Trimble 2004). One novelty of coral reefs, however, is that the positive feedback exerted by the weak competitor (corals) on the keystone consumer (parrotfish) occurs through habitat facilitation, leading to the reinforcement of a coral-dominated state. If similar positive feedbacks occur in other biogenic habitats, reciprocal facilitation may be a general mechanism for amplifying the engineering activity of an inferior-competitor.

Engineering activities sustained by reciprocal facilitation might be relatively vulnerable to dysfunction because disruption to any part of the feedback can destabilize the system. In the case of coral reefs, for example, the growth of engineers is directly impacted by climate change (Hoegh-Guldberg et al. 2007), and the facilitators are directly impacted by fishing; there are, therefore, multiple ways to disrupt the positive feedback we describe. The management of biogenic systems will clearly benefit from a good understanding of the nature of feedback mechanisms between the engineers and facilitators. Even subtle differences in the functional form of some relationships, such as the feeding intensity of the facilitator with rising complexity of the engineers, can have important consequences for the dynamics of the system and provide some insurance against short-term ecosystem degradation.

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