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REPORT

Multiple feedbacks and the prevalence of alternate stable states on coral reefs

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Abstract The prevalence of alternate stable states on coral reefs has been disputed, although there is universal agreement that many reefs have experienced substantial losses of coral cover. Alternate stable states require a strong positive feedback that causes self-reinforcing runaway change when a threshold is passed. Here we use a simple model of the dynamics of corals, macroalgae and herbivores to illustrate that even weak positive feedbacks that individually cannot lead to alternate stable states can nonetheless do so if they act in concert and reinforce each other. Since the strength of feedbacks varies over time and space, our results imply that we should not reject or accept the general hypothesis that alternate stable states occur in coral reefs. Instead, it is plausible that shifts between alternate stable states can occur sporadically, or on some reefs but not others depending on local conditions. Therefore, we should aim at a better mechanistic understanding of when and why alternate stable states may occur. Our modelling results point to an urgent need to recognize, quantify, and understand feedbacks, and to reorient management interventions to focus more on the mechanisms that cause abrupt transitions between alternate states.

Introduction

Many ecosystems exhibit marked regime shifts from one set of species to another, such as the transitions between clear and turbid lakes (Scheffer 1998), forest and grassland (Hirota et al. 2011; Staver et al. 2011), kelp beds and sea urchin barrens (Steneck et al. 2002; Watson and Estes 2011), or between tropical corals and assemblages of macroalgae and other weedy species (e.g., Done 1992; Hughes 1994; Mumby et al. 2007; Hughes et al. 2010). Positive and negative feedbacks play a critical role in shaping the stability of these ecosystems and in determining the responses they display to increases or decreases in anthropogenic drivers such as pollution, over-harvesting or climate change.

Positive feedback as a cause of alternate stable states

A feedback is defined as a closed-loop process where the results affect the inputs, influencing future results (DeAngelis et al. 1986). In complex ecosystems, feedbacks result from circular chains of interactions (e.g., A affects B and B affects A) between ecosystem components (e.g., species, abiotic conditions, humans). A feedback is negative when the results dampen an initial rate of change, causing the initial change to slow down (DeAngelis et al. 1986) (e.g., increase in A ⇒ increase in B ⇒ decrease in A). Positive feedbacks, on the other hand, amplify an initial small

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change, potentially propelling the system away from its previous state (DeAngelis et al. 1986) (e.g., increase in A ⇒ increase in B ⇒ further increase in A).

Deterministic models (i.e., excluding natural variability) can be used to study crucial system dynamics and states at which the system is in equilibrium. A stable equilibrium is established by a negative feedback that causes the system to return to the original equilibrium after a disturbance (i.e. a snowball effect). Negative feedbacks are therefore often called stabilizing feedbacks (Schröder et al. 2005). Negative feedbacks are ubiquitous in ecosystems; in their absence populations would grow infinitely. In contrast, an unstable equilibrium is established by a positive feedback that causes acceleration away from that equilibrium after a small disturbance (a snowball effect). In a system with alternate stable states, an unstable equilibrium separates two stable equilibria. For this reason, a strong positive feedback is a necessary (but not sufficient) condition for alternate stable states (Thomas 1981). Positive feedbacks are therefore often called destabilizing feedbacks (Schröder et al. 2005).

Due to positive feedbacks, systems can respond in unexpected ways to changing conditions or small disturbances (Fig. 1a). The equilibrium response of an ecosystem to a gradually increasing driver is often smooth, meaning that there is only one stable state for each level of driver (Fig. 1b). If a positive feedback is strong enough to generate alternate states, the response to a driver becomes hysteretic (Fig. 1c). In Fig. 1c there are two particular threshold values for the driver, also called 'tipping points', where a stable equilibrium collides with an unstable equilibrium and disappears. If the driver brings the system close to such a tipping point the unstable equilibrium approaches the stable equilibrium, implying that even a small perturbation may push the system across this unstable boundary invoking a critical transition to the alternate stable state. Reversing the change in the driver is not enough to induce a shift back to the original state, as the system tends to remain trapped in the new alternate state, a phenomenon known as hysteresis. Hysteresis thus increases with the strength of the positive feedback. The stronger the positive feedback, the larger the range of driver levels for which alternate stable states exist (Fig. 1a).

In reality, multiple positive and negative feedbacks act together and may counteract each other. This complex interplay of feedbacks, in combination with many random effects, will shape the actual response of an ecosystem to slowly changing conditions.

Feedback mechanisms in coral reef ecosystems

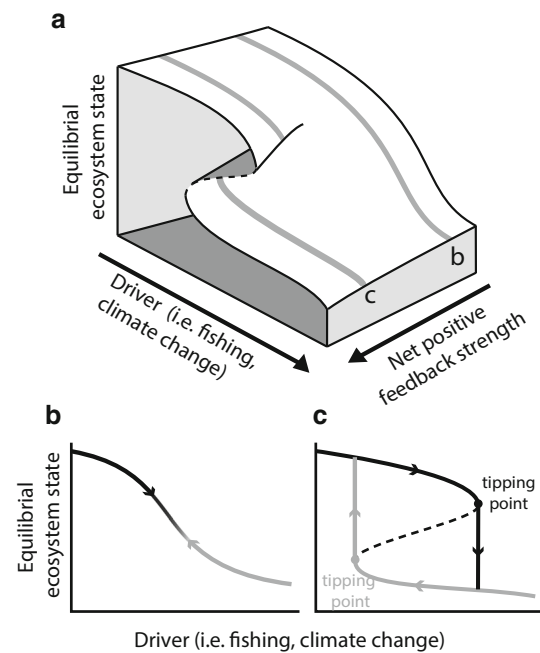Although the role of positive feedbacks in coral reef dynamics has previously been analysed (Mumby and

Fig. 1 The cusp-catastrophe plot. a A positive feedback can lead to a qualitatively different equilibrium response of an ecosystem to an external driver (e.g., fishing pressure and/or climate change), depending on the strength of the feedback. b Weak positive feedback may lead to a smooth response, and a single equilibrium, along the entire range of driver, from low to high. c Strong positive feedback may cause the response curve to fold inwards, such that two alternate stable states exist over the same intermediate range of drivers. The response of the system as a result of an increasing driver (in *black*) shows a tipping point at which the system will abruptly shift to another regime. If the driver is lowered again, the response will follow a different trajectory (in *grey*), because the system remains trapped in the alternate regime until the driver reaches a level at which the system is tipped back to its original state

Steneck 2008; Mumby 2009; Nyström et al. 2012), the fundamental consequences of the interplay between multiple feedbacks have hardly been addressed. To formulate a model that explores this interplay we first searched the literature to identify positive feedbacks that have been described for coral reef ecosystems (Table 1; see Electronic Supplementary Material, ESM Appendix 1 for list of references). We found that over 20 positive feedback mechanisms have been documented, although they have very seldom been quantified, and in most cases their potential role in promoting critical transitions or alternate states has not been recognized. The feedbacks can be classified into five general categories, based on the dominant process involved: predation; competition; density-dependent demography; facilitative interactions between species and/or between species and their environment; and social–ecological interactions (Table 1). These categories overlap and are not mutually exclusive.

Arguably, the best-known positive feedback arises from the interaction between corals and herbivores

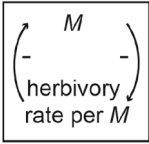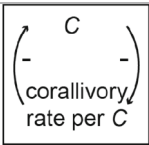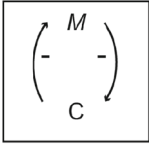**Table 1** Positive feedbacks on coral reefs suggested in the literature. (See ESM Appendix 1 for references)
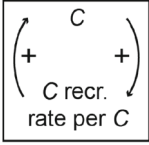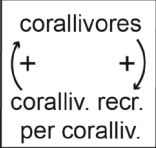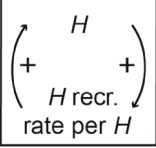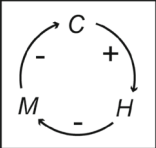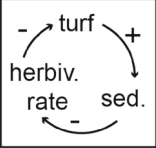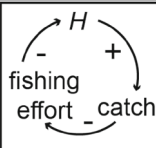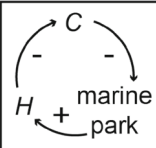
Scheme	#	Feedback mechanism	Refs
Predator-prey interactions: predation pressure per capita prey decreases with prey density			[1]
$\begin{pmatrix} M \\[2pt] - \quad - \\[2pt] \text{herbivory} \\ \text{rate per } M \end{pmatrix}$	1	Higher algal cover can lead to a saturated herbivore population (e.g. sea urchins, fish), and thus to a lower herbivory rate per algae. This may occur if the herbivore population does not change with algal cover: ■ If: population growth of herbivores is recruitment limited rather than food limited ■ If: preferred alternative food sources (e.g. turf algae) are available	[3,4] [5,6] [7]
	2	Higher algal cover can lead to more mature algae, which can lead to decreased food handling and digestion time of herbivores (e.g. decreased palatability of mature algae, increased dominance of algae that are mechanically or chemically defended).	[8–10]
	3	Higher algal cover can lead to dense stands, which may be avoided by adult herbivorous fish, leading to a decreased herbivory rate per algae.	[11]
	4	Higher algal cover can create nursery habitat for micropredators, leading to increased post settlement mortality of herbivorous echinoids (opposite has also been shown[2]).	[12]
$\begin{pmatrix} C \\[2pt] - \quad - \\[2pt] \text{corallivory} \\ \text{rate per } C \end{pmatrix}$	5	Higher coral cover can lead to a saturated corallivore population (e.g. *Drupella spp.*, *Acanthaster planci*, some parrotfish) and thus to a lower corallivory rate per coral. This may occur if the corallivore population does not change with coral cover: ■ If: preferred alternative food sources are available (i.e. many corallivorous fish are facultative instead of obligate corallivores)	[13–17] [18]
Competition: interspecific competition (e.g. between corals and algae) exceeds intraspecific competition (e.g. among corals, or among algae)			[23,24]
$\begin{pmatrix} M \\[2pt] - \quad - \\[2pt] C \end{pmatrix}$	6	Higher algal cover can lead to stronger inhibition of settlement of coral larvae.	[25,26]
	7	Higher algal cover can lead to stronger physical interference (e.g. overgrowing, overtopping, or abrasion) of juvenile or adult corals.	[26–33]
	8	Higher algal cover can lead to stronger chemical effects of algae on corals (e.g. allelopathy, enhanced microbial activity, disease transmission).	[34–37]
	9	Higher coral cover can lead to stronger physical interference (extrusion of mesenterial filaments) of algae, damaging algal segments.	[38]
Density dependent demographic processes: net growth rate increases with population size (Allee effect)			[39]
$\begin{pmatrix} C \\[2pt] + \quad + \\[2pt] C \text{ recr.} \\ \text{rate per } C \end{pmatrix}$	10	In a self-seeded population, loss or gain of adult brood stock can affect local recruitment disproportionately. Net recruitment per capita adult coral may decrease at low coral cover (Allee effect), if fertilization success decreases with distance between coral colonies, due to dilution of gametes.	[40–44]
	11	Higher coral cover can lead to increased settlement rates, because coral larvae move towards reef sounds.	[45]
	12	Higher coral cover can lead to increased herbivory, which can increase the presence of crustose corraline algae that facilitate settlement and post-settlement survival of coral larvae.	[46–48]

Table 1 continued

Scheme	#	Feedback mechanism	Refs
corallivores (+ +) coralliv. recr. per coralliv.	13	Lower corallivore (*Acanthaster*) population density can lead to reduced larval survival rates. A pulse of nutrient input, or predator removal, may lead to temporary increased recruitment rates, resulting in a long-lasting starfish outbreak.	49
H (+ +) H recr. rate per H	14	Lower herbivore population density (observed for *Diadema* and fish) can lead to reduced fertilization success.	50,51

Facilitative interactions between two species, or between a species and its environment

C (− +) M − H	15	Higher coral cover can have a positive effect on herbivore abundance, by providing shelter and food to herbivores, thereby lowering the competition pressure between macroalgae and coral.	52–63
− turf + herbiv. rate sed. −	16	Turf algae can trap sediment, which can decrease herbivory on turf algae. Algal turfs and sediment also reduce coral recruitment, which can, on the long term, also decrease herbivory on turf algae.	64,65

Social-ecological feedbacks: facilitative interactions between social and ecological system

H (− +) fishing effort − catch	17	A decreased herbivorous fish population can lead to a decrease in catches. Fishers need to reach a certain yield/ income, and lack alternatives for their income. Therefore, they may increase fishing effort, by fishing more often, or using other methods.	19,20
	18	A decreased herbivorous fish population can lead to a decrease in catch. To reach the yield needed, governments may subsidize fishers when incomes fall.	21,22
C (− −) H + marine park	19	Higher coral cover can influence the placement of new marine parks. The protection of herbivores can positively affect coral cover.	66

C coral, *M* macroalgae, *H* herbivores

See ESM Appendix 1 for references

(Table 1). Corals provide habitat and shelter to herbivores (Friedlander and Parrish 1998; Graham et al. 2006; Lee 2006), and in turn, herbivores have a positive effect on corals by grazing on algae that compete with them for space (e.g., Lirman 2001). This is a positive feedback loop where a decline in coral cover could lead to further decline through the following chain of events: coral cover decline ⇒ herbivore stocks decline ⇒ macroalgae increase ⇒ coral cover decline through increased competition with macroalgae (Fig. 2). The intensity of this feedback is likely to vary in response to variation in the morphological structure of different coral assemblages, the size and species composition of herbivores, and their reliance on corals.
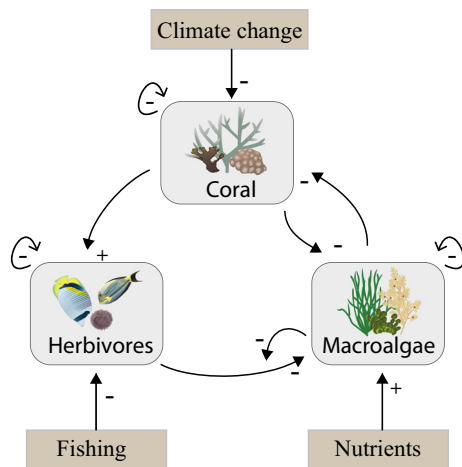
Fig. 2 An overview of the modelled feedbacks and drivers of change on coral reefs. The qualitative effect of each feedback route in the diagram can be determined by multiplying the signs on the *arrows* of the route taken. Two negative effects thus combine to cause a positive feedback. For instance, herbivores reduce the biomass of macroalgae, but abundant macroalgae can reduce the impact of herbivores if they swamp grazing pressure and become less palatable. Such a double negative effect can result in a positive feedback. A three-phase positive feedback occurs between corals, herbivores, and macroalgae (+, −, −). Negative feedbacks act to balance runaway change. For instance, maximum densities of all populations are ultimately limited by competition represented by small negative feedback loops that depict self-limitation. For a more extensive overview of documented positive feedbacks on coral reefs, see Table 1

An additional positive feedback arises from the interaction between herbivores and macroalgae (Table 1; Fig. 2). As herbivorous fishes become depleted by overfishing, grazing pressure per unit of macroalgae is reduced, and too few herbivores may become swamped by too much macroalgae (Mumby et al. 2007; Scheffer et al. 2008). Grazing pressure can become further reduced if algae become less palatable as they mature and grow (McClanahan et al. 2002). For example, on many overfished reefs in the Caribbean, regional-scale blooms of macroalgae occurred following mass mortality of grazing sea urchins due to disease because overfished stocks of herbivorous fishes were unable to consume enough algae (Hughes 1994). Similarly, a bloom of seaweed following a pulse of nutrients may also arise in part from a lower grazing pressure per unit of macroalgae (Scheffer et al. 2008). This feedback between herbivores and macroalgae could potentially lead to the replacement of corals by faster-growing seaweed (Hughes 1994; Mumby et al. 2007; Scheffer et al. 2008). However, on reefs with intact herbivore populations, this herbivore–macroalgae feedback may be very weak. For example, exposed reef crests on the Great Barrier Reef routinely lose most of their coral cover during recurrent cyclones, but return afterwards to high coral cover rather than flipping to a macroalgal state (Connell et al. 1997). Consequently, local variation in

fishing pressure on herbivores, in their species composition, and in palatability of macroalgae are all likely to influence the strength of this feedback.

Positive feedbacks on coral reefs can also arise from human behaviour (Table 1). For example, the intensity of fishing often increases in response to declining catch rates, which can drive stocks further downward. This positive feedback can occur, for instance, if government subsidies are linked to dwindling catches, if fishers switch to a more efficient type of gear when catches decline, or if they target seasonal spawning aggregations in depleted fisheries (Mackinson et al. 1997). As with feedbacks that are strictly biological, the strength of social feedbacks varies greatly from place to place and over time.

Importantly, empirical evidence for the existence of any specific positive feedback mechanism does not prove that alternate stable states occur, because the feedback may be too weak or intermittent. Also, empirical information on spatial and temporal variation in almost all of these feedbacks (Table 1) is either non-existent or very sparse. This makes it challenging to understand the response of any particular coral reef to accumulating stress. Our aim here is to improve the general understanding of the interplay of feedbacks in coral reefs in relation to the occurrence of alternate stable states, with an ultimate goal of preventing unexpected transitions to undesired states.

In this paper, we develop a simple model of a coral reef ecosystem to illustrate the interplay of multiple positive feedbacks, and to explore how differences in local environmental conditions, and thus in feedback strength, can affect the stability of coral reefs, leading in some circumstances to the emergence of alternate stable states. Previous work on alternate stable states on coral reefs has included more elaborate models examining hysteresis (e.g., Blackwood et al. 2010; Mumby et al. 2007), and the effect of multiple stressors (e.g., Blackwood et al. 2011; Fung et al. 2011). Here, we focus explicitly on a scenario in which multiple weak positive feedbacks interact. Because the strength of negative and positive feedbacks is contingent on synergies between them, and on the vagaries of local conditions, we conclude that a complex ecosystem such as a coral reef will likely exhibit a wide variety of responses to external drivers that may or may not include alternate stable states.

Model

To explore how multiple interacting feedbacks could affect the dynamics of coral reefs, we developed a model that explicitly incorporates three positive feedback mechanisms. We set the strength of each of these feedbacks in such a way that individually they were too weak to generate alternate stable states. Subsequently, we combined

the three weak feedbacks to study their collective effects. Parameter analyses to determine the stable and unstable states for each parameter value were performed in Matlab, using MatCont and Grind for Matlab.

Cover by corals (C) and macroalgae (M) are represented in our models as the proportion of space occupied, while herbivore abundance (H) is defined as a proportion of the carrying capacity of herbivores. Corals and macroalgae are assumed to compete for unoccupied space (S), with cover by corals, macroalgae and unoccupied space summing to 1 (Eq. 1). More complex models could add further benthic categories, or subdivide corals and macroalgae into functional groupings, but for our purposes we focus on the simplest case of shifts in dominance of corals and macroalgae.

$$S = 1 - C - M \tag{1}$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = (i_C + b_C C)S - d_C C \tag{2}$$

$$\frac{\mathrm{d}M}{\mathrm{d}t} = (i_M + b_M M)S - gHM \tag{3}$$

$$\frac{\mathrm{d}H}{\mathrm{d}t} = rH(1 - H) - fH \tag{4}$$

In this model, two mechanisms cause the expansion of coral and macroalgae, which are both proportional to the unoccupied space in the system. External import of propagules of coral and macroalgae has a constant rate (i_C and i_M, respectively) independent of the local cover of adults. This reflects demographically open populations with dispersal of juvenile stages. Additionally, local expansion of existing adults of both functional groups is proportional to the existing cover (with rates b_C and b_M). Mortality of corals is represented by a constant decay rate (d_C) (Eq. 2), and mortality of macroalgae by a constant grazing rate per herbivore (g) (Eq. 3). Herbivores (e.g., fish and sea urchins) are assumed to grow logistically (the density is scaled to the carrying capacity) with a relative growth rate of herbivores (r) that is independent of local macroalgal cover (Eq. 4). Herbivore mortality is represented by a constant fishing pressure (f) (Eq. 4).

Parameters of the default model without feedbacks are based on the following basic assumptions: (1) the macroalgal growth rate exceeds the coral growth rate; and (2) the mortality rate of macroalgae due to herbivory exceeds the mortality rate of corals, if the herbivore population is at carrying capacity (i.e., no fishing). We used the following default parameters for the illustrated cases: $b_C = 0.3$, $b_M = 0.8$, $i_C = 0.05$, $i_M = 0.05$, $d_C = 0.1$, $r = 1$, $g = 1$.

As in almost all ecological models, negative feedbacks prevent unlimited population growth. A familiar term for this effect is negative density-dependence. In our model, for example, macroalgae and coral cover are limited by space, and the herbivore population size has a carrying capacity (Fig. 2). In addition to these negative feedbacks, we incorporated three positive feedbacks in the model, described in detail in ESM Appendix 2 (Fig. S1).

First, we implemented a positive feedback between macroalgal cover and herbivory rate. This feedback arises from a decrease in the herbivory rate (per unit of algae) as macroalgal cover increases, representing a scenario where consumption by herbivores saturates when algae are abundant (Table 1, feedbacks 1–3). To model this 'herbivory-escape feedback', we introduced a Holling type II functional response, with parameter η representing the macroalgae handling time of herbivores (Eq. 5).

$$\frac{\mathrm{d}M}{\mathrm{d}t} = (i_M + b_M M)S - \frac{gHM}{g\eta M + 1} \tag{5}$$

Second, we incorporated a positive feedback arising from the direct negative effects of macroalgae on coral recruitment and growth (Table 1, feedbacks 6–7). This "competition feedback" is based on the classic insight that competition can cause alternate stable states if interspecific competition exceeds intraspecific competition (Volterra 1926; Lotka 1932). The competition effect of macroalgae on coral recruitment and growth is represented by αM (Eq. 6). If α is zero, coral recruitment and growth are only indirectly affected by macroalgae through space pre-emption. A value of α between 0 and 1 represents the proportion of macroalgae involved in the direct inhibition of corals.

$$\frac{\mathrm{d}C}{\mathrm{d}t} = (i_C + b_C C)S(1 - \alpha M) - dC \tag{6}$$

Third, we considered an indirect positive feedback between corals and herbivores. Herbivores graze on macroalgae, thereby reducing the negative effect of macroalgae on coral. A positive feedback exists if corals promote herbivores, for example by providing habitat and shelter (Table 1, feedback 15). We modelled this 'coral–herbivore feedback' by assuming a positive relationship between coral cover and herbivore carrying capacity. The strength of this relationship is represented by σ (Eq. 7). If σ is zero, herbivores are not affected by corals. If σ is 1, coral cover completely determines the carrying capacity of herbivores.

$$\frac{\mathrm{d}H}{\mathrm{d}t} = rH\left(1 - \frac{H}{(1 - \sigma) + \sigma C}\right) - fH \tag{7}$$

To illustrate how stability properties may change we varied parameters that reflect variation in (a) palatability of macroalgae (McCook and Price 1997) by varying the handling time of macroalgae by herbivores (η), and (b) recruitment levels of corals (Connell et al. 1997; Diaz-Pulido and McCook 2003; Ayre and Hughes 2004) by varying the density-independent inflow of coral recruits (i_C). Both factors (a and b) are known to vary widely in

nature. For instance, the proportion of unpalatable species varies enormously at multiple scales (e.g., McCook and Price 1997), affecting the food handling time of herbivores (Hoey and Bellwood 2011). Similarly, coral recruitment varies greatly in both space and time (e.g., Connell et al. 1997; Hughes and Tanner 2000; Halford and Caley 2009).

Results

In the absence of the specific positive feedbacks we address, the model exhibits a smooth response to fishing pressure (Fig. 3a). As fishing increases, the abundance of herbivores declines linearly, causing the grazing rate on macroalgae to decrease incrementally, resulting in a smooth and reversible replacement of corals by macroalgae. There is a single stable state for any given level of fishing pressure. Consequently, the system exhibits the same forward and backward trajectory in abundances of herbivores, macroalgae and corals as fishing pressure is increased or decreased.

Adding each of the weak positive feedbacks to the model individually has scarcely any effect, resulting merely in a slight steepening in the response of corals and macroalgae to fishing pressure (Fig. 3b–d). In the default parameter setting, none of the individual feedbacks is strong enough to result in alternate stable states.

In contrast, when the same individually weak feedbacks are allowed to act together a fundamentally different behaviour emerges. The model now has alternate stable states over a range of fishing pressures (Fig. 3e). Consequently, the threshold in fishing that triggers a collapse of corals is lower than the threshold for the reverse transition from macroalgae to corals. The system now shows hysteresis, and a gradual change in driver can lead to abrupt shifts between alternate stable states. Similar synergetic effects among feedbacks can also occur in all pairwise combinations of the three feedbacks (ESM Appendix 2, Fig. S2).

Whether the response of an ecosystem to a changing driver such as fishing or climate change is hysteretic or not obviously depends on the strength of all contributing feedbacks. The strength of these feedbacks depends on local conditions. For instance, variation in the species composition of macroalgae and levels of coral recruitment, both commonly observed, affect feedbacks in the model. We used the model to illustrate that variations in the parameters affecting the strength of positive feedbacks can cause the equilibrium response to drivers such as fishing pressure to change from smooth to hysteretic (Fig. 4). Specifically, these analyses suggest that reefs with a higher proportion of unpalatable macroalgae, or with lower levels of recruitment (e.g., isolated reefs) are more likely to exhibit alternate stable states.
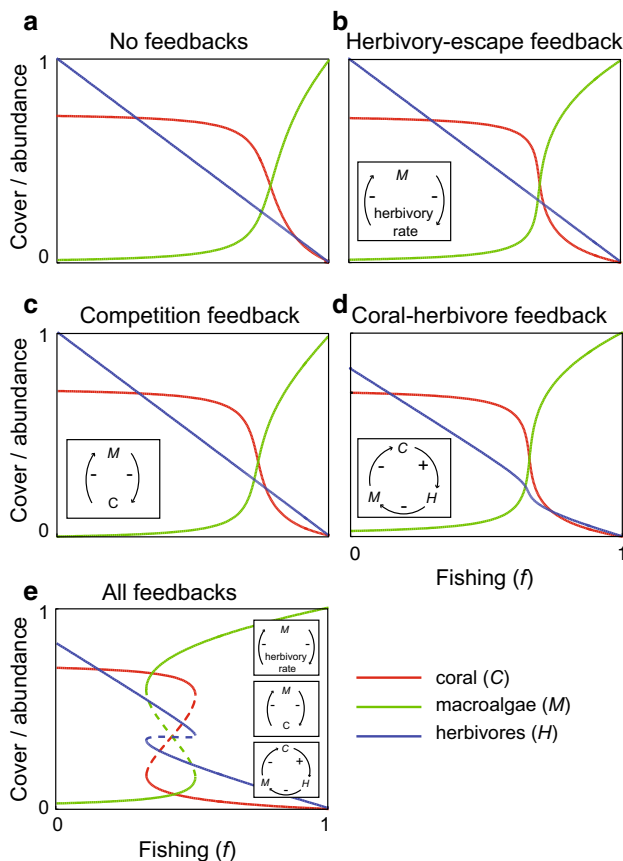

Fig. 3 The impact of multiple positive feedbacks on the equilibrium response of corals, macroalgae, and herbivores to changing fishing pressure. In (a), the model has no positive feedbacks, and only a single equilibrium exists for a given level of fishing pressure. In (b–d), a single positive feedback is introduced in the model, but each one is too weak to generate hysteresis and alternate stable states: b Herbivory-escape feedback ($\eta = 1$). c Competition feedback ($\alpha = 0.5$). d Coral–herbivore feedback ($\sigma = 0.6$). In (e), the same three weak feedbacks in (b), (c), and (d) are combined, generating hysteresis and alternate stable states at an intermediate level of fishing pressure
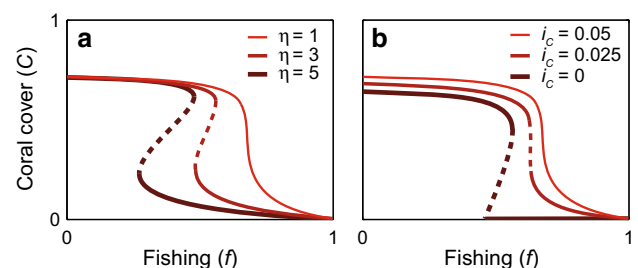

Fig. 4 The tendency of the system to show hysteresis in response to fishing pressure can be affected by locally varying factors such as: a Low palatability of fully grown algae (high η) (feedback parameters: $\alpha = 0.2$, $\sigma = 0$). b Low external recruitment of corals, i_C (feedback parameters: $\eta = 1$, $\alpha = 0.2$, $\sigma = 0$)

Discussion

Multiple causality

Our analyses illustrate that feedback mechanisms that individually have no qualitative effect on stability properties when they are experimentally tested or observed can nonetheless collectively cause an ecosystem to have tipping points. It is well known that reefs are more likely to shift to a degraded state such as a macroalgae-dominated state if stress on corals increases, for example due to climate change, high nutrient run-off, or intensive fishing. However, whether this shift will be gradual or abrupt (Fig. 1) will largely depend on the strengths of feedbacks in the ecosystem. Reefs with weakened negative feedbacks or strengthened positive feedbacks, or, as we have shown here, with multiple weak positive feedbacks, are more prone to have critical thresholds where they undergo collapses that are difficult to reverse.

Because the strength of the many commonly observed feedbacks (Table 1) varies from place to place and from time to time (Fig. 4), a corollary is that it is impossible to conclude that coral reefs in general will or will not have alternate stable states (Bruno et al. 2009; Dudgeon et al. 2010; Mumby et al. 2013). Consequently, while some coral reefs around the globe may respond smoothly to slowly changing anthropogenic drivers, others can unexpectedly collapse and fail to recover even when drivers are reduced (e.g., Connell 1997; Hughes et al. 2010; Graham et al. 2011).

Obviously, our model captures only a small part of the complexity of coral reefs. It is tempting to further elaborate and parameterize the model in order to capture more of the complexity and spatial variation found in the field. Indeed, the wish to describe ecosystems as realistically as possible has driven the development of detailed, spatially explicit models with specified environmental conditions for each location (e.g., Melbourne-Thomas et al. 2011). However, although more complex models can be of great help in evaluating the potential role of different processes, they remain challenging to parameterize and fully understand (Oreskes et al. 1994). Our model is intended to complement this approach. Rather than aiming to be complete, 'minimal models' such as the one we present may help to understand how non-linear mechanisms may interact to drive complex systems.

Managing ecosystem resilience

Many natural resource management agencies struggle to cope with multiple human impacts that are cumulative and potentially synergistic. Often the response of cash-strapped agencies is to manage "stressors" or drivers without a clear understanding of which interventions are likely to give the best environmental or social outcome. Our analysis illustrates that an understanding of how multiple feedbacks interact is essential to guide management decisions. Even mechanisms that are likely to be dismissed as unimportant can collectively destabilize an ecosystem. Therefore, efforts to reduce human impacts on reefs need to focus on understanding and managing interactive feedbacks (Bellwood et al. 2004; Nyström et al. 2012; Graham et al. 2013), such as the ones we have highlighted (see also Table 1). Our results show that management decisions for protecting coral reefs could be substantially improved by a better understanding of how multiple feedbacks interact to strengthen or weaken hysteresis. Currently, economic and social constraints rather than scientific knowledge often dominate the choice of management action, or inaction (Scheffer et al. 2015).

We conclude that to comprehend ecological resilience and alternate states more fully and to avoid unwanted critical transitions will require a new focus on the combined effects of positive and negative feedbacks, measuring the existence of and proximity to thresholds, and assessing the strength of hysteresis (e.g., Dakos et al. 2012; Scheffer et al. 2012). Importantly, our theoretical exploration of the importance of feedbacks highlights a critical knowledge gap in when and where they occur, how strong or weak they may be, and how they interact to influence the nature of critical transitions.

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