

Modeling alternative stable states in Caribbean coral reefs

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Abstract

The resilience of Caribbean coral reefs, which are an important source of biodiversity and provide essential ecosystem services, is constantly challenged by many reef stressors including ocean acidification, hurricane damage, and over-harvesting of herbivorous reef fish. The presence of two alternative stable states—a desirable state with high levels of coral cover and its coral-depleted counterpart—has been widely documented in the literature. Increasing coral resilience to prevent phase shifts to the undesirable state is a critical research priority, and mathematical models can serve as an important tool to not only better understand the underlying dynamics of observed coral communities, but also to evaluate the potential impacts of stressors and the outcome of management strategies designed to promote coral persistence. Here, we review the existing literature of mathematical models designed to understand the processes that generate alternative stable states. We focus on models that are comprised of ordinary differential equations and, at their core, capture algal–coral dynamics.

Recommendations for Resource Managers

- Evidence for the existence of alternative stable states and the associated presence of hysteresis implies a need for management designed to increase the resilience of coral reef ecosystems.
- In addition, holistic approaches to designing management strategies are required to both increase resilience of



coral reefs and maximize the benefits of the ecosystem services they provide.

- Due to the intrinsic complexity and spatial variability of coral reef ecosystems, management cannot be designed using a “one size fits all” approach. Instead, local dynamics and stressors need to be carefully considered.

KEYWORDS

community composition, hysteresis, phase shift, reef stressors

1 | INTRODUCTION

Caribbean coral reefs have recently suffered significant losses in coral cover as a consequence of the catastrophic die-off of the sea urchin *Diadema antillarum* in the early 1980s. The conventional wisdom has been that overfishing of herbivorous fish led to the pre-eminence of *Diadema* as the last remaining significant herbivore keeping algae at bay in the Caribbean prior to that die-off. Thus, overfishing led to the precarious dependence of herbivory on just the one species. The effectiveness of *Diadema* during the recent past in controlling macroalgae abundance has much support (Levitan, Edmunds, & Levitan, 2014; Miller, Kramer, Williams, Johnston, & Szmant, 2009). In fact, some reports suggest that *Diadema* may have been among the dominant herbivores for millennia (Lessios, Garrido, & Kessing, 2001; Levitan et al., 2014). However, the importance of these urchins as significant herbivores prior to human disturbance has been called into question by Cramer, Dea, Carpenter, and Norris (2017), who examined the subfossil spine assemblages of echinoids for the past 3000 years. They do confirm that *Diadema* is causally related to the abundance of at least one reef-building coral species (*Madracis mirabilis*), but not others (e.g., *Acropora cervicornis*). Moreover, recent studies suggest that bioeroding sponges may play a significant role in coral cover (Murphy, Perry, Chin, & McCoy, 2016). Thus, the relationship of coral abundance to herbivory, bioerosion, and macroalgae is likely to be complicated. In addition to biotic factors, numerous abiotic factors, including temperature, ocean acidification, and mechanical damage from hurricanes have been identified as coral reef stressors. These factors not only affect the coral but also the animals implicated in their resilience, or their ability to recover following a perturbation or disturbance (Holling, 1973). For example, in addition to the increased incidence of coral bleaching due to elevated temperatures (Donner, 2011), *Diadema* is likely to be negatively affected by temperatures predicted to occur due to global warming (Sherman, 2015). Nevertheless, in order to understand the mechanisms that are driving the observed macroalgae and coral dynamics and to uncover methods for promoting restoration and recovery, holistic approaches integrating field research, experimental work, and mathematical modeling are needed.

Many have hypothesized that there exist two stable states for coral ecosystems: the first is a desirable state that corresponds to high coral cover while the second is a degraded coral-depleted state that usually has high levels of macroalgae. It is clear that anthropogenic stresses can drive phase shifts from a state with high coral cover to one that is coral depleted, but a significant distinction is made based on whether the phase shift is continuous (a smooth transition between states) or discontinuous (a sudden jump from one state to another) as an exogenous factor is varied. In systems with a continuous phase shift, only a single stable state exists across all environmental conditions. In contrast, alternative stable states exist when there is a discontinuous phase shift such that multiple stable states can coexist



under the same environmental conditions. In this case, an undesirable shift between stable states due to changing environmental conditions cannot usually be undone easily; to return to the original state would require environmental parameters to shift beyond where the discontinuous change occurred (i.e., hysteresis). The existence of alternative stable states for coral communities has been extensively debated in the literature, with many arguing that the observed drastic shifts in community structure are due to changing environmental conditions that represent a continuous phase shift (Dudgeon, Aronson, Bruno, & Precht, 2010) and attempts to experimentally shift a community to an alternative stable state have not been successful without changing the environmental conditions (Connell & Sousa, 1983). In contrast, others argue that while we may not be able to see alternative stable states under identical environmental conditions, this does not mean that they are not present in this system.

Although progress is being made, the debate between whether there are two alternative stable states or whether the changes in community structure are the result of a continuous phase shift remains an open question. Mathematical modeling is an important tool for investigating the existence of alternative stable states because of the opportunity to construct a system in which the environmental conditions are kept unchanged while the community composition is shifted. For example, Mumby, Hastings, and Edwards (2007) developed a simple model of the interactions between coral, macroalgae, and algal turfs. Using this model, they demonstrated that alternative stable states exist and their stability depends on the rate at which herbivores graze macroalgae. When grazing is low, macroalgae is able to spread over turf and successfully outcompete coral leading to a stable coral-depleted state. In contrast, when grazing of algae is sufficiently high, the growth of macroalgae is sufficiently inhibited so that coral can recruit to and overgrow turf and stably persist at high levels. Moreover, the analysis of their model suggests that the phase shift between these stable states is discontinuous. Mumby et al.'s model provides a parsimonious explanation for the existence of alternative stable states, with feedbacks between coral and algae at its core. Hereafter, our emphasis in this paper is on related modeling studies that capture the presence of alternative stable states.

Due to the relative simplicity of the Mumby et al. model, its baseline assumptions provide a foundation to build upon in an attempt to better understand the complex dynamics of coral reef ecosystems. Consequently, a wealth of modeling studies have been performed over the past decade that build upon similar baseline assumptions. In this paper, we introduce the Mumby et al. model in detail and its key properties. We then review modeling efforts since then that are either directly based on the Mumby et al. model or have similar model structures. While many other studies exist that have considered, for example, delay differential equations (e.g., Blackwood & Hastings, 2011; Li, Wang, Zhang, & Hastings, 2014) or large-scale spatial simulation models (e.g., Mumby, 2006), we focus exclusively on models based on systems of ordinary differential equations (ODEs) that have coral–algal interactions at their core. Further, the majority of models we review consider the dynamical impacts of stressors to Caribbean reefs.

2 | BASELINE MODEL OF CORAL–ALGAL INTERACTIONS

Here, we describe the influential model of coral–algal interactions first introduced by Mumby et al. (2007). This model arguably provides the most parsimonious representation of interactions between coral and algae that leads to alternative stable states. The model is spatially implicit and is comprised of three ODEs that capture the dynamics of coral (C), macroalgae (M), and algal turfs (T). Each of the three state variables is described in terms of the fraction of seabed that they occupy. An important biological assumption made is that the seabed is covered entirely by coral, macroalgae, and algal turfs so that $C + M + T = 1$. Conveniently, this allows the system to be completely determined only by two

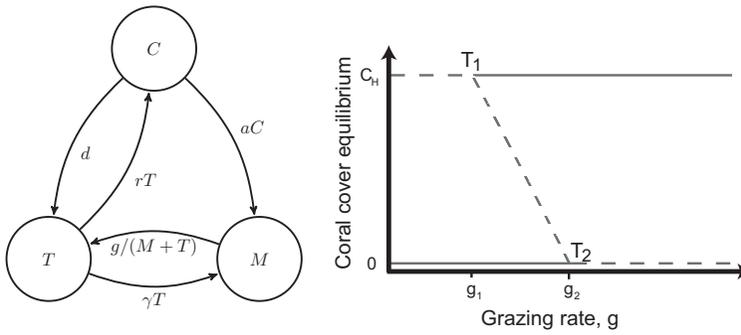


FIGURE 1 (A) Schematic representation of the interactions captured in the Mumby et al. (2007) framework; (B) bifurcation diagram of the equilibrium coral cover versus the grazing rate (g)

Note. Solid gray lines denote stable equilibria and dashed gray lines indicate unstable equilibria as well as saddles. This bifurcation diagram captures the presence of alternative stable states in the model with C_H denoting the desirable stable state with high levels of coral cover. g_1 and g_2 , which are found explicitly in the Appendix, represent the critical grazing rates at which the transcritical bifurcations T_1 and T_2 occur. These bifurcations are the points at which the system can switch to the alternative stable state.

of the state variables. In other words, the fraction of algal turf is defined by $T = 1 - C - M$ and can therefore be identified using the solutions for C and M .

The model captures five basic interactions: (i) macroalgae overgrows coral at a rate a , (ii) macroalgae spreads vegetatively over algal turfs at a rate γ , (iii) coral recruits to and overgrows algal turfs at a total rate of r , (iv) coral has a natural mortality rate of d , which then gives rise to algal turfs, and (v) grazers feed indiscriminately on both algal types at a fixed rate g (see schematic representation in Fig. 1A). For the latter interaction, it is assumed that grazing crops macroalgae and gives rise to turfs whereas grazing on algal turfs essentially maintains the turf. Using the fact that T is entirely determined by M and C , the model is given by:

$$\frac{dC}{dt} = rTC - dC - aMC, \quad (1)$$

$$\frac{dM}{dt} = aMC - \frac{gM}{M+T} + \gamma MT. \quad (2)$$

All parameters were estimated using empirical studies, with the exception of grazing, which may vary based on, for example, local fishing practices.

An advantage of this relatively simple model formulation is that a linear stability analysis can be explicitly carried out. While the details are left to the Appendix, it can be shown that there are four equilibria (a fifth equilibrium exists, but it takes on a negative value for our parameterization and is therefore ignored here). Recalling that $T^* = 1 - C^* - M^*$, the equilibria, (C^*, M^*) , are given by:

- (I) $(0, 0)$, or local extinction of both macroalgae and coral, which gives rise to a state entirely covered by algal turfs;
- (II) $(0, \frac{\gamma-g}{\gamma})$, or an algal-dominated state where the equilibrium level of coverage of macroalgae increases as the grazing rate decreases;
- (III) $(\frac{r-d}{r}, 0)$, or local extinction of macroalgae and persistence of coral; and
- (IV) (\hat{C}, \hat{M}) , where $\hat{C}, \hat{M} \neq 0$ corresponds to coexistence of both coral and macroalgae.



Importantly, linear stability analysis reveals that when grazing rates are sufficiently low, then equilibrium (II) is stable and (III) is unstable so that algae is able to outcompete coral (this is the degraded coral-depleted state). However, when the grazing rate is sufficiently high, then macroalgae is successfully kept at bay. In this case, the stability of these equilibria is reversed so that the state with high coral cover (equilibrium (III)) is stable.

As pointed out by Blackwood, Hastings, and Mumby (2012), this system exhibits hysteresis. That is, the critical grazing rate (g_2 in Fig. 1B) at which the system switches stability from equilibrium (II) to (III) is different from the critical rate (g_1 in Fig. 1B) at which stability switches from (III) to (II) (these critical rates are found analytically in the Appendix). In other words, both equilibria coexist and are stable for grazing rates between these critical values. In this region of parameter space, the basins of attraction for the stable equilibria are divided by a separatrix that connects the origin (equilibrium (I)) and a saddle (or semistable) point in which coral and macroalgae coexist (equilibrium (IV)). These behaviors are captured in a bifurcation diagram of the equilibrium level of coral cover versus the grazing rate (Fig. 1B).

In the sections that follow, we describe several modeling studies that have been performed since 2007 when the Mumby et al. model was introduced. In particular, we review models that focus on coral–algal interactions at their core and exhibit alternative stable states (i.e., discontinuous phase shifts between stable states). We note that in many cases, we adapt and/or simplify notation to be consistent with the model described above and therefore to ease model interpretation.

3 | ALTERNATIVE MODELS OF CORAL–ALGAL INTERACTIONS

3.1 | Turf, free space, and coral recruitment

Several studies use a similar framework to Mumby et al. (2007) but make alternative assumptions on what covers the seabed. For example, some authors have generalized the assumption that T represents algal turf; instead, it is often defined as F or S to represent a more generic term that captures any “free space” or substrata. One such example of this comes from another influential modeling framework that was introduced by Fung et al. in 2011. In this section, we discuss the models from Fung, Seymour, and Johnson (2011) to demonstrate a model formulation that is similar to Mumby et al. (2007) but makes some different key assumptions.

Fung et al. introduced three models with increasing complexity and, at their core, each of these models was also centered on describing coral–algal interactions. Their first model considered coral, algal turfs, and free space (denoted by F). In this setting, algal turfs can grow on to substrata but are not capable of competing with coral. In the second model, the algal class was generalized to include macroalgae and could therefore compete with existing coral. In the final model, macroalgae and algal turfs were considered separately. Here, we describe the final and most complex model in detail.

A key difference with Mumby et al. (2007) is that Fung et al. (2011) differentiates between algal turfs and free space and therefore requires four state variables. In this model, it is again assumed that the seabed is entirely covered by these four variables so that the fraction of free space can be found implicitly by $F = 1 - C - M - T$. Further, this model makes more explicit assumptions about coral growth and recruitment. It is assumed that spawning corals recruit onto space at a rate l_s , brooding corals recruit onto space at a rate l_b , which is also proportional to the existing coral C , and both coral types can recruit to algal turfs at a fraction ϵ of the rate at which they recruit to space. Next, they assume that coral grows laterally over both free space and algal turfs at rates r and αr (where $\alpha \in [0, 1]$),



respectively, but this growth is limited by the presence of macroalgae. As in Mumby et al. (2007), they assume that coral has a natural mortality rate of d , macroalgae can overgrow coral at a rate a and turf at a rate γ , and they additionally assumed that macroalgae and algal turfs can grow over free space at rate γ_F and ζ , respectively. They also assumed that coral growth can be directly suppressed by macroalgae at a rate β . Finally, they assumed that grazing of macroalgae and algal turfs occurs at fixed rates g_M and g_T , respectively. These assumptions are captured in the following model:

$$\frac{dC}{dt} = (l_s + l_b C)(F + \epsilon T) + r(1 - \beta M)(F + \alpha T)C - dC - aMC, \quad (3)$$

$$\frac{dM}{dt} = \gamma MT + \gamma_F MF + aMC - g_M M, \quad (4)$$

$$\frac{dT}{dt} = -\epsilon(l_s + l_b)CT - r\alpha(1 - \beta M)TC - \gamma MT - g_{TT} + \zeta F. \quad (5)$$

In addition to considering grazing as a term that is subject to change through variation of fish abundance (due to, e.g., changes in fishing effort), Fung et al. (2011) assumed that other model parameters are also subject to change due to other stressors (e.g., eutrophication and sedimentation). In all cases, they found that the stressors can lead to decreases in coral resilience and therefore increase the likelihood of phase shifts. However, discontinuous shifts (i.e., as exhibited in Fig. 1B at points T_1 and T_2) rather than continuous shifts through smooth transitions to higher (or lower) coral cover only occur for parameter values at the edge of their parameter ranges.

3.2 | Extending the community composition

While the vast majority of models that capture alternative stable states focus on algal and coral interactions and stressors to coral, there are other organisms that have competitive interactions with coral and algae. Consequently, it is plausible that these species play a fundamental role in preventing (or driving) phase shifts to undesirable states.

For example, sponges—which compete with coral—are known to play a functionally important role in Caribbean coral reef ecosystems (Bell, 2008; Suchanek, Carpenter, Witman, & Harvell, 1983; Wulff, 2001). González-Rivero, Yakob, and Mumby (2011) therefore extended the coral–turf–macroalgae framework to account the proportion of sponges S occupying a given area of seabed. Similar to other models presented in this paper, the proportion of algal turf can be found implicitly as $T = 1 - M - C - S$. In this model, natural coral mortality is ignored (i.e., $d = 0$ in Equation 1). It is also assumed that sponges outcompete coral for space at a rate a_2 , macroalgae can overgrow sponge at a rate a_3 , and sponge can overgrow turfs at a rate z . Finally, it is assumed that generalist predators may graze on both macroalgae and sponges so that a proportion of the total grazing b is allocated to sponges. This model is given by

$$\frac{dC}{dt} = rTC - aMC - a_2SC, \quad (6)$$

$$\frac{dM}{dt} = aMC - \frac{gM}{M + T + bS} + \gamma MT + a_3MS, \quad (7)$$

$$\frac{dS}{dt} = a_2SC + zST - a_3MS - \frac{gbS}{M + T + bS}. \quad (8)$$



In this model formulation, grazing pressure on macroalgae is diluted by the presence of sponges. Consequently, under most scenarios explored by González-Rivero et al. (2011), the presence of sponges increases the requisite level of grazing required to maintain high levels of coral cover and, consequently, decreases coral resilience. However, there might also be direct positive effects of sponges on coral cover. For example, sponges can enhance coral survival by binding the reef frame and temporarily stabilizing carbonate rubble following physical damage. Therefore, additional modeling studies of interactions between coral, algae, and sponge might be important to further our understanding of complex reef interactions.

Another example of a modeling study that extends the community composition is related to recruitment facilitation, which can also drive alternative states on temperate reefs. In particular, crustose coralline algae (CCA) facilitates recruitment of herbivores (e.g., sea urchins), which in turn feed on macroalgae that would otherwise outcompete CCA. This interaction was captured in the model of Baskett and Salomon (2010), who find that the closer to obligate the relationship between CCA and sea urchins is, the more hysteretic the system. In Baskett and Salomon (2010), CCA takes the place of tropical corals but the ecological dynamics are similar. The major difference between the two models is dimensionality: Baskett and Salomon (2010) include herbivore populations as a phase variable dependent upon CCA populations for recruitment, whereas Mumby et al. (2007)'s model treats herbivore populations as a control parameter. Other notable differences include the lack of an intrinsic death term for CCA and the assumption that macroalgae makes up the entirety of an urchin diet, as opposed to Mumby et al. (2007)'s inclusion of algal turf.

4 | MODELING THE EFFECTS OF REEF STRESSORS

The majority of ODE models that capture the dynamics of coral–algal interactions have been developed to both assess the impacts of stressors on the resilience of coral reefs as well as explore the dynamical responses to conservation efforts. For example, one major stressor to coral is the overharvesting of herbivorous reef fish and a method for mitigating this issue is to impose restrictions or even a complete moratorium on fishing. In this section, we describe modeling efforts that have focused on exploring the consequences of overfishing, hurricane impacts and other physical damages, ocean warming, and acidification. We also review the conclusions drawn about the dynamical effects of interventions. We note that while we separate these stressors into two different sections, there is some overlap between them. For example, some models consider combinations of multiple stressors.

4.1 | Grazing rates and harvesting of herbivorous reef fish

Several modeling studies have considered the effects of changes in grazing rates on coral reef resilience. Some of these studies have considered structural aspects of the coral–algal system that may impact grazing rates while others directly consider the dynamics of herbivorous reef fish and their relationship to the grazing rate.

One important aspect of coral–algal systems not captured in the original baseline model is external coral and algal recruitment and its relationship to grazing rates. Including recruitment is one way in which spatial aspects of the system can be considered, and an analysis of such a system was performed by Elmhirst, Connolly, and Hughes (2009). Adapting the model of Mumby et al. (2007), they assumed that coral and algal recruitment onto algal turfs occurs at rates of ζ and e , respectively, and that recruitment is proportional to the amount of settlement space (i.e., turf) available so that the model can be



rewritten as

$$\frac{dC}{dt} = rTC - dC - aMC + \zeta T, \quad (9)$$

$$\frac{dM}{dt} = aMC - \frac{gM}{M+T} + \gamma MT + \epsilon T. \quad (10)$$

These authors constructed bifurcation diagrams of the equilibrium coral cover versus grazing intensity, similar to Figure 1(B), and then demonstrated how this bifurcation diagram is modified when ζ and ϵ take on positive values. Including external recruitment of coral causes the transcritical bifurcation (at T_1 in Fig. 1B) to become a saddle node bifurcation, creating a second stable equilibrium with small— but positive—levels of coral cover between g_1 and g_2 . Additionally, the value of g_2 decreases. In contrast, external recruitment of macroalgae causes the transcritical bifurcation at T_2 to become a saddle node bifurcation and increases g_1 , thereby causing a decline in coral resilience.

In other settings, the grazing term g has been directly related to fish biomass. For example, Blackwood et al. (2012) explicitly modeled herbivorous fish dynamics and assumed that the fish (assumed to be parrotfish, the primary grazer of Caribbean reefs) abundance (P) grows logistically but that there is an associated harvesting rate f . This can be written as

$$\frac{dP}{dt} = sP \left(1 - \frac{P}{K} \right) - fP, \quad (11)$$

where s is the *per capita* growth rate, f captures mortality due to fishing, and K is the carrying capacity. They assumed that K may vary with coral cover based on various assumptions. Importantly, they defined grazing to be a function of P (i.e., $g(P)$) so that sustainable levels of fishing effort could be determined based on its impacts on the ecosystem dynamics. Consequently, this model provides a relatively simple example of ecosystem-based management. This model formulation was extended in Bhattacharyya and Pal (2015), who additionally accounted for external recruitment of macroalgae. In their model, they assumed that macroalgae produces inhibitory toxins to coral growth. The authors demonstrate that reef resilience declines with increases in macroalgae toxicity.

There are many other assumptions made in Blackwood et al. (2012) that have been relaxed in other settings. For example, van de Leemput, Hughes, van Nes, and Scheffer (2016) argue that there is not necessarily a single strong feedback—such as the positive feedback between coral and grazers—but that there are several feedbacks whose strength varies in both time and space. Therefore, it is essential to consider local dynamics of individual reefs and assess what feedbacks may be present. To test this, van de Leemput et al. (2016) constructed a model with three weak feedbacks; that is, each feedback is not independently capable of generating alternative stable states. The model they constructed makes a couple of key assumptions: both coral and macroalgae can both grow through importation at rates i_C and i_M , and they grow proportionally to the amount of coral and macroalgae present at rates r and γ , respectively. Similar to other models described in this review, they assume that there is a natural mortality rate of coral (d). Finally, they explicitly model herbivore (assumed to include all reef grazers) population dynamics and assume they take the same structure as Blackwood et al. (2012). Finally, it is assumed that macroalgae is removed at a rate proportional to the number of grazers and present algae so that

$$\frac{dC}{dt} = (i_C + rC)T - dC, \quad (12)$$

$$\frac{dM}{dt} = (i_M + \gamma M)T - gMP, \quad (13)$$



$$\frac{dP}{dt} = sP \left(1 - \frac{P}{K} \right) - fP. \quad (14)$$

They then modified this model accordingly to test three different feedbacks: saturation of herbivore consumption with sufficiently high algal coverage, competition between coral and macroalgae, and increases in herbivores corresponding to increases in coral cover through, for example, more suitable habitat conditions. In analyzing this model, the authors importantly concluded that it is possible for multiple weak feedbacks to collectively generate phase shifts.

In another modeling study, Bozec, Yakob, Bejarano, and Mumby (2013) did not model grazer dynamics explicitly (as in Equation 11) but they relaxed some assumptions about grazing and fishing behaviors. For example, they considered two different genres of parrotfish (*Scarus* and *Sparisoma*) that had associated grazing rates of G_{scar} (for *Scarus*) and G_{spar} (for *Sparisoma*). Each of these terms directly depended on properties related to each genus of parrotfish. For example, Bozec et al. (2013) tested two assumptions on how parrotfish abundance—and therefore grazing rates—may change with changes in rugosity (a measure of structural complexity of a reef). Specifically, they tested both a linear response and a Type II Holling response in which increases in parrotfish abundance eventually saturates with a high enough rugosity. Such saturation may occur from, for example, density dependent competition among parrotfish for food resources and habitat. Additionally, each species has different grazing behavior; *Scarus* preferentially consume algal turf whereas *Sparisoma* graze indiscriminately on both algal types (as in the original model). Now, the differential equation for macroalgal dynamics can be written as

$$\frac{dM}{dt} = aMC - \frac{G_{\text{spar}}M}{M+T} + \gamma MT - \left(G_{\text{scar}} + \frac{G_{\text{spar}}T}{M+T} \right) MT. \quad (15)$$

Due to the way in which both species graze on turf, the rate of macroalgal overgrowth of turf is slowed down due to grazing (as reflected in the final term in this equation). Finally, these authors also consider losses due to hurricane impacts. These authors highlight that coral resilience increases with the strength of the positive feedback between coral and grazing: if rugosity increases then parrotfish abundance increases, which leads to an increase in grazing and, in turn, coral faces less competition and maintains greater rugosity.

While the models described in this section directly look at the effect of changes in the grazing rates, other models consider whether grazing rates near the critical grazing threshold—the grazing rate at which the system shifts to a coral-depleted state—can be detected in time series data. For example, Fung, Seymour, and Johnson (2013) expanded the model introduced by Fung et al. (2011) (see Equations 3–5) to account for demographic stochasticity. They used stochastic simulations to assess whether early warning signals (Scheffer et al., 2009) arise when the grazing rate is approaching its critical threshold. While they conclude that some early warnings indicators appear near the critical grazing threshold (such as an increase in variance), other early warning indicators (such as skewness) do not.

4.2 | Climate change

Climate change and related increases in ambient CO₂ levels have led to increased ocean temperatures, increased frequency and severity of hurricanes, and ocean acidification, each of which distinctly impacts the coral reef ecosystem. When water temperatures are too high, coral lose beneficial symbiotic algae resulting in what is called coral bleaching. Bleaching events reduce coral survival, growth, and reproduction (Hoegh-Guldberg, 1999). Warmer ocean temperatures have increased the frequency



and severity of bleaching events (Heron, 2016). Increasing ambient CO₂ concentrations are causing the ocean to become more acidic, which may reduce calcification rates and accelerate the disintegration of coral skeletons and calcified substrate (Hoegh-Guldberg et al., 2007). Increased temperatures as a result of climate change can also lead to higher hurricane frequencies and intensity, which lead to discrete physical disturbances to the organisms and calcium substrate.

There are many models of the alternative stable states between coral and algae that consider reef stress under climate change in different ways. For example, Edmunds et al. (2014) developed a metapopulation model to determine the relative importance of coral traits in responding to thermal stress as a proxy for climate change. They model macroalgae, coral recruits, and coral adults on n patches, which are connected through dispersal of coral and algal recruits. The model assumes that a fraction of coral recruits stay in the patch they originate from and the rest are evenly distributed among all other patches. We forgo the modeling details here, but the authors captured several processes that could differ between coral species such as general life history traits (e.g., dispersal and mortality rates), resistance to overgrowth by macroalgae, and tolerance to thermal stress. Through simulations and sensitivity analyses, the authors identified thermal tolerance, growth rate, and lifespan of corals as the primary predictors of coral resilience in the face of increasing thermal stress.

Following this study, Fabina, Baskett, and Gross (2015) developed a model to explore the consequences of bleaching events as they increase in severity or frequency. Similarly to Edmunds et al. (2014), these authors start with a nonspatial stage-structured model of coral and macroalgae, which differentiates between coral adults and juvenile recruits. This stage structure of coral provides the flexibility to capture stage-specific differences between responses to bleaching events. The three base differential equations in the Fabina et al. (2015) model are omitted here, but have many components similar to other basic differential equations models discussed in this paper. However, in their model, grazing of macroalgae is broken into two components: one that captures density-independent grazing at a fixed rate and another for density-dependent grazing that saturates as adult coral cover increases. These authors added an additional layer to their model that stochastically captured bleaching events. To develop this component of their model, they used climate models to determine how bleaching frequency and magnitude would increase with changes in climate. Their findings indicate that severe bleaching events lead to greater overall damage as compared to higher frequency but less severe events. Based on their results, the authors delineate two primary findings related to reef conservation: protection of corals that are less resistant to bleaching events should be prioritized when bleaching events are relatively mild, and more resistant corals should be prioritized when bleaching events are severe.

In another study that investigated coral responses to thermal stress, Baskett, Fabina, and Gross (2014) extended Mumby et al. (2007) to assume that there are up to two types of coral: one capable of withstanding higher levels of stress (referred to as “resistant” coral, C_S), and a second that experiences faster recovery following disturbance (referred to as “resilient” coral, C_L). In the setting constructed by these authors, a given community can have either one type or both types present and it is therefore assumed that $T = 1 - C_S - C_L - M$. Additionally, the coral types compete with each other for space which is captured by competition parameters α_S and α_L . The other parameters associated with each coral type can differ according to their specific properties; for example, the rate at which macroalgae overgrows coral is specific to whether the coral is resistant or resilient. These authors additionally assume that there is a density-independent external recruitment rate for both coral types in addition to macroalgae ($r_{ex,S}$ and $r_{ex,L}$ for resistant and resilient corals, respectively, and $r_{ex,M}$ for macroalgae). Under these assumptions, the model is given by:

$$\frac{dC_S}{dt} = r_{ex,S}T + r_S(1 - M - C_S - \alpha_S C_L)C_S - d_S C_S - a_S M C_S, \quad (16)$$



$$\frac{dC_L}{dt} = r_{ex,L}T + r_L(1 - M - \alpha_L C_S - C_L)C_L - d_L C_L - a_L M C_L, \quad (17)$$

$$\frac{dM}{dt} = r_{ex,M}T + a_S M C_S + a_L M C_L - \frac{g}{M + T} + \gamma M T. \quad (18)$$

Finally, they stochastically implement damage to each species of coral due to the consequences of thermal stress (e.g., coral bleaching). These authors conclude that coral resilience increases when both coral types are present under two main conditions: the resilient coral does not outcompete the resistant coral, and disturbances are sufficiently severe so that resilient corals cannot survive independently. Moreover, the authors conclude that management needs to account for both site diversity and connectivity.

In general, modeling the dynamical effects of ocean warming and acidification is constrained by both uncertainty and complexity in the underlying processes that drive them. Therefore, a common way in which to explore the impacts of these stressors to reefs is through “implicit” approaches in which the parameters within a model can vary as environmental conditions change. For example, Anthony et al. (2011) adapted the model of Mumby et al. (2007) and used it to investigate how combinations of different levels of CO₂ and fishing pressure may impact reef communities. They included stochastic background mortality as a proxy for accounting for other stressors that do not directly correlate with CO₂ (e.g., hurricane damage). In their parameterization, they assumed that ocean acidification impacts coral calcification (and therefore coral growth rates), ocean warming affects coral mortality (through, e.g., bleaching events), grazing pressure affects algal mortality rates, and nutrient enrichment affects the growth rate of algae. Anthony et al. (2011) modified the original model by converting the coral colonization rate of free space (r) and coral mortality rate (a) into functions that are parameterized based on ocean acidification (as measured by the aragonite saturation state, which is a measure of carbonate ion concentration) and sea surface temperature. These authors concluded that both ocean warming and high levels of acidification are capable of lowering coral resilience.

While Anthony et al. (2011) and some of the models in Section 4.1 consider hurricane impacts as a part of their analyses, we highlight several papers that focus on them more exclusively. For example, Blackwood, Hastings, and Mumby (2011) considered multiple stressors to reefs: fishing and hurricane damage. Fishing was implemented as described above (Equation 11) and they added an equation for coral rugosity—which can be substantially impacted by hurricane impacts—so that it increases with the presence of living coral (C) and decreases from bioerosion. They then implement hurricanes stochastically using stochastic jump processes such that hurricane impacts follow a Poisson distribution and occur at a rate λ . In their model, hurricanes instantaneously cause decreases in coral cover, macroalgal cover, and rugosity. These authors concluded that management should be adapted according to local conditions: if hurricane impacts are relatively low, stronger regulations on fishing should be enforced. In contrast, if hurricane damage is high, efforts should be focused on restoration.

Related constructions of models with hurricane impacts have used the Dirac delta function to impose an instantaneous reduction to coral, macroalgae, and turf (Ippolito, Naudot, & Noonburg, 2016). However, they did not consider rugosity. In another modeling study, Obolski, Hadany, and Abelson (2016) performed a follow-up analysis to Blackwood et al. (2011) in which they performed a cost–benefit analysis to analyze the potential for fish restocking as a control method. These authors concluded that a moratorium on fishing coupled with restocking programs may improve reef health.

Many of the models we have discussed so far focus on just one or two environmental factors or include them in simplified ways. Baskett, Nisbet, Kappel, Mumby, and Gaines (2010) attempt to quantitatively prioritize the most important actions we can take to protect corals by constructing a fairly complex model, synthesizing and extending the models presented in Mumby et al. (2007), Baskett,



Gaines, and Nisbet (2009), and more. Their model accounts for many of the most important dynamics on coral reefs, including symbiont thermal sensitivity, coral competition with macroalgae, size structure of coral populations, and the potential effects of multiple symbiont strains, multiple coral species, and multiple spatial patches. This model was able to reproduce most major historical trends and bleaching events in the locations modeled (the Bahamas), and the authors used both model sensitivity and model dynamics to inform their conclusions. While the authors of Baskett et al. (2009) do not claim that their model should be used for quantitative prediction, they use qualitative comparisons of the model predictions to inform their management recommendations. They conclude that the most important management goals should be (i) conservation of diverse coral communities rather than homogeneous but thermally tolerant communities, (ii) mitigation of anthropogenic impacts that affect coral–macroalgal competition and juvenile coral survivorship, and (iii) protection of both locations and connectivity to locations with oceanographic features that lead to lower thermal stress.

5 | DISCUSSION

Coral reefs support an incredible amount of biodiversity and provide numerous ecosystem services ranging from fisheries production to coastal defense from storms (Moberg & Folke, 1999). In the Caribbean, many stressors including those related to declines in algal grazing following the great urchin die-off of the early 1980s provide a constant challenge to the resilience of reefs. In particular, the existence of two alternative stable states—a desirable state with high levels of coral cover and a degraded coral-depleted state—has been frequently hypothesized in the literature. Understanding the mechanisms that may lead to the presence of alternative stable states as well as processes that underlie phase shifts between them is a central research priority for managing coral reef ecosystems.

In this review paper, we highlighted several modeling studies that are centered on the most parsimonious explanation for the presence of alternative stable states. In particular, declines in grazing of macroalgae by herbivorous reef fish allow macroalgae to outcompete coral and proliferate, ultimately resulting in a phase shift to the degraded algal-dominated state. Subsequent increases in grazing gives rise to algal turfs and thereby frees up space for coral to recruit to and then proliferate, leading to a stable state with high levels of coral cover. Early influential models of algal–coral interactions centered almost exclusively on these processes (e.g., Fung et al., 2011; Mumby et al., 2007). Since the initial conception of these models, many more studies have been performed that build upon the central algal–coral interaction framework. This review provides a summary of these related modeling studies to date, ranging from models that expand the community composition to evaluating the resilience of coral when faced with one or more of its many stressors.

While many modeling studies exist, several considerations remain that may be important for future research. For example, while some studies explicitly integrate algal–coral dynamics with the population dynamics of herbivores, interactions between trophic levels of fish are typically not accounted for. Such studies that include additional trophic interactions could reveal important considerations for designing management strategies. As a second example, a recent paper used the Fung et al. (2011) framework to demonstrate that the bottom-up processes of sedimentation and eutrophication (which can result from coastal development) are capable of driving phase shifts to alternative stable states in reef ecosystems (Arias-González et al., 2017). The importance of these stressors has also been empirically documented (e.g., Lapointe, 1997). However, sedimentation and eutrophication have been given much less attention as potential drivers of phase shifts in modeling studies centered on algal–coral dynamics. Further research is therefore needed to better understand potential management implications.



While the focus of this study is on models of ODEs, several other frameworks exist to investigate coral–algal dynamics in more complex settings. For example, several approaches have been utilized to explicitly model populations spatially. Mumby (2006) developed a spatial simulation model in which coral–algal interactions occur over a large grid of cells. In another setting, Melbourne-Thomas et al. (2011) developed a large-scale model on a spatial grid where local dynamics were determined by differential equations describing the dynamics of eight key organisms and larval transport connected patches regionally. Spiecker, Gouhier, and Guichard (2016) implemented their integro-difference equations on 200 coupled patches, which were connected through material transport and dispersal and analyzed the dynamics to test the effectiveness of various configurations of marine reserves.

In addition to focusing on models constructed of ODEs, our emphasis here is on models derived predominantly from studies of Caribbean coral reefs. Nevertheless, the same stressors of overfishing, bioerosion, elevated temperatures, increasing ocean acidity, local impacts of human habitation, etc., affect the reefs of the Indo-Pacific as well with concomitant increases in macroalgae cover and decreases in coral cover (Bruno & Selig, 2007; Glynn & Manzello, 2015; Nordström, Nordström, Lokrantz & Folke, 2009). Thus, it is likely that this modeling approach is applicable to reef dynamics in the Indo-Pacific as well. The Indo-Pacific did not experience the great *Diadema* die-off of the Caribbean but the consequences of the loss of herbivory afflicts reefs in both regions. Perhaps the most important unique stressor of the Indo-Pacific is the recurrence of *Acanthaster* predation outbreaks (Clements & Hay, 2017), which might need to be accommodated in models for greater predictive power in Indo-Pacific reefs.

More generally, mathematical models serve as a complementary tool to field and experimental studies. We highlight a range of mathematical models that have contributed to the growing body of literature on coral–algal interactions and phase shifts in Caribbean reefs. Further studies that expand upon these ideas will be important in obtaining a more holistic understanding of complex coral ecosystem dynamics.

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APPENDIX A: STABILITY ANALYSIS OF BASELINE CORAL-ALGAL MODEL

In this section, we provide a detailed stability analysis for the original model of Mumby et al. (2007). First, we can identify the model equilibria by setting the right-hand side of Equations (1) and (2) equal to zero or, equivalently, define:

$$f_1 = (rT - d - aM)C, \quad (\text{A1})$$

$$f_2 = \left(aC - \frac{g}{M+T} + \gamma T \right) M, \quad (\text{A2})$$

and identify the points at which $f_1 = f_2 = 0$. Replacing T with $1 - M - C$, from Equation (A1), we obtain the equilibrium conditions that $C^* = 0$ and $r(1 - M^* - C^*) - d - aM^* = 0$. Similarly, from Equation (A2) we have that $M^* = 0$ and $aC^* - \frac{g}{1-C^*} + \gamma(1 - M^* - C^*) = 0$. From this, we can obtain five equilibria:

$$(C^*, M^*) = \left\{ (0, 0), \left(0, \frac{\gamma - g}{\gamma} \right), \left(\frac{r-d}{r}, 0 \right), (\hat{C}_1, \hat{M}_1), (\hat{C}_2, \hat{M}_2) \right\}, \quad (\text{A3})$$

where $\hat{C}_i, \hat{M}_i \neq 0$ for $i = 1, 2$. For the second two equilibria to have biological relevance, we require that $\gamma > g$ (macroalgae spreads over turf faster than it is grazed) and $r > d$ (coral overgrows turf faster than it succumbs to natural mortality). The final two equilibria are found by simultaneously solving $r(1 - M^* - C^*) - d - aM^* = 0$ and $aC^* - \frac{g}{1-C^*} + \gamma(1 - M^* - C^*) = 0$. After simplifying, these equilibria can be found explicitly as the roots of a quadratic in C . As shown in Figure 1B, the final equilibrium only exists for a range of values of g . Additionally, only the larger of these two equilibria is non-negative for the parameterization used in Figure 1B; therefore, hereafter we only consider the larger of the two and redefine it as (\hat{C}, \hat{M}) .

To analyze the stability of these equilibria, we first find the Jacobian matrix, J :

$$\begin{bmatrix} \frac{\partial f_1}{\partial C} & \frac{\partial f_1}{\partial M} \\ \frac{\partial f_2}{\partial C} & \frac{\partial f_2}{\partial M} \end{bmatrix} = \begin{bmatrix} r(1 - 2C - M) - d - aM & -(r+a)C \\ (a-\gamma)M - \frac{g}{(1-C)^2}M & aC - \frac{g}{1-C} + \gamma(1 - C - 2M) \end{bmatrix}.$$

The stability of each equilibrium can be found by determining the sign of the eigenvalues of J evaluated at the equilibrium. At the origin, the eigenvalues are given by $\lambda_1 = r - d$ and $\lambda_2 = \gamma - g$. By our assumption that $\gamma > g$ and $r > d$, both eigenvalues are positive. Recalling that an equilibrium is locally unstable if both eigenvalues positive, then the origin is unstable.

For the equilibrium corresponding to healthy state with high levels of coral cover, we find that the eigenvalues are:

$$\begin{aligned} \lambda_1 &= d - r, \\ \lambda_2 &= a \left(\frac{r-d}{r} \right) - \frac{gr}{d} + \frac{\gamma d}{r}. \end{aligned}$$

In this case, the first eigenvalue is always negative (by our assumption that $r > d$). The second eigenvalue is negative only when

$$g > \frac{ad}{r} \left(\frac{r-d}{r} \right) + \frac{\gamma d^2}{r^2}. \quad (\text{A4})$$



Recalling that an equilibrium is locally stable if all of its eigenvalues are negative valued, then this equilibrium is only stable when the grazing rate is sufficiently high. Moreover, notice that when the grazing rate is equal to the right-hand side of Equation (A4), it is exactly equal to g_1 in Figure 1B.

For the equilibrium corresponding to a degraded coral-depleted state, we find that the eigenvalues are:

$$\lambda_1 = (r - d) - (r + a)\frac{\gamma - g}{\gamma},$$

$$\lambda_2 = g - \gamma.$$

While $\lambda_2 < 0$, $\lambda_1 < 0$ only when

$$g < \gamma \left(\frac{a + d}{a + r} \right). \quad (\text{A5})$$

This equilibrium is locally asymptotically unstable when both eigenvalues are negative; therefore, the coral-depleted state is stable for sufficiently low levels of grazing and unstable otherwise. Note the grazing rate takes on the value on the right hand side of Equation (A5), this is exactly the value g_2 as displayed in Figure 1B.

The final equilibrium where both coral and macroalgal cover are nonzero, (\hat{C}, \hat{M}) , is much more algebraically complicated, so we omit the details here. However, it can be shown that under our parameterization this equilibrium (when biologically relevant) is always a saddle point. Importantly, this stability analysis demonstrates the presence of alternative stable states.