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Authors

Fabina, Nicholas S
Baskett, Marissa L
Gross, Kevin

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The differential effects of increasing frequency and magnitude of extreme events on coral populations

Nicholas S. Fabina,[1,4] Marissa L. Baskett,[2] and Kevin Gross[3]

[1]*Department of Evolution and Ecology, University of California, One Shields Avenue, Davis, California 95616 USA*
[2]*Department of Environmental Science and Policy, University of California, One Shields Avenue, Davis, California 95616 USA*
[3]*Biomathematics Program, North Carolina State University, Box 8203, Raleigh, North Carolina 27695 USA*

Abstract. Extreme events, which have profound ecological consequences, are changing in both frequency and magnitude with climate change. Because extreme temperatures induce coral bleaching, we can explore the relative impacts of changes in frequency and magnitude of high temperature events on coral reefs. Here, we combined climate projections and a dynamic population model to determine how changing bleaching regimes influence coral persistence. We additionally explored how coral traits and competition with macroalgae mediate changes in bleaching regimes. Our results predict that severe bleaching events reduce coral persistence more than frequent bleaching. Corals with low adult mortality and high growth rates are successful when bleaching is mild, but bleaching resistance is necessary to persist when bleaching is severe, regardless of frequency. The existence of macroalgae-dominated stable states reduces coral persistence and changes the relative importance of coral traits. Building on previous studies, our results predict that management efforts may need to prioritize protection of "weaker" corals with high adult mortality when bleaching is mild, and protection of "stronger" corals with high bleaching resistance when bleaching is severe. In summary, future reef projections and conservation targets depend on both local bleaching regimes and biodiversity.

Key words: alternative stable states; climate change; coral bleaching; ecological projection; global sensitivity analysis; population dynamics; random forests; species distribution model; Symbiodinium.

INTRODUCTION

Global climate change is expected to have substantial effects on ecological systems (Parmesan 2006), motivating accurate ecological forecasts for future climate scenarios. Ecological forecasts typically focus on the effects of changes in mean environmental variables, but changes at the extremes may also push ecological systems beyond their tolerances (Jentsch et al. 2007). The frequency and magnitude of extreme events are projected to continue changing over the next century (Hoegh-Guldberg 2000, Jentsch et al. 2007) with substantial spatial and temporal variance (Hoegh-Guldberg 2000, Selig et al. 2010). While static models suggest the distributional effects of changing extremes (Jentsch et al. 2007), disentangling the relative effects of changing frequency and magnitude of extreme events on population persistence requires a consideration of dynamic populations.

The effects of climate change on Scleractinian corals demonstrate the potential for extreme events to influence ecological systems. Hard corals are the foundation of tropical coral reefs, and they are severely impacted by extreme temperature events associated with a warming climate (Hoegh-Guldberg 2011). Sustained temperature increases can cause mass bleaching events and coral mortality (Douglas 2003). These events have contributed to widespread reef degradation (Pandolfi et al. 2005), especially with projected increases in bleaching frequency and magnitude over the next century (Hoegh-Guldberg 2000, Donner et al. 2005, Baker et al. 2008). However, recent research has highlighted spatial and temporal variance in bleaching across reef locations (Hoegh-Guldberg 2000, Selig et al. 2010) and corals vary in their responses to thermal stress (Obura 2005, Fabricius et al. 2011, Pandolfi et al. 2011, van Woesik et al. 2011, Darling et al. 2013). These circumstances raise the possibility that some reef locations or coral species may be relatively buffered from warming seas.

The ability to identify oceanographic features and coral phenotypes that enhance reef resistance or resilience to bleaching could facilitate focused management efforts (West and Salm 2003, Obura 2005, Game et al. 2008). While many reef ecosystems could experience frequent and severe bleaching events by mid-century under business-as-usual emissions scenarios, some locations may experience fewer and/or milder events (Donner et al. 2005). It is unclear whether the frequency or severity of bleaching events has the greater impact on coral persistence. In addition, the effects of bleaching frequency or magnitude may depend on coral traits or life histories. Coral persistence is hypothesized to be maximized by high recruitment rates and other recovery-

related attributes when disturbances are frequent (e.g., growth or asexual recruitment), and by low adult mortality and other survival-related attributes when disturbances are severe (West and Salm 2003, Obura 2005). However, this hypothesis has not been tested under a range of bleaching regimes, nor has the relative importance of recovery- and survival-related attributes been compared.

Complicating matters further, the presence of coral-dominated and macroalgae-dominated alternative stable states can influence coral reef community dynamics (Mumby et al. 2007, Baskett et al. 2010, Anthony et al. 2011, Fung et al. 2011). High coral cover can be associated with high rates of herbivory, while high macroalgal cover is linked to low herbivory and inhibited coral recruitment (McCook et al. 2001). Competitive interactions between coral and macroalgae have the potential to influence coral responses to bleaching events, as coral mortality from extreme temperatures can lead to increased macroalgal cover (McCook et al. 2001). This effect may depend on bleaching frequency and magnitude, as well as coral traits like survivorship and growth. Although the relevance of alternative stable states to coral reef dynamics remains controversial (Bruno et al. 2009, Roff and Mumby 2012, Mumby et al. 2013), these connections are relevant to reef communities with more evidence for competitive interactions (e.g., Caribbean vs. Indo-Pacific; Roff and Mumby 2012).

In this study, we coupled climate projections and a dynamic population model to explore the effects of increasing bleaching frequencies and magnitudes on coral populations. First, we quantified how coral persistence and cover depended on bleaching frequency and magnitude. Second, we determined whether the relative importance of different coral life history traits depended on bleaching regime, as well as whether traits contributed differentially to coral persistence or cover. Finally, we tested whether the existence of stable macroalgae dominance could influence the effect of bleaching regime and different coral traits.

METHODS

We constructed a stage-structured population model of a coral species with a macroalgae competitor by building on existing theory (Mumby 2006, Mumby et al. 2007, Blackwood and Hastings 2011, Blackwood et al. 2011, 2012, Fung et al. 2011). We parameterized our model with values gathered from the literature and simulated coral responses to projected ranges of bleaching frequencies and magnitudes. To analyze our results, we conducted a global sensitivity analysis to explore the effect of coral attributes on persistence and cover, and investigated whether the presence of alternative stable states influenced our results. We will describe the (1) coral population model, (2) implementation of bleaching events, (3) model simulation, and (4) model analysis.

Deterministic population dynamics: coral–macroalgal interactions

We used a stage-structured model coral and macroalgae competition because it captures the essential biological and ecological dynamics relevant to our questions (Fig. 1a; model modified from Mumby et al. 2007, Baskett et al. 2014). Moreover, the stability of our model is easily determined (Appendix A). Our model tracks the proportion cover of coral adults (A) and recruits (R), as well as macroalgae (M) and the remaining free space ($F = 1 - R - A - M$) in a single coral reef patch. Coral adults and macroalgae colonize free space via recruitment and growth at rates proportional to their cover (r_A for coral recruitment, g for coral growth, and r_M for macroalgae recruitment and growth). Coral recruits do not contribute to recruitment or growth, but mature to adulthood at a fixed rate a. Macroalgae has a competitive advantage over coral such that it can overgrow adult colonies at a rate β ($\leq r_M$) and overgrow juvenile corals at the same rate as growth into free space r_M. However, adult corals can indirectly compete by increasing herbivory (e.g., by providing habitat for herbivorous fish; Mumby 2006). Total herbivory is the sum of baseline herbivory at a constant rate h_b (which encapsulates macroalgae loss to other density-independent processes as well) and supplementary herbivory at a rate h_s that saturates with adult coral cover according to the parameter ω. Coral mortality occurs at a constant rate, where adult mortality d_A is less than recruit mortality d_R and accounts for mortality resulting from all causes other than extreme thermal stress. Both coral and macroalgae mortality create free space, which can then be recolonized via recruitment or growth.

Thus, our system is described by

$$\frac{dR}{dt} = r_A A(1 - R - A - M) - aR - r_M RM - d_R R$$

$$\frac{dA}{dt} = aR + gA(1 - R - A - M) - \beta AM - d_A A$$

$$\frac{dM}{dt} = r_M M(1 - R - A - M) + r_M RM + \beta AM$$
$$- h_b M - h_s M \frac{\omega A}{1 + \omega A}. \tag{1}$$

We determined ranges and values for model parameters from the literature (Table 1) and fixed macroalgae parameters as constants to focus on coral attributes. Model explorations indicated that our results were not sensitive to changes in parameter ranges or constants, the inclusion of external coral recruitment, or multiple reef patches.

Stochastic population dynamics: bleaching events

We used climate models to identify projected increases in bleaching frequency and magnitude, and then ran simulations under various bleaching regimes. We
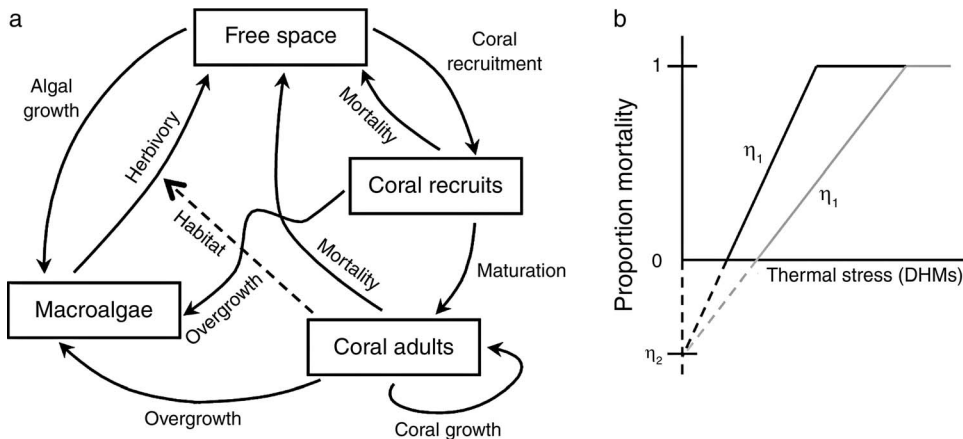
Fig. 1. (a) Demographic processes govern changes in state variables in the model, and (b) the parameter eta (η) controls the relationship between thermal stress and coral mortality. In our model (a), free space is colonized by either corals or macroalgae via recruitment and growth. Coral recruits advance to adulthood at a fixed rate. Free space is created when corals or macroalgae experience mortality. Coral mortality occurs at a constant rate and during density independent bleaching events. Macroalgae death is composed of natural mortality, baseline herbivory, and supplemental herbivory, the latter being a function of coral cover. Macroalgae outcompetes coral for space and can overgrow adults and recruits. Bleaching resistance (b) is calculated by converting degree heating months (DHMs) to proportion mortality via the parameters η_1 and η_2. The parameter η_1 can differ between coral species, while η_2 is held constant, so that coral species with lower η_1 have greater bleaching resistance.

measured coral bleaching severity with the cumulative stress metric of degree heating months (DHMs; Donner 2011), where 1 DHM is defined as a temperature increase of 1°C over the mean monthly temperature for a single month. One DHM may signify a 1°C increase that persists for four weeks or a 2°C increase for two weeks, but the temperature increase in a given week needs to be greater than 1°C to count toward a DHM. DHM accumulate over a rolling 12-week summer period

and the greatest DHM value determines the severity of the bleaching events in a given year.

For our model, we assumed that coral mortality is a linear function of DHM and that corals have a bleaching threshold, below which DHM values are not sufficient to cause mortality (Fig. 1b; Douglas 2003, Donner 2011). We defined coral bleaching mortality as a function of DHM with slope η_1 and intercept $-\eta_2$, bounded between zero and one:

TABLE 1. Model parameters adapted from Fung et al. (2011).

Parameter	Notation	Min	Max	Constant	Units
Coral parameters					
Coral recruitment	r_A	0.0005	0.05		time^{-1}
Recruit maturation	a	0.2	0.65		time^{-1}
Adult growth	g	0.1	0.4		time^{-1}
Recruit mortality	d_R	0.25	1.5		time^{-1}
Adult mortality	d_A	0.002	0.4		time^{-1}
Macroalgae parameters†					
Macroalgae recruitment‡	r_M			0.4	time^{-1}
Baseline macroalgae mortality§	h_b			0.2	time^{-1}
Supplemental macroalgae mortality	h_s			0.4	time^{-1}
Competition					
Recruit overgrowth‡	r_M			0.4	time^{-1}
Adult overgrowth	β	0	0.4		time^{-1}
Herbivore habitat provisioning	ω	0	4		prop. coral adult cover
Bleaching					
Slope of bleaching sensitivity	η_1	0	0.25		prop. mortality × DHM^{-1}
Intercept of bleaching sensitivity	η_2			0.375	prop. mortality

Note: Abbreviations are: prop., proportion; and DHM, degree heating month.

† The minimum (min) and maximum (max) possible values are provided for all parameters that were varied for the global sensitivity analysis, while macroalgae parameters were held constant.

‡ We assume macroalgae recruitment and overgrowth of coral recruits are equivalent, and the same symbol and value represents both.

§ We assume that baseline macroalgae mortality incorporates natural mortality and baseline herbivory.

$$\mu = \begin{cases} 0, & \text{if } \eta_1\text{DHM} - \eta_2 \leq 0 \\ 1, & \text{if } \eta_1\text{DHM} - \eta_2 \geq 1 \ . \\ \eta_1\text{DHM} - \eta_2 & \text{otherwise} \end{cases}$$

To focus the analysis of bleaching sensitivity on a single parameter, we fixed the intercept η_2 and varied the slope η_1 (Table 1). Thus, greater values of η_1 increase coral sensitivity to changes in DHM, and also lower the DHM necessary to induce bleaching or cause complete coral mortality. This approach allowed us to test how coral sensitivity to bleaching initiation and accumulated mortality influence population responses, but further analyses could distinguish between these effects by also modifying the intercept η_2 or by testing nonlinear accumulation functions.

We determined the ranges of projected bleaching frequencies and magnitudes via DHM datasets generated from climate models (Donner et al. 2005, Logan et al. 2013). These data indicated that bleaching frequencies of four out of every five years and DHM of 8 were reasonable upper bounds to test. These upper bounds approximate AR4 end-of-century projections (Donner et al. 2005) and AR5 mid-century projections (Logan et al. 2013), and therefore reflect disturbance expected in management-relevant time spans. Model explorations demonstrated that our qualitative results are consistent outside these ranges.

We implemented stochastic bleaching events by iterating through the deterministic population dynamics model (System 1) for one year. Bleaching survivorship was applied to adult and juvenile cover (Eq. 2) by drawing DHMs from a normal distribution with mean equal to the simulation's bleaching magnitude and standard deviation equal to 0.05. Formally, our model is a semi-discrete system with the inclusion of stochastic, discrete bleaching events (see Appendix B for the formal model notation; Mailleret and Lemesle 2009).

Simulation structure and output

Our model has four possible stability structures in the absence of bleaching events. Depending on parameter values, coral can exclude macroalgae, macroalgae can exclude coral, the two can coexist, or dominance is determined by initial conditions (alternative stable states; see Appendix A). We focused our analyses on parameter sets that resulted in coral dominance or alternative stable states. Under these conditions, bleaching events can flip the system from coral dominance to macroalgae dominance either temporarily or permanently. We directly contrasted results under each stability structure by holding coral parameters constant and increasing macroalgae mortality and baseline herbivory (h_b) from 0.2 to 0.4 (additional stability calculations confirmed this change was sufficient; see Appendix A). Parameter sets for macroalgae dominance were irrelevant because corals could not persist regardless of bleaching, and those for coexistence represented a very small range of parameter space ($<1\%$).

We ran 1000 simulations for each combination of bleaching frequency and magnitude, with unique coral parameters drawn for each individual simulation. Coral cover was initiated at the dominant, equilibrium values (see Appendix A) and macroalgae at 10% cover (or at 90% of the remaining cover if equilibrium coral cover was greater than 90%). Each simulation lasted for 250 time steps, and the first 100 time steps were discarded to reduce the effect of initial condition-dependent transients. Coral persistence was defined as adults and recruits having greater than 1% cover for the last five time steps. Coral cover was calculated as the mean sum of recruit and adult cover for the last 150 time steps. Numerical simulations were conducted with the *ode*() function in R (*desolve* package, Runge-Kutta methods; Soetaert et al. 2010, R Development Core Team 2013). Qualitative model results were not sensitive to the choice of simulation length, initial macroalgae cover, or extinction threshold.

Global sensitivity analysis using random forests

We conducted a global sensitivity analysis (GSA) for parameter values using random forests (Breiman et al. 1984, Breiman 2001, Boulesteix et al. 2012). Random forests use multiple classification or regression trees to analyze randomly selected subsets of data. Here, the main advantages of random forests are increases in GSA accuracy and evaluations of parameter importance when all coral traits are perturbed simultaneously, rather than one at a time. For our GSA, we used coral parameter values to predict coral persistence with categorical trees and mean coral cover with regression trees (*randomForest* package in R; Liaw and Wiener 2002, R Development Core Team 2013).

We used parameter importance values to demonstrate how coral traits were related to coral persistence and mean cover (*randomForest* package; Liaw and Wiener 2002, R Development Core Team 2013). Importance values quantify how often a parameter is selected for splits within classification and regression trees, as well as how informative that parameter is for prediction (i.e., the loss in predictive ability by deletion of that parameter; Breiman 2001). We used training and testing sets at 80% and 20% of the data, respectively, to ensure that our random forest was calibrated appropriately (Breiman 2001). Our explorations suggested predictive power and error metrics approached their asymptotic values at 100 trees with 100 branches.

We created a random forest for each bleaching regime to understand qualitative trends in parameter importance and then highlighted four regimes to demonstrate these trends. The highlighted bleaching regimes spanned the entirety of the frequency and magnitude combinations, with bleaching either infrequent (0.25 probability) or frequent (0.70) and mild (2.5 DHM) or severe (7.0). We refer to once-every-four-years bleaching frequency and 2.5 DHM bleaching severity as "infrequent" and "mild" because these values were on the low end for
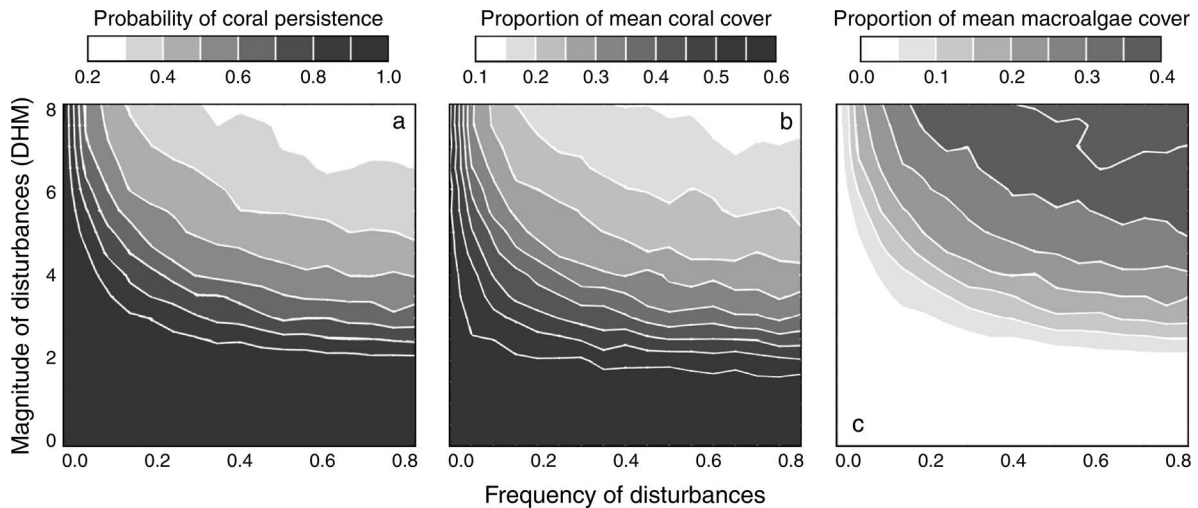
FIG. 2. Increasing bleaching frequency and magnitude affects the (a) probability of coral resistance, (b) mean proportion of coral cover, and (c) mean proportion of macroalgae cover. Coral persistence was defined as adults and recruits having greater than 1% cover for the last five time steps. Increasing magnitudes (y-axes) have a greater effect on coral population dynamics than increasing frequencies (x-axes; a, b), e.g., coral cover changes more from bottom to top (increasing magnitude) than from left to right (increasing frequency; b). Coral persistence and cover follow the same trend (a, b), while mean macroalgae cover exhibits an opposing trend due to competition for space (c).

future thermal regimes; note that these conditions are not infrequent or mild in the historical sense. We conducted an additional 10 000 simulations for these four regimes to ensure our results were robust to further simulation data.

Results

Increasing bleaching frequencies vs. magnitudes

Our model predicted that severe bleaching is more detrimental to Scleractinian corals than frequent bleaching (Fig. 2). The results in this section and the following two sections focus on scenarios where corals are dominant and alternative stable states do not exist. Increasing bleaching magnitude had the greatest effect on coral persistence and cover when events occurred more frequently than a very low threshold (approximately one bleaching event every 20 years; Fig. 2a, b). Increasing bleaching frequency had little effect when events were mild because each event had a negligible impact on coral populations. Increasing bleaching frequency also had little effect when events were severe because a small number of severe events could drastically reduce coral cover. Additional severe events did not alter model dynamics. The effects of increasing frequency were maximized when bleaching magnitudes were intermediate. Under these conditions, individual bleaching events were severe enough to have a noticeable effect on coral populations, but also mild enough to leave remnant coral cover for additional events to act upon. The effects of increasing bleaching frequencies saturated when bleaching happened once every two years, on average. Macroalgae cover followed an opposing trend to coral persistence and cover, reflecting

competition for space and a transition to macroalgae-dominated states in highly disturbed regimes (Fig. 2c). Again, alternative stable states did not exist in this subset of simulations and macroalgae domination was not stable; instead, disturbances prevented corals from recovering and macroalgae were opportunistic competitors.

The relative importance of coral traits across bleaching regimes

Survival-related attributes were more important than recovery-related attributes across all bleaching regimes, but the overall and relative importance of specific coral traits depended on the bleaching regime. When bleaching was infrequent and mild relative to business-as-usual future thermal regimes, coral adult (baseline, non-bleaching) mortality and growth rates were the most important parameters for determining mean coral cover (Fig. 3a). As bleaching frequency increased, the importance of bleaching resistance increased relative to other traits (Fig. 3b). Bleaching resistance eventually surpassed coral growth and macroalgal overgrowth rates in importance, but was still secondary to adult mortality. As bleaching magnitude increased, bleaching resistance became the primary trait for determining mean coral cover and coral adult mortality became relatively unimportant (Fig. 3c). Parameter importance was similar between frequent and severe regimes and infrequent and severe regimes (Fig. 3d), so increases in the frequency of severe bleaching events had little effect on parameter importance.

Coral parameters were divided into three distinct tiers based on importance. Adult mortality and growth were in the first tier, but their absolute importance depended
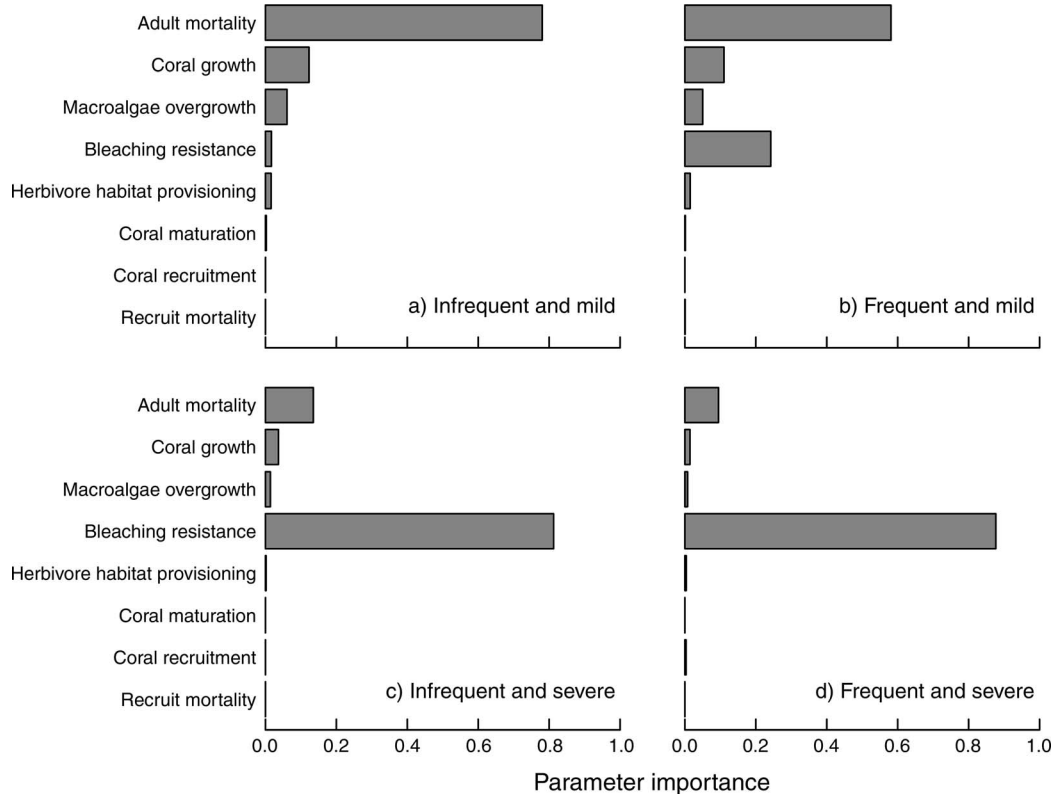
FIG. 3. Results of a global sensitivity analysis (GSA) quantify the importance of model parameters to determining mean proportion of coral cover. GSA results are shown for coral traits under four bleaching regimes: (a) infrequent and mild (0.25 probability, 2.5 DHM), (b) frequent and mild (0.70, 2.5), (c) infrequent and severe (0.25, 7), and (d) frequent and severe (0.70, 7). Survival-related attributes are more important than recovery-related attributes across all regimes. Coral life history traits (adult mortality, growth rate, and competitive ability) are most important in regimes with mild bleaching events, regardless of frequency (a, b), while bleaching resistance is the most important attribute when bleaching is severe (c, d). Four parameters are not strongly related to mean coral cover in any bleaching regime: recruitment rates, advancement to sexual maturity, recruit mortality, and herbivore habitat provisioning.

on the relative importance of bleaching resistance in a given bleaching regime (Fig. 3). Macroalgae overgrowth and herbivore habitat provisioning appeared to be moderately important when bleaching events were mild (Fig. 3a, b). However, these two parameters were in the second tier because the random forest algorithm always preferred adult mortality or growth when branching (results not shown). Coral recruitment rate, recruit mortality, and maturation rate were in the third tier. These three parameters were not important under any bleaching regime and the random forest algorithm preferred macroalgae overgrowth and herbivore habitat provisioning when branching.

The relative importance of coral traits to coral persistence and cover

Coral traits also differed in their contributions to coral persistence vs. cover, and we illustrate this general qualitative result with an example from the infrequent and severe regime in Fig. 3c. Again, bleaching resistance was the best overall predictor of coral persistence and cover in severe bleaching regimes (Fig. 3c, d). We

explored this in more depth by classifying simulated corals according to whether their populations persisted through bleaching events (Fig. 4a). Bleaching resistance was the primary predictor of coral persistence (Fig. 4b). However, adult mortality was the primary predictor of mean coral cover when corals persisted (Fig. 4a, c). Thus, corals with high bleaching resistance could persist, but other traits were still essential for high coral cover.

Coral responses with vs. without alternative stable states

The stability structure of the coral–macroalgae system had subtle interactions with bleaching regime and coral traits. The results described up to this point cover scenarios where corals were dominant, which we now contrast with scenarios where alternative stable states exist. Coral adult mortality, growth rate, herbivore habitat provisioning, and macroalgae growth all predicted the existence of alternative stable states (i.e., whether coral and macroalgae dominance were both stable; Fig. 5a). Notably, herbivore habitat provisioning was important for determining stability structure, but not coral persistence or mean coral cover. Within the

a) Random forests fit
(low frequency/high magnitude)

b) Parameter importance for persistence   c) Parameter importance for cover
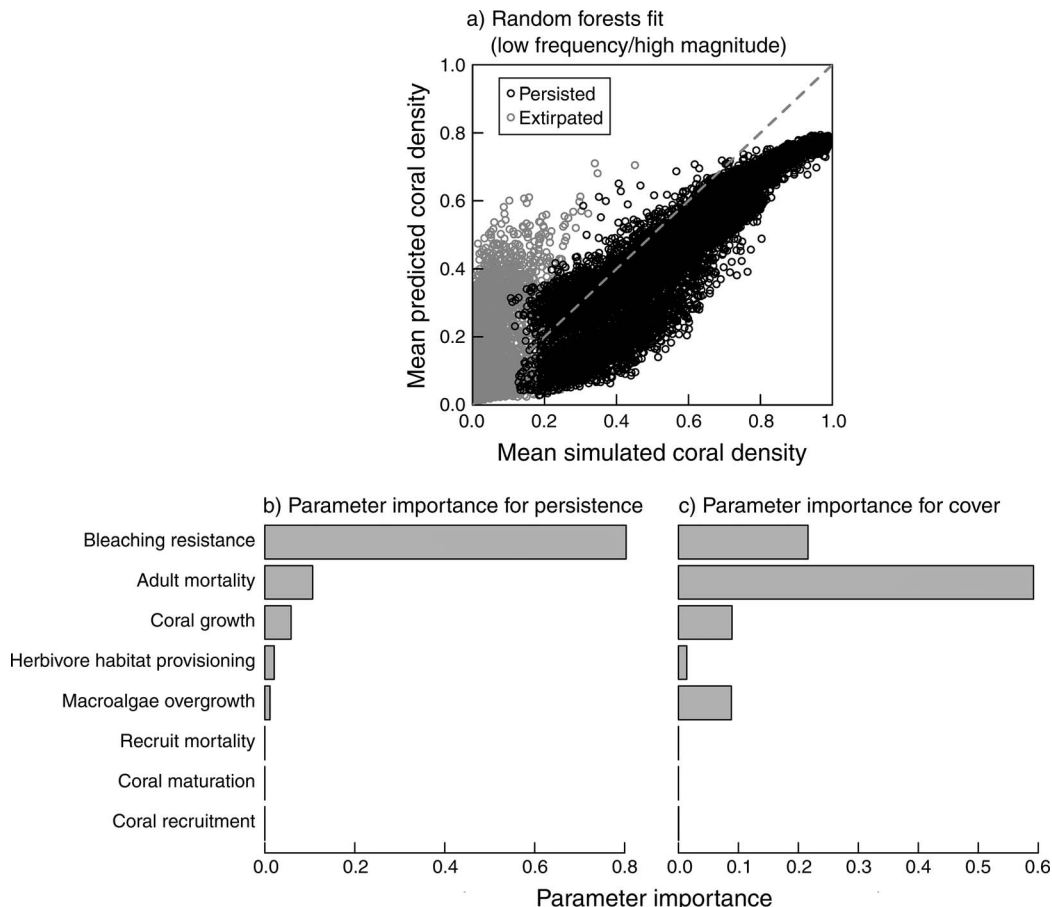

FIG. 4. Detailed explorations reveal the nuances of parameter importance for model predictions when bleaching disturbance is infrequent and severe. (a) The GSA predictions are relatively consistent with simulated results, but underestimate cover for corals that persist (black cluster) and overestimate cover for corals that are lost due to stochastic bleaching events (gray cluster). (b) GSA explorations indicate that bleaching resistance is most important to coral persistence; i.e., distinguishing between the black and gray clusters in (a). (c) However, conditional on persistence, adult mortality is the most important to coral cover; i.e., discriminating between corals in the black cluster in (a). Thus, corals with high bleaching resistance may persist, but still have low cover. In other words, both characteristics are needed for corals to persist with high cover under severe disturbances. Other regimes have qualitatively similar results.

parameter ranges explored, 11.2% of systems resulted in coral dominance, 60.1% in macroalgae dominance, 28.6% in alternative stable states, and <1% in stable coexistence of corals and macroalgae (Appendix A).

Intuitively, coral persistence and cover increased when macroalgae dominance was not locally stable (Fig. 5b for persistence; cover results are not shown, but are qualitatively similar). Corals could recover in systems with unstable macroalgae dominance, but coral losses were irreversible in systems with alternative stable states. Stability differences had the greatest effect in intermediate bleaching regimes, when bleaching events of 3–6 DHM occurred once every 3–10 years. It is likely that bleaching events in this region had the potential to greatly reduce coral cover, but still allowed for recovery when macroalgae dominance was unstable. Beyond this region, differences between alternative stable state and coral-dominated outcomes were less pronounced. Coral

cover decreased because bleaching regimes were too intense regardless of stability structure. Macroalgae cover increased even when macroalgae dominance was not stable because intense bleaching regimes mimicked a loss of coral stability and allowed for unstable macroalgae dominance.

The importance of coral traits to coral persistence and cover depended on stability structure (Fig. 5c). Bleaching resistance was more important when alternative stable states existed. In this case, lower macroalgae mortality allowed macroalgae to colonize and maintain benthic cover when coral cover was abruptly lost. Therefore, greater bleaching resistance prevented macroalgae colonization. Bleaching resistance was less important when coral was dominant and coral adult mortality, coral growth rate, and macroalgae overgrowth rate increased in importance.

a) Parameter influence on stability

Adult mortality
Coral growth
Herbivore habitat provisioning
Macroalgae overgrowth
Coral recruitment
Recruit mortality
Coral maturation

0.00   0.09   0.18   0.27   0.36   0.45

Parameter importance

c) Absolute change in parameter importance

Bleaching resistance
Adult mortality
Coral growth
Macroalgae overgrowth
Herbivore habitat provisioning
Recruit mortality
Coral recruitment
Coral maturation

−0.06   −0.04   −0.02   0.00   0.02

Change in parameter importance

Absolute change in
persistence probability

0.00   0.05   0.10   0.15   0.20

Magnitude of disturbances

b

0.0   0.2   0.4   0.6   0.8
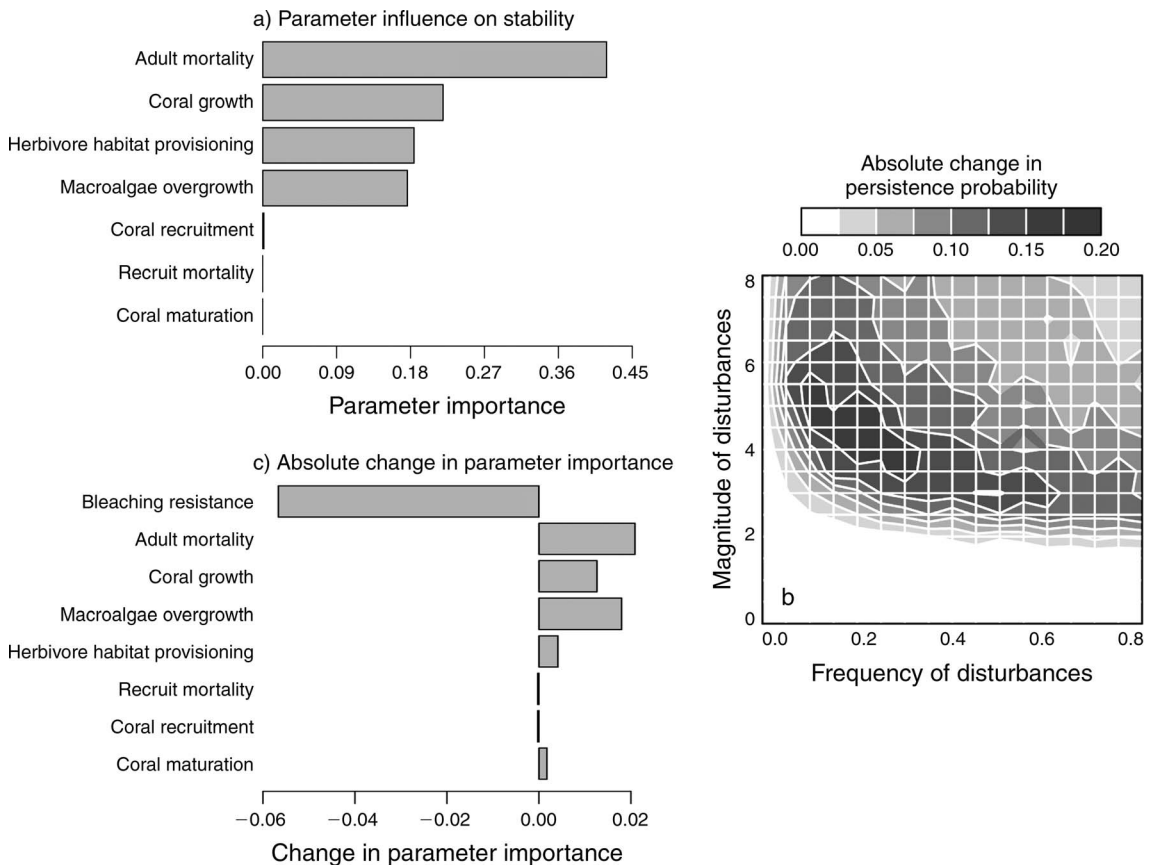
Frequency of disturbances

FIG. 5. The presence of alternative stable states influences both the importance of (a, c) model parameters and (b) predicted coral persistence. The results from our classification GSA indicate that the stability of macroalgae-dominated states strongly depends on adult mortality and moderately depends on growth rate, herbivore habitat provisioning, and competitive abilities (a; Appendix A). Systems without alternative stable states (i.e., coral-only states are stable, but macroalgae-only states are unstable) have increases in coral persistence relative to systems with alternative stable states, and these effects are greatest in intermediate bleaching regimes (b). Differences between the two are minor when bleaching events are mild or frequent and severe. Parameter importance also depends on the stability of macroalgae-dominated states, with bleaching resistance being less important for coral persistence in systems without alternative stable states (c). Instead, adult mortality, coral growth, macroalgae overgrowth, and herbivore habitat provisioning are more important.

DISCUSSION

Our results demonstrate that increases in the frequency and magnitude of extreme events can have disparate effects on ecological communities. Specifically, our model of coral–macroalgae competition predicts that coral persistence and cover are most sensitive to increasing bleaching magnitudes (Fig. 2). This outcome may be general for ecological systems with mortality-recovery dynamics; i.e., populations or communities that experience mortality due to pulse disturbances and have the opportunity to recover between events. Mild disturbances can have little effect on population sizes, while one severe disturbance can reduce a population to relatively low levels and therefore slower recovery rates. Although comparisons of disturbance frequency and magnitude are rare, one example of a similar dynamic could be changes in extreme precipitation events, such as floods or droughts, and consequences for plant survivorship and reproduction (Mueller et al. 2005, Jentsch et al. 2007, Allen et al. 2010). Our model suggests that increases in flood or drought severity could be more influential than increases in frequency due to direct effects on plant mortality. However, our model does not account for direct effects on reproduction or somatic growth, and these pathways could increase the relative importance of the frequency of extreme precipitation events.

Model comparisons and assumptions

Our quantitative results can be sensitive to the definition of persistence and the duration of simulations. We defined persistence as coral cover remaining above a fairly low cover value, 1%, but corals are no longer reef-dominating structures at such low cover. In addition, the long transients in models of this time (Blackwood et al. 2012) mean that some of the corals considered persistent at the end of our simulations might not persist under longer time scales. While these decisions were central to

performing our global sensitivity analyses and understanding qualitative community dynamics, the use of these ranges can bias the absolute values for persistence and cover. For example, we bound our bleaching tolerance (η_2) by zero susceptibility in order to contain the full range of possibilities, but including extreme tolerance values in this range will overrepresent the likelihood of highly resistant corals occurring in the calculations for average persistence and cover. Therefore, the absolute values in persistence and cover are not representative of forecasts for real coral communities. Rather, it is the relative trends across different disturbance magnitudes and frequencies (and sensitivity to different trait values, as described in the next subsection below) that our analysis is designed to elucidate.

Two mechanisms drive the relative sensitivity of corals to increased bleaching severity in our model (Fig. 2). The first mechanism is that corals can resist bleaching during mild events both in the field and in our model (Hoegh-Guldberg 2000, Baker et al. 2008, Donner 2011). Intuitively, our model predicts that increases in bleaching frequency are only detrimental when minimum bleaching thresholds are exceeded (i.e., see DHM values from approximately 0 to 3 on Fig. 2a, b). The subtle corollary is that corals with lower bleaching thresholds are likely to be more impacted by increases in frequency, while corals with higher thresholds are likely to be more impacted by increases in magnitude. The second mechanism is that macroalgae responded nonlinearly to supplemental herbivory following Mumby et al. (2007). The nonlinearity increases the mean value of supplemental herbivory relative to a model with only a linear scaling between supplemental herbivory and coral cover (Jensen's inequality). Thus, frequent, minor bleaching events tend to be associated with greater levels of supplemental herbivory because coral cover is not greatly reduced at any given point. On the other hand, even infrequent, severe bleaching events cause greater reductions in coral cover and result in lower levels of supplemental herbivory. Mumby (2006) explores coral persistence under various hurricane frequencies and magnitudes. In his model, one additional hurricane each year is approximately equivalent to a 5% increase in coral mortality from hurricanes (Fig. 11 in Mumby 2006). His results show that hurricane frequency and magnitude interact more than our bleaching frequency and magnitude. The key differences are that Mumby 2006 focuses on a specific parameter space, while we conduct a global stability analysis, and that Mumby has a more detailed model of herbivore grazing processes governing recovery between disturbances. However, our models generally agree that increases in disturbance magnitude can strongly influence coral persistence.

The relative importance of coral adult mortality and recruitment parameters is consistent between our study and others, even though few explicitly included bleaching resistance. Matrix modeling approaches have often found that coral populations are most sensitive to changes in adult mortality and least sensitive to changes in recruitment rates, maturation rates, or recruit mortality (Hughes 1984, Hughes and Tanner 2000, Edmunds and Elahi 2007, Edmunds 2010). Similarly, simulation studies have found that coral cover under future climate change is most sensitive to mortality-related parameters (Riegl and Purkis 2009, Baskett et al. 2010) and those related to bleaching resistance (Baskett et al. 2010). A recent field study corroborated these modeling results by demonstrating that isolated coral populations could recover from disturbances via adult growth and survival, even with low external recruitment (Gilmour et al. 2013). The authors concluded that, in some cases, the costs of low connectivity and external recruitment for isolated reefs might be eclipsed by the benefits of low anthropogenic stressors and increased adult fitness.

In contrast, other models have highlighted the importance of coral traits found to be less influential here. Coral recruits strongly influenced population growth rates in an early coral matrix model (Hughes 1984) and a more recent study (Smith et al. 2005), but the former did not report sensitivity or elasticity values and the latter specifically sought to compare variance in recruitment parameters. Mumby (2006) used a model similar to ours and his local stability analysis showed that the strength of herbivorous fish grazing had an overwhelming effect on coral population dynamics. While we did not test the sensitivity of our results to herbivorous fish grazing because it is not a coral trait, Mumby's results were secondarily sensitive to adult mortality and relatively insensitive to changes in all other parameters (e.g., growth rate, juvenile mortality).

Our model does not include certain mechanisms that may play a large role in coral reef community dynamics. That is, in our model, we assume that (1) reef rugosity (herbivore habitat) is always proportional to coral cover, and (2) grazer populations immediately respond to changes in reef rugosity. In reality, disturbances can reduce reef rugosity and new coral colonies may cover the benthos without providing much herbivore habitat (Bellwood et al. 2004). Furthermore, herbivore populations do not immediately respond to changes in reef rugosity because of lags in recruitment and growth, and fishing pressures may reduce population sizes despite habitat availability (Blackwood and Hastings 2011, Blackwood et al. 2012). We hypothesize that inclusion of these mechanisms could increase the relative importance of herbivore habitat provisioning and coral growth rate, but bleaching resistance would remain most important under severe bleaching.

Implications for management

The effects of extreme events on ecological systems can be moderated by life history traits, suggesting that the success of management efforts will depend on the

interaction between environmental conditions and ecological dynamics. Specifically, management of a given species or population may be viable under all, some, or no disturbance regimes, due to change in the relative importance of adult mortality, growth rate, and bleaching resistance (Figs. 3, 4, and 5). Management of corals with high bleaching resistance and low adult mortality may be successful in all bleaching regimes, while management of corals with low adult mortality may be successful in all but the most severe bleaching regimes. On the other hand, management of corals with "weedy" life history traits is unlikely to be successful under any increase bleaching frequency or magnitude. These projections are consistent with long-term empirical studies that have identified successful corals, or "winners," as those that are thermally tolerant and long lived (Loya et al. 2001, van Woesik et al. 2011).

Yet the appropriate management action based on these projections also depends on management goals. Game et al. (2008) asked whether management efforts should prioritize protection of reef locations based on greatest need (protecting the weak) or triage (protecting the strong). To this end, the authors modeled the probability that a reef would either be in a healthy or degraded state at any point in time. Low-risk reefs (the strong) were more likely to be healthy and high-risk reefs (the weak) were more likely to be degraded. The authors found that protecting low-risk reefs optimized a management goal of maximizing the probability of having at least one healthy reef. However, to achieve a management goal of maximizing the number of healthy reefs, the answer depends on how frequently reefs are likely to be in a degraded state. High-risk reefs can be prioritized when reefs are generally healthy because low-risk reefs are likely to remain healthy even without management action. Low-risk reefs can be prioritized when reefs are generally degraded because management action is unlikely to maintain the health of high-risk reefs.

Using this framework, the success of coral life histories in our model establishes specific management priorities. High- and low-risk reefs in the Game et al. model (2008) are analogous to high- and low-risk coral life histories in our model. Here, the risk of a coral life history is defined by the probability of extirpation or significantly reduced cover due to coral bleaching. In mild bleaching regimes, risk depends most on adult mortality and growth rates; low-risk species have low adult mortality and high growth rates. In severe bleaching regimes, risk depends most on bleaching resistance; low-risk species have high bleaching resistance. Management efforts may target only the lowest risk coral species if the goal is to ensure that at least one coral species persists through bleaching events, but the species with the lowest risk of extirpation will depend on the severity of bleaching, as described in the previous paragraph. However, it is more likely that management goals will be to maintain reef biodiversity and ecosystem services by maximizing the number of coral species that

persist through bleaching events. In this case, when bleaching is mild, management efforts can target high-risk corals with high adult mortality and low growth rates because corals are generally expected to persist. When bleaching is severe, management efforts can target low-risk corals with high bleaching resistance, as coral persistence decreases on average and management efforts are unlikely to be effective for high-risk corals.

In addition to coral community composition, high- and low-risk reefs will depend on local oceanographic factors that can influence the thermal stress that determines bleaching likelihood and therefore can also inform conservation targets (West and Salm 2003). For example, in climate change generally (Keppel et al. 2012) and coral reefs specifically (Reigl and Piller 2003, Baskett et al. 2010, Mumby et al. 2011), locations with buffered environmental conditions might act as refuges and provide source populations when bleaching is severe. Prioritizing protection of such refuges represents an approach of protecting low-risk reefs (the strong) in the Game et al. (2008) framework. Our results here suggest that oceanographic factors that influence the magnitude of thermal stress are likely to be more important than those that influence the frequency of thermal stress in determining whether a given location might act as a refuge.

These guidelines are contingent, however, on additional trait and community context. First, management goals may be to maintain high coral cover, rather than just ensure persistence. Our results suggest that species or populations may need both high bleaching resistance for persistence and low adult mortality for high cover (Fig. 4). Tradeoffs in life history strategies may reduce viable management options if persistence with low cover is undesirable. Second, the presence of a strong competitor or alternative stable states can alter coral projections and the importance of life history traits (Fig. 5). For instance, management targets may differ between reefs with more evidence for competitive interactions (Bruno et al. 2009, Roff and Mumby 2012, Mumby et al. 2013), such as the Caribbean relative to the Indo-Pacific (Roff and Mumby 2012). However, the degree to which species can be targeted will depend on the management options. A marine protected area, for instance, impacts all species within an area and not just the highest value management target. However, one can choose where to place a marine protected area based on the species composition, of which high value management targets may be an essential component. That is, local conditions may suggest that bleaching resistant species are critical management targets, so management efforts would indirectly target those species by selecting reefs where they are at higher densities.

Although the oceanographic and trait criteria for coral persistence appear restrictive, reef biodiversity could be maintained due to environmental and phenotypic variation. Hoegh-Guldberg (2000) integrated

observed bleaching thresholds and climate models to forecast bleaching events for the coral reefs of 12 Pacific nations. His projections suggest that bleaching frequency and magnitude will increase at different rates across these reefs, with the reefs of Nauru, Palau, and the Solomon Islands experiencing once-a-year bleaching events several decades earlier than the reefs of the Cook Islands, Kiribati, or New Caledonia. In addition, Selig et al. (2010) used a 21-year data set to analyze global long-term bleaching patterns. Their results showed that bleaching frequency and magnitude exhibit a great deal of fine-scale variance, with most events occurring on scales smaller than 50 km^2. Together, variation in reef environments (Hoegh-Guldberg 2000, Selig et al. 2010) and coral responses (Figs. 3 and 4) may sustain some coral biodiversity. However, this biogeographic bleaching mosaic also suggests that effective management targets will depend on fine-scale oceanographic and biodiversity features, and that one-size-fits-all approaches may be less effective. As one example, there may be a limited capacity for protected reefs to serve as a source for populations with different bleaching regimes. Finally, it is critical to point out that these considerations depend on environmental variation, and are moot in the event that business-as-usual emissions lead to widespread and severe bleaching events.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-0273.1.sm