

Response Diversity Can Increase Ecological Resilience to Disturbance in Coral Reefs

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ABSTRACT: Community-level resilience depends on the interaction between multiple populations that vary in individual responses to disturbance. For example, in tropical reefs, some corals can survive higher stress (resistance) while others exhibit faster recovery (engineering resilience) following disturbances such as thermal stress. While each type will negatively affect the other through competition, each might also benefit the other by reducing the potential for an additional competitor such as macroalgae to invade after a disturbance. To determine how community composition affects ecological resilience, we modeled coral-macroalgae interactions given either a resistant coral, a resilient coral, or both together. Having both coral types (i.e., response diversity) can lead to observable enhanced ecological resilience if (1) the resilient coral is not a superior competitor and (2) disturbance levels are high enough such that the resilient coral would collapse when considered alone. This enhanced resilience occurs through competitor-enabled rescue where each coral increases the potential for the other to recover from disturbance through external recruitment, such that both corals benefit from the presence of each other in terms of total cover and resilience. Therefore, conservation management aimed at protecting resilience under global change requires consideration of both diversity and connectivity between sites experiencing differential disturbance.

Keywords: alternative stable states, coral bleaching, coral reefs, dynamical model, resilience, response diversity.

Introduction

Both basic and applied ecologists seek to understand how ecosystems respond to natural and anthropogenic disturbance. The overall response of an ecosystem arises from the interactive responses of the individual species that inhabit the community, such that ecological communities act as complex adaptive systems (Levin and Lubchenco 2008). Part of the overall response depends on whether

an ecosystem exhibits alternative stable states, where multiple qualitatively distinct states are locally stable under a given set of environmental conditions and disturbance can cause the ecosystem to cross an unstable threshold in population densities and shift between states (Scheffer et al. 2001; Beisner et al. 2003). When alternative stable states occur, a central component of disturbance response is then ecological resilience *sensu* Holling (1973), or the probability of an ecosystem maintaining a given state follow a disturbance. The resilience of such ecosystems depends on multiple ecosystem characteristics, including heterogeneity, redundancy, modularity, and feedback loops (Levin and Lubchenco 2008; Bernhardt and Leslie 2013). While the effect of diversity on some aspects of ecosystem stability has been extensively studied, the effect of biodiversity on resilience has received much less attention (Ives and Carpenter 2007).

One element of diversity that is expected to drive ecological resilience is response diversity, where different species or populations within a functional group vary in their response to disturbance (Chapin et al. 1997; Walker et al. 1999; Elmqvist et al. 2003). For example, some species exhibit resistance through an ability to withstand disturbance, while others exhibit engineering resilience through an ability to recover quickly. (Note that resilience has two separate but related definitions: the ecological resilience defined above as the probability of maintaining a given state, and the engineering resilience defined as the rate of return to a given state following a disturbance [Peterson et al. 1998].) Plant ecosystems epitomize response diversity, from resistance to engineering resilience to multiple disturbances. For example, some plants resist fire through avoidance and tolerance while others recover rapidly from fire through regeneration (Lavorel and Garnier 2002). In addition, in arid ecosystems, some plants resist grazing through low palatability and thorns while others recover rapidly from grazing through vegetative reproduction and dispersal (Chillo et al.

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2011). While such response diversity might enhance ecological resilience (Chillo et al. 2011), ecosystems dominated by species particularly well equipped to resist or recover from disturbance might have greater ecological resilience than diverse ecosystems (Silver et al. 1996). Furthermore, if the different species or populations compete, then the negative effects of competition might compromise individual population responses to disturbance (Sundstrom et al. 2012) and lower overall disturbance response in diverse communities compared to in communities dominated by the most resistant species (Ives and Cardinale 2004). Therefore, the ecological resilience will depend on both the strength of competition between species and the amount of ecological function provided by each (Peterson et al. 1998).

Whether response diversity enhances or degrades ecological resilience is a particularly critical question in the context of tropical coral reefs and climate change. Corals with different morphologies exhibit different susceptibility to stress (resistance) and different growth rates (engineering resilience) in response to disturbances such as thermal-stress-driven bleaching and hurricanes. Specifically, massive and encrusting corals (e.g., massive *Porites*) grow more slowly than branching and tabular corals (e.g., branching *Acropora*) but can withstand greater disturbances, most likely due to differences in structural strength, tissue thickness, and mass transfer (Jackson and Hughes 1985; Hughes and Connell 1999; Loya et al. 2001; Bhagooli and Yakovleva 2004; Nyström 2006). Whether coral reefs exhibit alternative stable states between coral-dominated states and those dominated by other species such as macroalgae has mixed evidence (e.g., Dudgeon et al. 2010; Zychaluk et al. 2012; Mumby et al. 2013), with greater support for alternative stable states in Caribbean reefs (Bruno et al. 2009; Hughes et al. 2010; Roff and Mumby 2012). One mechanism that can theoretically drive alternative stable states is a positive association between coral cover and grazing rates on macroalgae that would otherwise overgrow corals (Mumby et al. 2007). Empirical evidence supports the potential for corals to attract grazers that would otherwise avoid macroalgal-dominated patches (Williams and Polunin 2001; Hoey and Bellwood 2011), macroalgal overgrowth of corals in the absence of grazers (Hughes et al. 2007), and macroalgae prevention of coral recruitment (McCook et al. 2001); corals also compete directly with one another via injuries to soft tissue and overtopping (Lang and Chornesky 1990). Under this mechanism, competing corals experience indirect facilitation through negative effects on a shared noncoral competitor. Therefore, the effect of response diversity on ecological resilience in coral reefs depends on a complex interplay of indirect facilitation between different coral types via increased grazing, direct coral-coral competition

for space, and the nonlinear feedback in the coral-algae interaction that might promote alternative stable states.

This question for tropical corals is particularly interesting in a management context, where anticipated increases in bleaching disturbance caused by climate change has motivated research to inform management aimed at protecting the resistance and resilience of coral reefs (e.g., West and Salm 2003; Obura 2005; McLeod et al. 2009; Baskett et al. 2010; Hughes et al. 2010). Typically, recommendations based on resilience theory focus on the importance of diversity to resilience (e.g., Bellwood et al. 2004; Nyström et al. 2008). However, some suggest a focus on resistance to disturbance because of the high level of disturbance expected in the future (Côté and Darling 2010; McClanahan et al. 2012). Resolving this debate of whether to focus conservation efforts on diverse communities or those dominated by resistant types requires a deeper understanding of the interaction between the potential positive role of response diversity in ecological resilience and the negative effects of competition between types.

Here we use a mathematical model of coral reefs to examine how the presence of and interactions between resistant and resilient coral species affect the overall resilience of the reef ecosystem to environmental disturbances expected in the near future. We build on an existing theoretical framework of coral-macroalgal interactions by Mumby et al. (2007) that has been extended in a number of ways (e.g., to include multiple anthropogenic stressors and dynamical grazer populations; Anthony et al. 2011; Blackwood et al. 2012). Here, we extend it to include two contrasting coral types: a resistant coral that tolerates stress and a resilient coral that recovers quickly. In addition, we explore a variety of recruitment dynamics because recruitment can contribute to the recovery dynamics that drive individual resilience (Hughes et al. 2010). We use this model to explore how community properties (ecological resilience and stability of coral cover) depend on community composition in terms of these two types, their competitive interactions, their recruitment dynamics, and the magnitude of disturbances caused by coral bleaching.

Methods

We seek to construct the simplest possible model that has the dynamics relevant to our question of how ecological resilience depends on community composition. In doing so, we extend the model in Mumby et al. (2007; the model is analytically investigated in app. A.1; apps. A–C available online) to include two coral species, stochastic bleaching disturbance, and the potential for external recruitment (fig. 1). We choose this model because it provides a relatively simple and well-explored (extensions include Anthony et al. 2011; Blackwood and Hastings 2011; Blackwood et al.

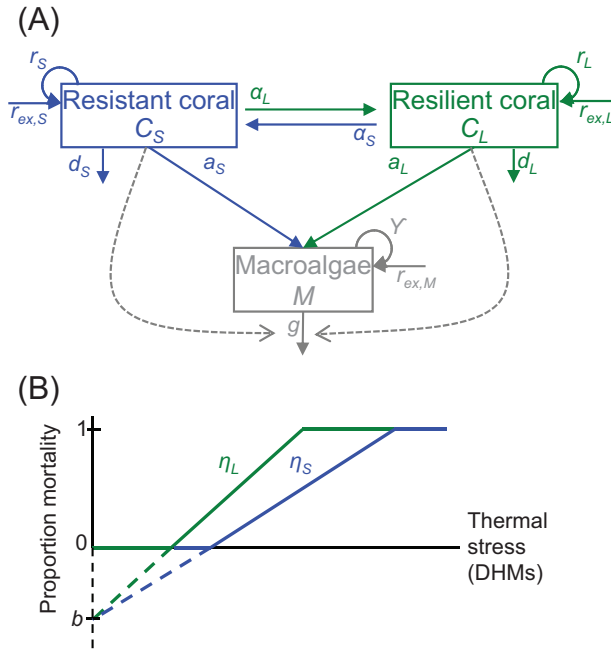


Figure 1: A, Diagram of the model dynamics, which include competition between corals (α_k), algal overgrowth of corals (a_k), herbivorous grazing (g) enhanced by corals, internal (r_k , γ) and external ($r_{ex,k}$) recruitment/growth, and coral mortality (d_k). B, Illustration of stochastic (disturbance) mortality as it depends on thermal stress for the resilient coral (steeper slope η_L) and the resistant coral (shallower slope η_S). In both panels, the parameters relevant to the resistant coral are in blue, resilient coral in green, and macroalgae in gray.

2011, 2012) theoretical framework with alternative stable states, which are, by definition, necessary for any exploration of ecological resilience. In this framework, the alternative stable states are a coral-dominated state and macroalgae-dominated state, where a positive association between coral cover and the grazing rate on macroalgae provides the feedback mechanism that can maintain each state. Under high coral cover, the associated high levels of grazing can prevent macroalgae intrusion to maintain the coral-dominated state. Under high macroalgal cover, lower grazing allows for macroalgal overgrowth of corals and the maintenance of a macroalgal-dominated state. Our novel extension to include bleaching disturbance and two competing coral species with different disturbance responses allows us to explore how response diversity affects the ecological resilience of the coral-dominated state. Because the effect of response diversity will inevitably depend on the balance between the negative effects of competition and the positive effects of indirect facilitation (via increased grazing negatively affecting the shared macroalgal competitor), we explore the effect of different competitive interactions between the two corals.

To model the above-described dynamics, we follow the

proportion cover of two coral types, the resistant coral C_S and the resilient coral C_L , as well as macroalgae M . Because these state variables represent proportion cover, they all have values $\in [0,1]$, with their sum $C_S + C_L + M \leq 1$. Either coral can colonize any area not covered by these three populations ($1 - C_S - C_L - M$; e.g., bare substrate or turf algae) at a rate r_k ($k = S$ for the resistant coral and $k = L$ for the resilient coral). The two coral types directly compete, where α_k indicates the relative competitive effect of the other coral type on type k . In some simulations, corals also recruit from external sources to free (colonizable) space at a rate $r_{ex,k}$. Corals lose cover from natural baseline mortality at rate d_k , and macroalgae can overgrow corals at a type-dependent rate a_k . Macroalgae also colonize unoccupied space ($1 - C_S - C_L - M$) at a rate γ , externally recruit at a rate $r_{ex,M}$ in some simulations, and lose cover due to grazing at a rate $g/(1 - C_S - C_L)$ that increases with coral cover (see app. B for a derivation of the functional form for grazing and an exploration of an alternate functional form).

In addition to these continuous-time dynamics (fig. 1A), we add a discrete, stochastic, species-specific annual survivorship from thermal stress-induced bleaching (fig. 1B). Following the semidiscrete model notation of Mailleret and Lemesle (2009), each summer indicated by time τ we translate the thermal stress represented by degree heating months (DHMs; following Donner 2009) into survivorship assuming a linear relationship between annual mortality and DHMs given slope η_k and intercept b , bounded at $[0,1]$ (no or 100% mortality, with a value in between representing partial bleaching). DHMs measure total number of degree-months that the temperature exceeds the average summer maximum (i.e., 1 DHM can mean 1 degree above the average summer maximum for 1 month or 2 degrees above the average summer maximum for 2 weeks), thus taking into account both the magnitude and duration of a thermal stress event. The full model is then:

$$\begin{cases} \frac{dM}{dt} = r_{ex,M}(1 - M - C_S - C_L) + M \left[a_S C_S + a_L C_L + \gamma(1 - M - C_S - C_L) - \frac{g}{1 - C_S - C_L} \right] & t \neq \tau \\ \frac{dC_S}{dt} = r_{ex,S}(1 - M - C_S - C_L) + C_S[r_S(1 - M - C_S - \alpha_S C_L) - d_S - a_S M] & t \neq \tau \\ \frac{dC_L}{dt} = r_{ex,L}(1 - M - C_S - C_L) + C_L[r_L(1 - M - C_L - \alpha_L C_S) - d_L - a_L M] & t \neq \tau \\ M(\tau^+) = M(\tau) \\ C_S(\tau^+) = \{1 - \min[1, \max(0, \eta_S * \text{DHM}(\tau) - b)]\} C_S(\tau) \\ C_L(\tau^+) = \{1 - \min[1, \max(0, \eta_L * \text{DHM}(\tau) - b)]\} C_L(\tau) \end{cases}, \quad (1)$$

where τ^+ indicates the moment immediately following τ , that is, the end of the summer.

In addition to testing either including ($r_{\text{ex},k} > 0$) or excluding ($r_{\text{ex},k} = 0$) open recruitment, we examine a two-patch model where disturbance varies across patches. In the two-patch model, dispersal of recruits to colonizable space occurs from patch i to patch j for type k at a rate $m_{ij,k}$ such that the dynamics of coral type k in patch i are

$$\begin{cases} \frac{dC_{ik}}{dt} = m_{ji,k}C_{jk}(1 - M - C_{ik} - C_{il}) - m_{ij,k}C_{ik} \\ \quad + C_{ik}[r_k(1 - M - C_{ik} - \alpha_k C_{il}) - d_k - a_k M] & t \neq \tau. \\ C_{ik}(\tau^+) = \{1 - \min[1, \max(0, \eta_k * \text{DHM}_i(\tau) - b)]\} C_{ik}(\tau) \end{cases} \quad (2)$$

Note that all parameters are independent of the patch but the thermal stress can vary between patches.

Model Parameterization

We focus our model parameterization on parameter space with bistability in the one-coral-type plus macroalgae cases (i.e., for each of the resistant or resilient coral considered separately) because alternative stable states are necessary for the effect of community composition on ecological resilience to be relevant (see Fung et al. 2011 for an exploration of the parameter range where alternative stable states occur in a model of this type). Within this space, we use the size of the basin of attraction to define the parameters for each coral, with a large basin for the resilient coral C_L and a small basin for the resistant coral C_S (fig. 2). Parameters that increase the size of the basin of attraction for the coral-dominated state (ecological resilience) also increase stability (return time; app. A.2). Among the parameter combinations that lead to differences in the size of the basins of attraction for each coral, we focus on the corals exhibiting differences in coral growth ($r_L > r_S$) and macroalgal overgrowth ($a_L < a_S$) to reflect the expectation that faster growth confers the greater resilience to branching-type corals as compared to the more stress-tolerant, massive-type corals (Jackson and Hughes 1985; Hughes and Connell 1999). Therefore, the resilient coral exhibits both ecological and engineering resilience. In test model runs, alternative parameterizations with a similar difference in the size of the basins of attraction between corals led to the same conclusions described here (app. A.4). When incorporating external recruitment, we assume higher external recruitment for the resilient coral ($r_{\text{ex},S} < r_{\text{ex},L}$) as one of the properties of resilience (Hughes et al. 2010). Similarly, when incorporating dynamics across two patches, we assume higher exchange rates for the resilient coral as one of the properties of

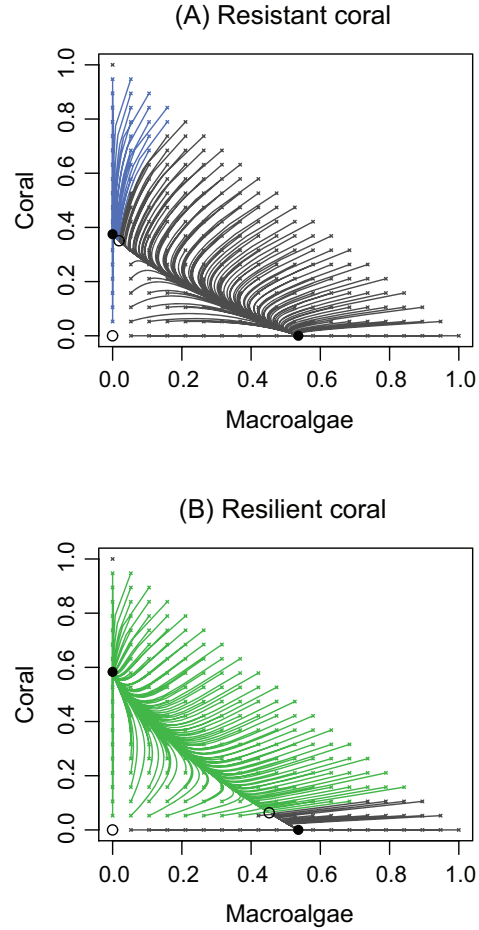


Figure 2: Phase-plane diagrams of deterministic time series simulations for the one-coral model without external recruitment and stochastic disturbance given each of the resistant (A) or resilient (B) coral. Circles indicate equilibria points, with open circles for locally unstable equilibria and filled circles for locally stable equilibria. The Xs indicate starting points of each simulation. To illustrate the basin of attraction for each equilibrium, gray lines indicate simulations that end in the macroalgae-dominated equilibrium, and colored lines (blue for resistant coral, green for resilient coral) indicate simulations that end in the coral-dominated equilibrium. Parameter values are $r_S = 0.4$, $r_L = 0.6$, $a_S = 0.13$, $a_L = 0.09$, $d_S = d_L = 0.25$, $\gamma = 0.55$, and $g = 0.255$. In order to have a trade-off between the resilience (size of the basin of attraction as well as growth rate r_k) and resistance (susceptibility to thermal stress), we let $\eta_S = 0.1$ and $\eta_L = 0.25$ (i.e., faster increase in mortality with degree heating months for the resilient coral), with $b = 0.25$, for all numerical simulations with bleaching mortality. See appendix A.3, available online, for a numerical local stability analysis of the two-coral model and investigation of the effect of additional mortality analogous to stochastic bleaching disturbance.

resilience ($m_{ij,S} < m_{ij,L}$); we also assume symmetrical migration ($m_{ij,k} = m_{ji,k}$) within each type for simplicity.

To model a difference in resistance between the coral types, the resistant coral experiences lower mortality for

the same amount of thermal stress than the resilient coral ($\eta_s < \eta_L$). For the random DHM values in stochastic simulations, we draw values from the DHM trajectories in the National Oceanic and Atmospheric Administration's Geophysical Fluid Dynamics Laboratory Earth System Model 2 climate model for Belize (data from Logan et al. 2014). Within this model and location, we compare different disturbance levels that draw from the RCP 2.6 (representative concentration pathway to a radiative forcing level of 2.6 W/m²) climate scenario and sample annual DHM values from those in four different time ranges (1985–2020, which has a mean of DHM of 0.72; 1985–2030, which has a mean of DHM of 1.23; 1985–2035, which has a mean of DHM of 1.44; and 1985–2050, which has a mean of DHM of 2.01). Sampling farther into the future increases mean disturbance because of increased climate change. This approach allows exploration of the disturbance level across a range from each coral having the potential to persist alone to stress levels high enough to cause the loss of the resilient coral when considered alone. Even greater disturbance leads to extinction of both corals under all circumstances; note that our model does not include acclimatization, genetic adaptation, or other processes relevant to the question of longer-term persistence under more severe climate change. Also, we only use one climate model and location in order to draw from a realistic distribution of DHMs given different levels of stress; our model is not intended as a forecast under these or other conditions. In two-patch simulations, we assume one patch has half of the disturbance magnitudes of the other in order to model two connected locations with consistent differences in disturbance regimes due to oceanographic features (West and Salm 2003; Obura 2005; Thompson and van Woesik 2009).

Model Analysis

We implement stochastic simulations with annual bleaching mortality in system 1 (see app. A.4 for details), where we compare simulations with both coral types to those with each coral type alone in competition with macroalgae. We analyze the effect of community composition on three community-level metrics: total coral cover, ecological resilience (measured as the proportion of simulations with final coral cover above a given threshold), and stability (inverse of the coefficient of variation in coral cover over time, a commonly used metric of stability for ecological time series; May 1974; Tilman 1996). In addition to exploring the different disturbance levels and recruitment dynamics (closed, open, two-patch) described above, we explore four different competitive arrangements: (1) equivalent intraspecific and interspecific competition ($\alpha_L = \alpha_s = 1$), (2) equivalent interspecific competition

smaller than intraspecific competition ($\alpha_L = \alpha_s < 1$), (3) the resilient coral is the superior competitor ($\alpha_L < 1 < \alpha_s$), and (4) the resistant coral is the superior competitor ($\alpha_s < 1 < \alpha_L$). In each simulation, we initialize the model with each coral at the coral-dominated equilibrium for each coral species when considered alone and the macroalgae at a nominal level of cover ($M = 0.0001$). We then run the model for 150 years and analyze the data over the last 50 years for metrics that require a time series (stability) in order to eliminate the effect of transients due to our choice of initial conditions (see app. C.1 for verification that 100 years is an adequate burn-in period). We perform 5,000 simulations per parameter set and model.

Results

For corals, the combination of both a resistant type and resilient type can lead to greater community cover and resilience given intermediate disturbance, interspecific competition that is weaker than intraspecific competition, and external recruitment (fig. 3). In addition to increased cover and ecological resilience on the community level, each coral individually is more abundant and resilient when the other coral is present than when occurring alone (fig. 3A, 3B). In scenarios where collapse is possible but not inevitable, the distribution of final coral cover across simulation runs is strongly right skewed, especially for the resilient coral (fig. 3A). This skew arises because of the attraction to the two states, where many runs end with little to no coral cover, and a few runs end with abundant coral cover. Our metric of ecological resilience (the probability of coral persistence) depends on both individual resistance (bleaching susceptibility) and individual engineering resilience (recovery rate), such that the lower resistance of the resilient coral drives its lower persistence under intermediate disturbance (fig. 3B). The resistant coral is also more stable when occurring in combination than when occurring alone (fig. 3C), while the resilient coral is less stable in combination because almost all simulations have near-zero resilient coral cover (and therefore low variability) when considered alone. To explore the effect of different assumptions for the disturbance frequency, competitive interactions, and recruitment dynamics, we focus on community cover and resilience in the remaining results.

Effect of Disturbance Level

At low disturbance (with weaker interspecific than intraspecific competition and external recruitment), the negative effect of competition when corals are in combination outweighs any positive effects of augmenting herbivory, leading to reduced cover for each coral in competition

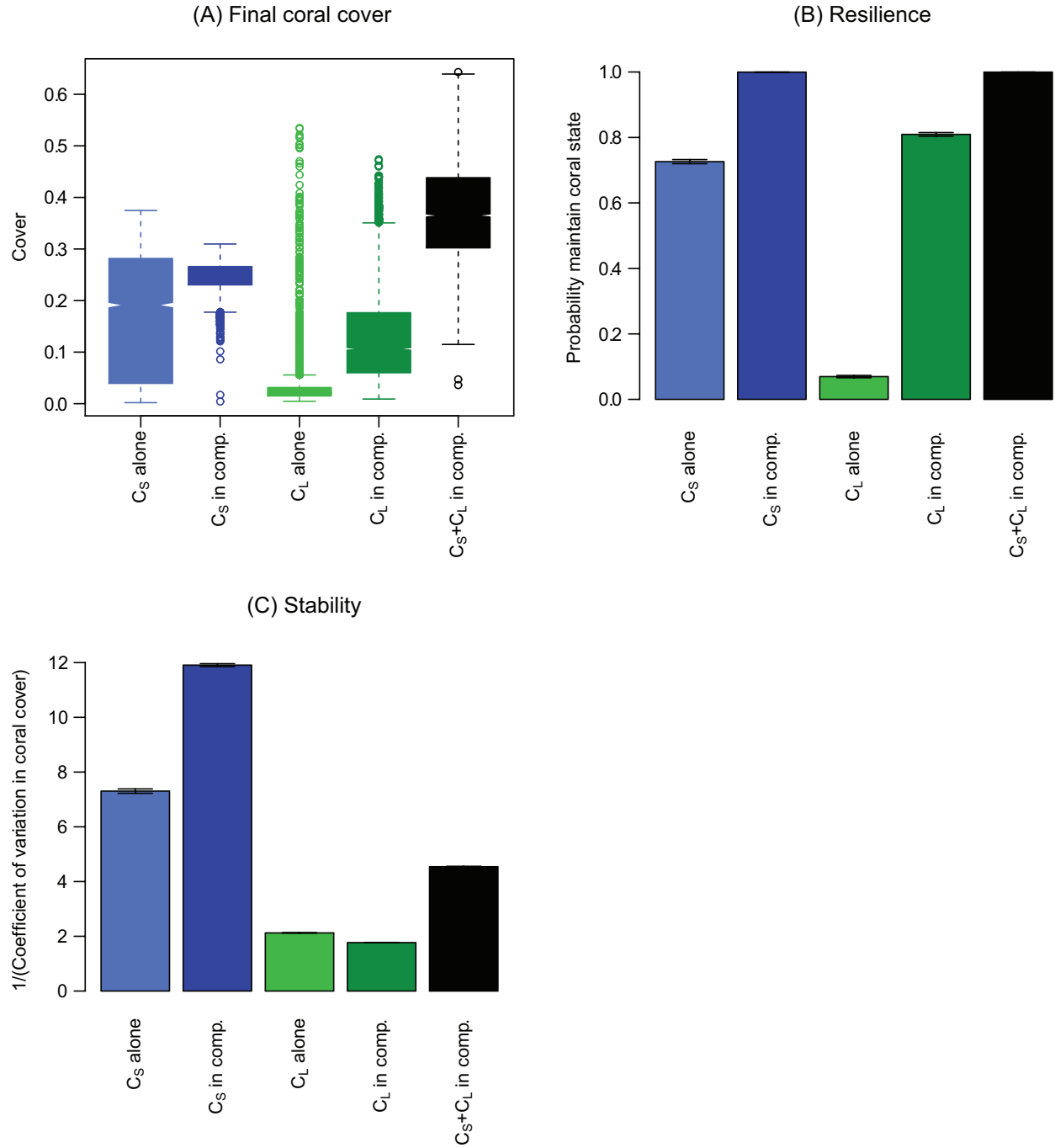


Figure 3: All metrics for the case of intermediate disturbance (mean degree heating months = 1.44), lower interspecific competition than intraspecific competition ($\alpha_s = \alpha_L = 0.6$), and external recruitment for corals ($r_{ex,S} = 0.001$, $r_{ex,L} = 0.01$, $r_{ex,M} = 0$): *A*, boxplot of the distribution of cover at the endpoints of the 5,000 simulations; *B*, resilience measured as the proportion of the replicate simulations where proportional coral cover is greater than 0.05 at the endpoint; and *C*, stability measured as the inverse of the coefficient of variation in cover over the last 50 years for each simulation and then averaged across simulations. In *B* and *C*, error bars indicate standard errors across all simulations. Here and in all remaining plots, blue indicates the resistant coral and green indicates the resilient coral, with light shading indicating the coral when considered alone (one-coral and macroalgae model) and dark shading indicating the cover the coral when considered in combination (two-coral and macroalgae model); black indicates the total of both corals when considered in combination. All other parameter values are as in figure 2.

compared to when considered alone (fig. 4A). However, total coral cover is higher when both corals are in combination at low disturbance levels given lower interspecific than intraspecific competition, and the negative effects of competition do not decrease resilience given the low likelihood of a state shift under low disturbance levels regardless of community composition. At intermediate and high disturbance levels, the positive effects of augmented herbivory outweigh the negative effects of competition, such that each coral is more abundant and resilient when part of a multicolored community than when alone (first realized for the resilient coral, fig. 4B, and then as disturbance increases for the resistant coral as well, fig. 4C, 4D; also observed in the analogous deterministic model with increasing mortality in app. A.3). For all disturbance levels, the coral community as a whole is equally or more resilient than a monoculture of either coral type. Analogous results (not shown) occur for simulations with exchange between two patches, one of which experiences disturbance on levels half the magnitudes of the other, compared to the results presented here with external recruitment for the corals.

Effect of Recruitment Dynamics

When individual reefs are considered in isolation (one patch, no external recruitment), intermediate levels of disturbance typically drive the resilient coral to collapse regardless of whether it is considered alone or in competition with the resistant coral (fig. 5A). In this case, the resilient coral has a beneficial legacy effect on the resistant coral: the resistant coral has higher cover on average, less variable cover, and greater resilience if the resilient coral were initially present, thus benefiting total coral cover as well. This result indicates that the original presence of the resilient coral can provide a transient but long-term benefit for the resistant coral well after its collapse by reducing the macroalgal cover over decadal timescales (app. C.2). When adding coral external recruitment (without or with macroalgal external recruitment) given intermediate levels of disturbance, both the resistant and resilient coral are more abundant and resilient in the presence of the other coral than when occurring alone (fig. 5B, 5C). With two connected patches, one with low disturbance and one with intermediate disturbance, the negative effect of competition reduces the resilient coral cover and resilience in the low-disturbance patch and therefore on average, but total coral cover and resilience is greater with both corals than with either alone (fig. 5D).

Effect of Competitive Interaction

Benefits of the presence of each coral to the other in terms of resilience and total cover under intermediate disturbance rely on either the absence of a superior competitor, that is, equivalent or lower interspecific than intraspecific competition (fig. 6A, 6B), or the resistant coral being the superior competitor (fig. 6D). If the resilient coral is the superior competitor, then it typically drives the resistant coral to collapse when considered together and subsequently collapses itself under intermediate-to-high disturbance, to the detriment of the resistant coral cover and resilience (with total cover and resilience of both corals together in between the resilient coral alone and resistant coral alone; fig. 6C). Under lower disturbance levels, lower interspecific than intraspecific competition is necessary for the coexistence of both corals when considered together in both one-patch and two-patch simulations under the parameter values explored here.

Discussion

We find that enhanced ecological resilience via response diversity across resistant and resilient types can occur in coral reef systems if (1) disturbance levels are high enough that the resilient type would collapse otherwise (fig. 4), and (2) the resistant type is an equivalent or superior competitor to the resilient type (fig. 6). The modeled mechanism for this enhanced resilience is through a positive association between coral cover and grazing on macroalgae that would otherwise invade and prevent coral recruitment after a disturbance: the resistant type is less likely to decline during disturbance and therefore maintains grazing intensity to benefit the recovery of the resilient coral, and the faster resilient coral recovery means a faster increase in grazing intensity following disturbance to benefit the persistence of the resistant coral. In other words, the balance between direct competition and indirect facilitation through effects on a shared competitor depends on disturbance level, where competition reduces individual cover at low disturbance but indirect facilitation enhances ecological resilience to disturbance at all levels (fig. 4). In the absence of external recruitment or multi-patch dynamics, even if disturbance levels are high enough to cause the resilient coral to collapse, the resilient coral can have a long-term (decadal-scale) legacy effect of reduced macroalgal cover that benefits the resistant coral due to the slow transients inherent to the model (app. C.2; analogous to the slow transients observed in Blackwood et al. 2012). The simulations with external recruitment or exchange between patches indicate the potential for competitor-enabled rescue (using “rescue effect” in the broad sense of Brown and Kodric-Brown 1977) where the role

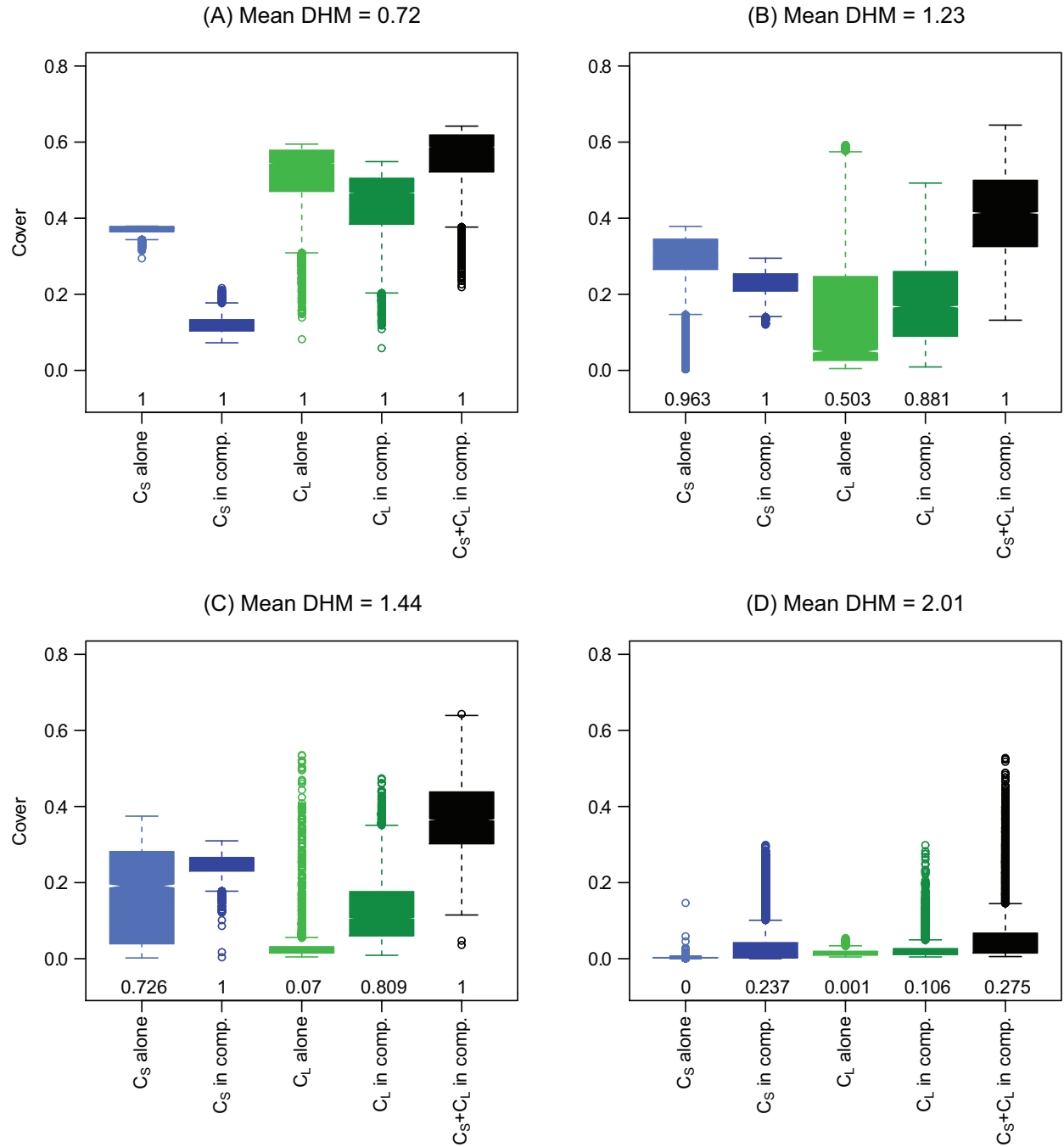


Figure 4: Boxplots of coral cover at the simulation endpoint and mean resilience (proportion of simulations ending with proportional coral cover greater than 0.05; numbers along the bottom of each plot) given different values of disturbance. Disturbances are sampled from the RCP 2.6 (representative concentration pathway to a radiative forcing level of 2.6 W/m^2) climate scenario for 1985–2020 (A), 1985–2030 (B), 1985–2035 (C), and 1985–2050 (D). In these simulations, interspecific competition is lower than intraspecific competition ($\alpha_s = \alpha_l = 0.6$) and the corals recruit externally ($r_{ex,S} = 0.001$, $r_{ex,L} = 0.01$, $r_{ex,M} = 0$), and all other parameters are as in figure 2. DHM = degree heating month.

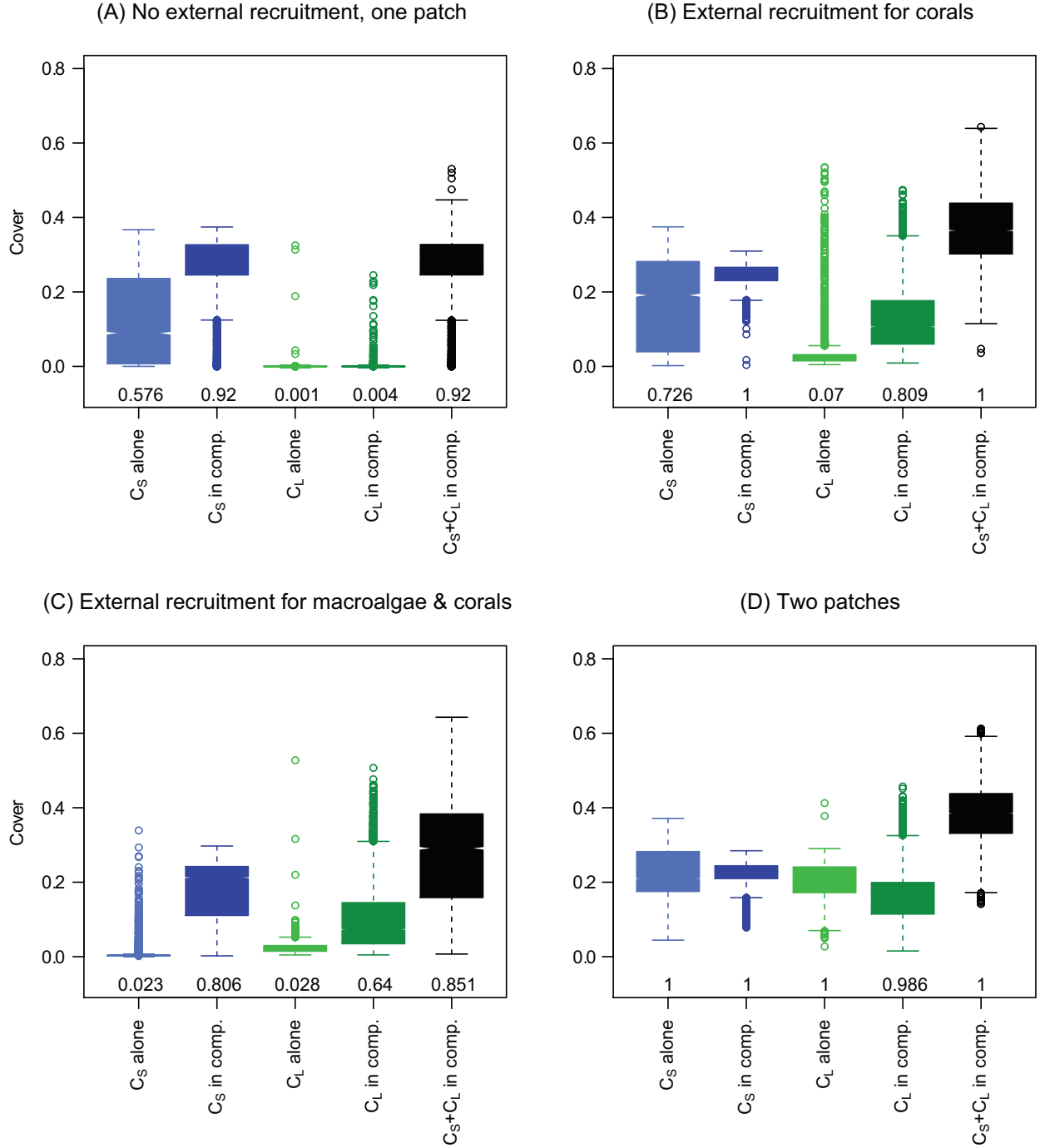


Figure 5: Boxplots of coral cover at the simulation endpoint and mean resilience (proportion of simulations ending with proportional coral cover greater than 0.05; numbers along the bottom of each plot) given different dynamics for recruitment. Recruitment dynamics are one patch with no external recruitment ($r_{ex,k} = m_{ij,k} = 0$; A), one patch with external recruitment for both coral types but no external recruitment for macroalgae ($r_{ex,S} = 0.001$, $r_{ex,L} = 0.01$, $r_{ex,M} = 0$; B), one patch with external recruitment for both corals and macroalgae ($r_{ex,S} = 0.001$, $r_{ex,L} = 0.01$, $r_{ex,M} = 0.0001$; C), and two patches with exchange between patches for both coral types ($m_{ij,S} = 0.001$, $m_{ij,L} = 0.01$; D) and where one patch experiences half of the disturbance magnitudes of the other. In these simulations, interspecific competition is lower than intraspecific competition ($\alpha_S = \alpha_L = 0.6$), mean disturbance is 1.44 degree heating months, and all other parameters are as in figure 2.

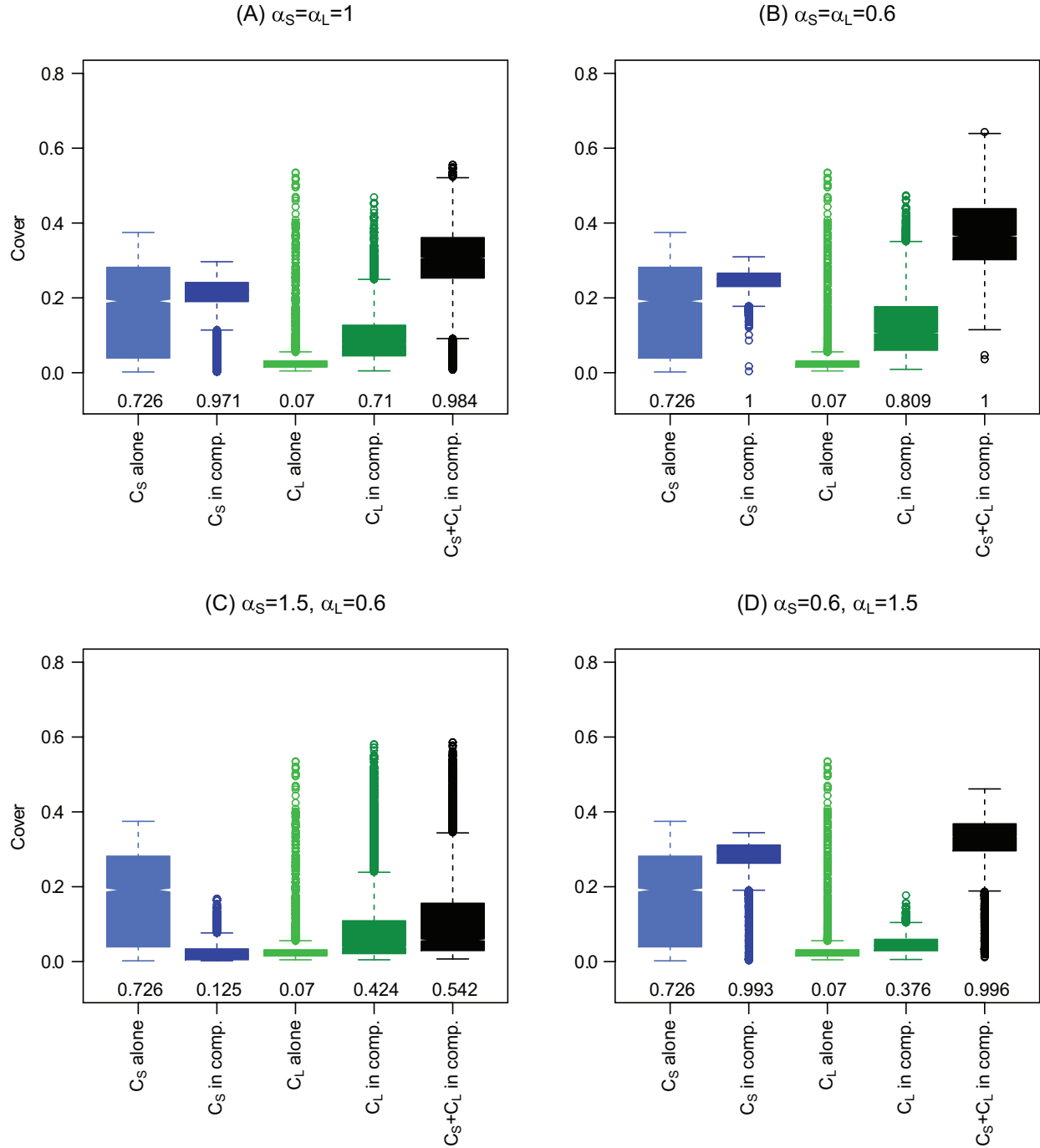


Figure 6: Boxplots of coral cover at the simulation endpoint and mean resilience (proportion of simulations ending with proportional coral cover greater than 0.05; numbers along the bottom of each plot) given different competitive interactions. Competitive interactions are equivalent interspecific and intraspecific (A), lower interspecific than intraspecific (B), resilient coral is the superior competitor (C), and resistant coral is the superior competitor (D). In these simulations, the corals recruit externally ($r_{ex,S} = 0.001$, $r_{ex,L} = 0.01$, $r_{ex,M} = 0$), mean disturbance is 1.44 degree heating months, and all other parameters are as in figure 2.

of each coral type in reducing the likelihood or rate of macroalgae invasion allows the local recovery of the other via recruitment from other sites (fig. 5).

Indirect facilitation can outweigh direct competition to increase ecological resilience given lower interspecific than intraspecific competition (i.e., niche partitioning), equivalent intraspecific and interspecific competition (i.e., a lack of a competitive hierarchy), and the resistant coral as the superior competitor (fig. 6A, 6B, 6D). However, if the resistant coral is the inferior competitor, the reduction in resistant coral cover due to competition in combination with its slow growth can prevent the resistant coral from reaching a density great enough to affect community-level dynamics at intermediate-to-high disturbance levels. Therefore, coral cover and ecological resilience can be greater with the resistant coral alone than with both corals (although both corals exceeds the resilient coral alone in cover and resilience) in this competitive case (fig. 6C). In contrast, the resilient coral's faster growth can allow it to contribute to ecological resilience when it is the inferior competitor (fig. 6D).

Enhanced resilience through response diversity despite the potential negative effect of competitive interactions has been observed in a wide variety of ecological communities, such as arid plant resilience to grazing (Walker et al. 1999; Chillo et al. 2011), tropical bird resilience to land use (Karp et al. 2011), and insect pollinator resilience to habitat loss (Winfree and Kremen 2009). Here, we show that one possible mechanism for this enhanced resilience occurs through the different roles played by resistant and resilient types, a specific categorization of response diversity that could apply beyond the coral reefs modeled here. For example, in boreal forests, aspen represent the resilient type through fast growth and spruce represent the resistant type through drought tolerance, and interspecific competition is likely lower than intraspecific competition due to differences in shade tolerance. Greater biomass in mixed stands during drought suggests enhanced resilience of these two species in combination, where the drought-tolerant spruce maintain soil moisture for the drought-susceptible aspen and the aspen might reduce the drought stress experienced by spruce through canopy provision (Man and Greenway 2013).

Ecological resilience is one of several dimensions of ecological stability (Ives and Carpenter 2007). More generally, the relationship between stability and diversity has long fascinated ecologists (Elton 1958). The extensive literature on this topic (reviewed by McCann 2000) includes a flurry of activity in the past 20 years focused on examining the relationship between biological diversity and ecosystem functioning (Loreau et al. 2002; Hooper et al. 2005; Cardinale et al. 2012). While our understanding of the relationship between diversity and some dimensions of eco-

logical stability (e.g., variance in biomass production) is now fairly deep (Gross et al. 2014), the relationship between diversity and ecological resilience has proven more difficult to characterize. Indeed, in a recent literature survey, Ives and Carpenter (2007) catalogued 64 different published empirical diversity-stability relationships and found that none of these addressed ecological resilience (while 12 of 64 relationships examined ecological resistance). The dearth of empirical data describing how diversity affects ecological resilience is at least partially attributable to the difficulty of measuring resilience in the field. In light of these difficulties, theoretical studies such as this one can foster understanding by identifying ecological conditions under which the response diversity of different species is likely to endow an ecosystem with enhanced resilience.

Requirements for Enhanced Ecological Resilience

The existence and detection of enhanced ecological resilience, therefore, depends on the context of competitive interactions, disturbance level, and recruitment dynamics, all in the presence of feedbacks that endow a system with alternative stable states. In this section we evaluate each of these requirements.

First, alternative stable states are, by definition (Holling 1973), a necessary component of any exploration of ecological resilience. Whether alternative stable states occur in a model of this type depends on a variety of parameter values, especially macroalgal growth and grazing rates (Fung et al. 2011). Empirically, the existence of alternative stable states is difficult to demonstrate (Petrakis and Dudgeon 2004), and the evidence for them in tropical reefs is greater for Caribbean than Indo-Pacific reefs due to a combination of potential factors such as lower herbivore diversity and abundance, faster macroalgal growth and recruitment, and loss of faster-growing corals in the Caribbean (Roff and Mumby 2012). Our model confirms that the loss of the faster-growing resilient types can erode ecological resilience (as can the loss of the resistant type). Also, tropical reefs might exhibit alternative states to coral dominance other than macroalgal dominance (Bellwood et al. 2004; Norström et al. 2009), ignored here for simplicity. If alternative stable states do not occur, a community-level benefit to the presence of both resistance and resilient types might still occur through increased stability in coral cover over time. Accordingly, enhanced community stability, measured in terms of aggregate variability in community properties or processes given environmental fluctuations, due to response diversity can occur in models that do not necessarily exhibit alternative stable states (e.g., Ives et al. 1999; Yachi and Loreau 1999; Norberg et al. 2001).

Second, enhanced ecological resilience via response diversity only occurs in our model when the resistant type is an equivalent or superior competitor to the resilient type (fig. 6). Corals exhibit direct and indirect competition for space and associated resources such as light and substrate-associated nutrients (Lang and Chornesky 1990). While one might expect fast-growing, branching (resilient) corals to be superior competitors due to their morphological structure that allows overtopping of slow-growing, massive-type (resistant) corals (Hughes and Connell 1999), massive-type corals tend to display greater aggression through digestive filaments as compared to faster-growing corals, which can serve as a defense against overtopping (Lang 1973). Overall, the variety of direct and indirect competitive interactions between corals leads to a lack of a clear hierarchy in coral competitive abilities (Lang and Chornesky 1990). In addition, different coral types might occupy different habitat or niches in terms of characteristics such as wave exposure, depth, light, and turbidity (Done 1982; Jackson and Hughes 1985; Anthony and Connolly 2004), which would decrease competitive interactions. Therefore, either niche partitioning or a lack of competitive hierarchy, both of which can lead to enhanced ecological resilience with response diversity (fig. 6A, 6B), might be relevant to coral competitive dynamics. Niche and habitat segregation can further enhance response diversity by diversifying the environmental variables that the different populations respond to, as occurs with seabird response diversity to variability in prey abundance (Fauchald et al. 2011).

Third, enhanced ecological resilience via response diversity is evident only when disturbance occurs at high enough levels that the resilient coral has a high likelihood of collapse in the absence of the resistant type (fig. 4). When bleaching is mild or infrequent, competition for space primarily drives the interaction between coral types. Conversely, as disturbance becomes more severe and more frequent, indirect facilitation between corals via augmented herbivory comes to outweigh competition. This shift matches the predictions of the stress-gradient hypothesis (Bertness and Callaway 1994; Callaway 2007), which suggests that facilitation should be a more important force in structuring ecological communities when the environment is harsh, and competition should be more important when the environment is benign. Therefore, our results suggest that indirect facilitation between coral species will become increasingly important to structuring tropical reef communities as climate change increases in the near future. As disturbance levels shift to those high enough to observe enhanced ecological resilience, community composition shifts toward greater composition of resistant type, a finding in line with previous modeling studies of coral reef response to increased thermal stress

(Wooldridge et al. 2005; Baskett et al. 2009; Riegl and Purkis 2009) as well as corresponding field data (Riegl and Purkis 2009). A potentially counterintuitive conclusion from these results is that the resilient type is more important to the community-level properties when it is more threatened.

Finally, outside recruitment is necessary for the continued persistence of both coral types under intermediate or higher levels of disturbance (i.e., to observe the competitor-enabled rescue effect; fig. 5), which requires the spatial scale of the disturbance to be smaller than the spatial scale of larval connectivity. Thermal stress does display fine-scale spatial variability (Selig et al. 2010) such that larval dispersal can connect areas that experience different levels of stress (Mumby et al. 2011), and empirical evidence supports the expectation that areas with high recruitment from undisturbed sites have greater recovery from bleaching disturbances (Underwood et al. 2007). The importance of recruitment found here echoes other models showing the importance of open recruitment or larval exchange between locations experiencing differential stress to coral response to disturbances (e.g., Hughes and Tanner 2000; Riegl and Purkis 2009; Riegl et al. 2009; Baskett et al. 2010). For example, the model of one coral type in competition with macroalgae by Elmhirst et al. (2009; including the potential for alternative stable states) indicates that external coral recruitment can lead to coral recovery from disturbance given high-enough grazing levels. The results here indicate that the combination of different coral types allows maintained grazing levels for recruitment to play this role.

While empirical support exists for each of the conditions described above, a direct empirical test of the relationship between response diversity and ecological resilience in the field or laboratory would require additional investigation. Specifically, it would require a system with established alternative stable states and response diversity, replicated cases with different community assemblages, and data on long-term persistence under disturbance across replicates. Long-term data are crucial because the immediate response to disturbance can be misleading: a community composed of both resistant and resilient types will, by definition of the types, experience greater proportional declines directly following a disturbance than a community composed of the resistant type only, but the recovery of the resilient type can play a role in overall ecological resilience across both types as shown here. Given these requirements, tropical coral reefs, with their slow growth and long life spans, may not provide the most opportune system for empirical tests of diversity-resilience relationships as a general ecological phenomenon. Rather, systems with faster turnover and the potential to experimentally

manipulate disturbance are likely to be more amenable to empirical exploration of our central conclusions.

Model Assumptions

Our model represents a stylized coral community of two coral types interacting with macroalgae in order to focus on the question of how the community composition in terms of these two types affects ecological resilience. We therefore ignore many additional dynamical components of tropical reef systems. For example, we simplified the vast array of coral diversity into two stylized types. Even when categorizing coral diversity into broad groups based on a variety of morphological and life history traits, Darling et al. (2012) posit three or four general categories: competitive types characterized by fast growth and stress susceptibility, weedy types characterized by rapid reproduction, and stress-tolerant types characterized by slow-growth, with a possibly distinct subgroup of generalist types characterized by moderate growth, competitive ability, and stress tolerance. Including more species would likely lead to similar results as long as species occur along a trade-off between resistance to disturbances and recovery rate from disturbance (engineering resilience). Analogously, in the model of phytoplankton communities by Norberg et al. (2001), diversity buffers the effect of variation in predation intensity on community biomass given an arbitrary number of species on a continuous trade-off between predator defense and faster growth.

In addition, we include the dynamics of herbivorous fish implicitly rather than explicitly. Explicit herbivore dynamics in models of this type still lead to alternative stable states (Blackwood et al. 2012). Such dynamics might include a time lag between coral loss and the loss of grazing on macroalgae, which can shift the basins of attraction (Blackwood and Hastings 2011); time lags would increase the time over which competitor-enabled rescue could occur in our model. Herbivore dynamics might also depend on the rugosity of the reef structure, where increasing herbivore attraction with increasing rugosity can increase the resilience of the coral-dominated state (Blackwood et al. 2011). Given the greater rugosity typically provided by branching and plating corals than massive and encrusting corals, incorporating a rugosity effect on grazing intensity would likely increase the potential benefit of the resilient coral to the resistant coral via grazer habitat provisioning. If rugosity affects grazer diversity more than density (as suggested empirically; Messmer et al. 2011), then coral diversity will play an additional role in ecological resilience beyond response diversity because grazer diversity affects the overall resilience of coral-dominated state as well (Bellwood et al. 2004; Nyström 2006).

Within the coral population dynamics, we ignore size

structure, different reproductive types, evolutionary responses to disturbance, and disturbances beyond thermal stress. Size structure can influence susceptibility to disturbances such as bleaching and hurricanes in addition to coral dynamics in general (Hughes 1984; Shenkar et al. 2005) and therefore would likely alter the sizes of the basins of attraction but not necessarily the relative effect of community composition, modeled here. While we model coral recruitment dynamics as a constant rate, the different coral reproductive strategies in terms of brooding or broadcast spawning will change the variability of recruits in time and can influence coral competitive interactions and coexistence (Darling et al. 2012). Dynamical evolutionary changes in stress susceptibility can increase the persistence of corals under high disturbance, depending on the rate of climate change (Baskett et al. 2009, 2010). By reducing the likelihood of a shift to a macroalgal-dominated state, the dynamics of competitor-enabled rescue found here would allow more time for such adaptation to increased thermal stress to occur. Finally, the disturbance modeled here, thermal stress-induced bleaching, is one of many effects of global change on tropical coral reefs (Bellwood et al. 2004; Hughes and Connell 1999). Ocean acidification, by reducing coral growth, would reduce overall resilience and therefore have the potential to interact synergistically with disturbances such as bleaching and storms (Anthony et al. 2011). Compounding this effect, reduced growth in the resilient coral in particular might reduce its role in ecological resilience shown here. The morphological traits considered to confer resistance or resilience to bleaching also confer resistance or resilience, respectively, to storms and predatory sea star outbreaks (Jackson and Hughes 1985; De'ath and Moran 1998; Hughes and Connell 1999), which would lead to analogous enhanced ecological resilience via response diversity to that found here.

Management Implications

Understanding the drivers of ecosystem response to disturbance can inform management in the context of global environmental change by providing insight into how to protect the capacity for ecological systems to absorb and recover from anthropogenically driven disturbance (Folke et al. 1996, 2004; Levin and Lubchenco 2008; Bernhardt and Leslie 2013). Here we show that a complex adaptive system perspective that takes into account not just individual-level responses but also how those responses interact with each other reveals a role for response diversity in ecological resilience under high disturbance. These results build on models that indicate a role for response diversity in buffering the effect of environmental variability on community properties in general (e.g., Ives et al. 1999;

Yachi and Loreau 1999; Norberg et al. 2001) to indicate that such buffering can be realized as increased ecological resilience specifically. Therefore, diverse regions can provide a target for protection in order to enhance resilience to expected future disturbance (West and Salm 2003; Obura 2005; McLeod et al. 2009). Because this enhanced resilience occurs through the recovery dynamics of competitor-enabled rescue, such protection will not necessarily reduce mortality following disturbances such as bleaching (Selig et al. 2012; in fact, greater mortality might occur due to the persistence of stress-susceptible types), but rather can affect the probability and rate of return to a coral-dominated state. Finally, the dynamics of competitor-enabled rescue require a network of protected areas with larval connectivity across locations experiencing different levels of stress (as in Mumby et al. 2011).

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