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# Conservation management approaches to protecting the capacity for corals to respond to climate change: a theoretical comparison

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## Abstract

Multiple anthropogenic impacts, including bleaching from climate change-related thermal stress, threaten coral reefs. Protecting coral capacity to respond to the increase in future thermal stress expected with climate change can involve (1) protecting coral reefs with characteristics indicative of greater resistance and resilience to climate change, and (2) reducing other anthropogenic impacts that are more likely to reduce coral resistance and resilience to climate change. Here, we quantitatively compare possible priorities and existing recommendations for protecting coral response capacity to climate change. Specifically, we explore the relative importance of the relevant dynamics, processes, and parameters in a size-structured model of coral and zooxanthellae ecological and evolutionary dynamics given projected future thermal stress. Model results with varying initial conditions indicate that protecting diverse coral communities is critical, and protecting communities with higher abundances of more thermally tolerant coral species and symbiont types secondary, to the long-term maintenance of coral cover. A sensitivity analysis of the coral population size in each size class and the total coral cover with respect to all parameter values suggests greater relative importance of reducing additional anthropogenic impacts that affect coral–macroalgal competition, early coral life history stages, and coral survivorship (compared with reproduction, growth, and shrinkage). Finally, model results with temperature trajectories from different locations, with and without connectivity, indicate that protection of, and connectivity to, low-thermal-stress locations may enhance the capacity for corals to respond to climate change.

*Keywords:* coral bleaching, coral reefs, global climate change, quantitative genetic model, size-structured matrix model

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## Introduction

Given the substantial impact of climate change on ecological communities (Walther *et al.*, 2002), accounting for how climate change affects population persistence, community structure, and the sustainable delivery of ecosystem services presents a major challenge for conservation biology and ecosystem manage-

ment (McCarty, 2001). Accounting for the ecological impacts of climate change in management decisions requires an understanding of potential ecological and evolutionary dynamical responses to climate change (e.g., movement, acclimatization, and genetic adaptation) and how they depend on interactions between climate change and additional anthropogenic impacts (McCarty, 2001; Parmesan, 2006). Through this understanding, local management may alleviate the impact of global climate change (Heller & Zavaleta, 2009). Specifically, management may focus protection on populations and communities with a greater capacity to respond to climate change, i.e., those with biological and environmental characteristics that may lead to

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reduced severity of climate change impacts. In addition, management may reduce additional anthropogenic impacts that are more likely to impede ecological responses to climate change.

Coral reef ecosystems face multiple anthropogenic impacts, including climate change (Smith & Buddemeier, 1992; Done, 1999; Wilkinson, 1999; Pandolfi *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007). One of the primary ways in which climate change threatens coral reefs is through an increase in coral bleaching, the potentially fatal loss of symbionts (principally dinoflagellates of the genus *Symbiodinium*) from the coral animal in response to stressors such as extreme temperatures (Smith & Buddemeier, 1992; Brown, 1997b; Hoegh-Guldberg, 1999). Assuming constant thermal stress thresholds, climate change-related coral bleaching may lead to precipitous coral declines within decades (Ware, 1997; Huppert & Stone, 1998; Hoegh-Guldberg, 1999; Sheppard, 2003; Donner *et al.*, 2005, 2007; Wooldridge *et al.*, 2005). However, corals may be able to respond to climate change through shifts in community composition, acclimatization, and genetic adaptation (Baird *et al.*, 2007; Brown, 1997a; Hughes *et al.*, 2003; Baker, 2004; Hoegh-Guldberg *et al.*, 2007).

In addition to thermal stress, global climate change threatens coral reefs through increased ocean acidification (with increased carbon dioxide concentrations) and associated reduced coral calcification, increases in temperature-related coral diseases, and possibly increased disturbance from greater storm intensity (Smith & Buddemeier, 1992; Done, 1999; Wilkinson, 1999; Pandolfi *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007). Locally, coral reefs face impacts from fisheries-related habitat degradation and disruption of community structure (e.g., declines in herbivorous fish) as well as terrestrial runoff-related sedimentation, eutrophication, and pollution; these impacts affect corals directly and indirectly through effects on competing macroalgae and predatory corallivore populations (Smith & Buddemeier, 1992; Wilkinson, 1999; Pandolfi *et al.*, 2003). Such local impacts have the potential to decrease coral resistance and resilience to the global impacts (Nyström *et al.*, 2000; Knowlton, 2001; Bellwood *et al.*, 2004). Note that here we employ the Holling (1973) definition of resilience as the capacity for a system to avoid shifts between alternative states after disturbance. For example, by increasing macroalgal growth, herbivorous fish fisheries and nutrient runoff may decrease the resilience to a shift from a coral-dominated state to a macroalgae-dominated state after a disturbance such as coral bleaching (Nyström *et al.*, 2000; Knowlton, 2001; Hughes *et al.*, 2007; Mumby *et al.*, 2007).

Local management may help protect the capacity for coral response to global climate change by reducing

additional anthropogenic impacts that may otherwise impede this response (Bellwood *et al.*, 2004). Furthermore, management can focus such efforts on locations with biological and environmental characteristics indicative of greater coral resistance and resilience to climate change (West & Salm, 2003). The long list of such possible characteristics, based on conceptual deductions from a scientific understanding of coral bleaching (West & Salm, 2003; Obura, 2005), leads to multiple possible, and sometimes contradictory, management priorities, detailed in the following paragraphs. To help inform priorities and resolve contradictions, the goal of this study is to use a dynamical model to compare these management recommendations in a single quantitative framework.

The conceptual analysis of alternative priorities for conserving coral response capacity has led to a number of conflicting targets with respect to coral and symbiont diversity, location, and connectivity. For example, one possible conservation target is diverse coral communities, as a potential indicator of ecosystem health (West & Salm, 2003) and functional redundancy that may enhance disturbance response capacity (Nyström *et al.*, 2000). Alternatively, less diverse communities with a higher prevalence of thermally tolerant coral species and symbiont types may have greater resistance to climate change (West & Salm, 2003). Therefore, locations where past thermal stress has resulted in high thermal tolerance in community and genetic composition may deserve prioritization for protection (Cook *et al.*, 1990; West & Salm, 2003). However, areas with historically high temperatures may also have higher future temperatures due to their oceanographic properties, which would increase susceptibility to future climate change, especially if adaptation is slow (Hoegh-Guldberg, 1999). Accordingly, another possible management goal is protecting areas with oceanographic features that lead to less temperature stress (West & Salm, 2003; McClanahan *et al.*, 2008). Finally, connectivity between high-stress and low-stress locations may enhance recovery after bleaching events, which suggests management goals such as protecting locations with oceanographic features that enhance recruitment (Obura, 2005; Salm *et al.*, 2006). However, such connectivity may also lead to an input of recruits poorly adapted to local conditions and therefore slow adaptive response to climate change (i.e., 'migration load,' Lenormand, 2002).

Furthermore, given limited resources for conservation, a clearer prioritization is needed. Specifically, different oceanographic and biological characteristics differentially affect coral demographic processes (e.g., oceanographic features that flush toxins that build up during bleaching events affect mortality rates, while

those that promote connectivity affect recruitment; West & Salm, 2003), and therefore may differentially indicate which locations would allow greater coral resistance and resilience to bleaching. Similarly, different anthropogenic impacts (e.g., ocean acidification, temperature-related disease outbreaks, sedimentation, eutrophication, herbivore fisheries) differentially affect various coral demographic processes (e.g., growth, recruitment, mortality, fragmentation, and competition with macroalgae; Smith & Buddemeier, 1992; Done, 1999; Wilkinson, 1999; Pandolfi *et al.*, 2003). Therefore, such impacts may differentially affect the capacity for coral response to thermal stress (Marshall & Schuttenberg, 2006) and deserve differential prioritization for mitigation.

In order to analyze these potential contradictions and inform possible priorities, we quantitatively compare the influence of the relevant processes and parameters on theoretical coral response to climate change. To this end, we build on our existing model of temperature-dependent symbiont population and genetic dynamics and symbiont-dependent coral population dynamics (Baskett *et al.*, 2009); new dynamics include coral size structure, coral–macroalgae competition, and coral larval exchange between multiple locations. Then we explore model predictions of coral cover given future climate scenarios (1) with different initial conditions to determine the relative importance of a higher prevalence of stress-tolerant coral species or symbiont types compared with overall diversity, (2) across multiple locations to determine the relative potential for past stress to shape stress-tolerance compared with its possible association with future stress levels, and (3) with and without larval connectivity to determine the relative importance of the amount of recruitment compared with the maintenance of local adaptation. Finally, sensitivity analysis of coral cover to the various coral demographic and coral–macroalgae competition parameter values that are differentially affected by different local anthropogenic impacts allows insight into which processes may most affect the capacity for corals to respond to climate change. Overall, this quantitative comparison helps to understand which characteristics better indicate coral capacity to respond to future climate change and which additional anthropogenic impacts are more likely to impede coral response to thermal stress.

## Materials and methods

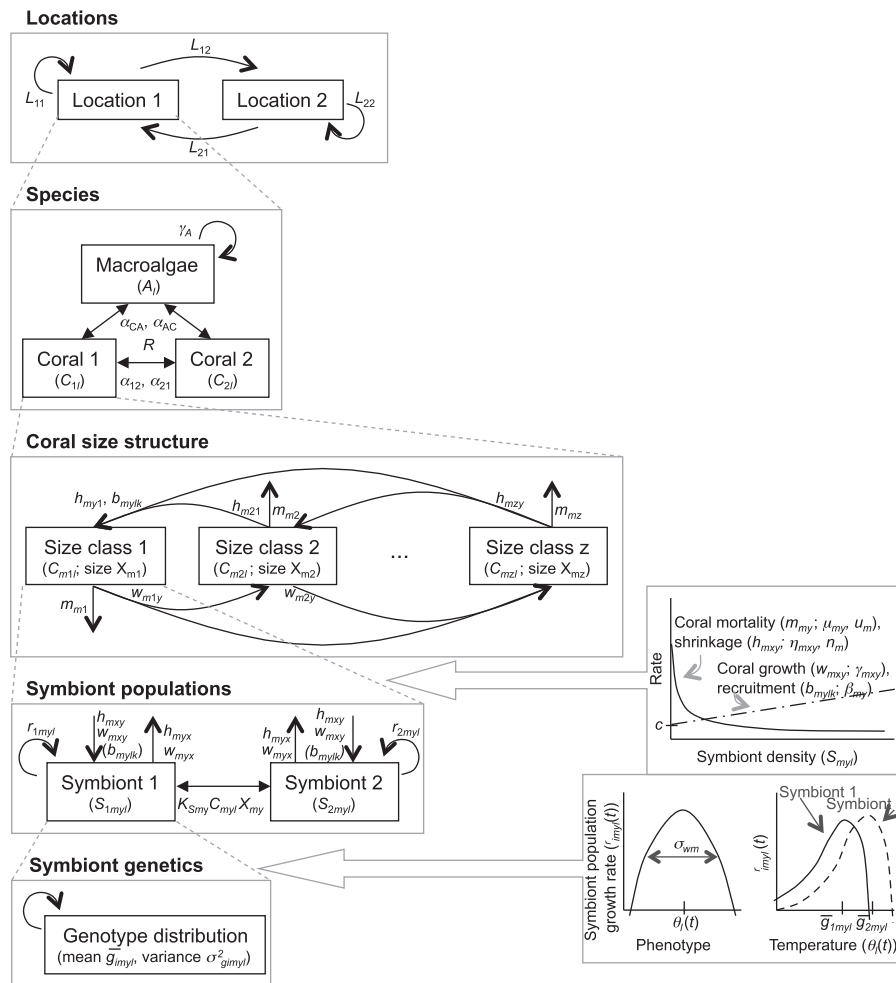
Below, we first provide a conceptual overview of the coral–symbiont model; see Appendix S1 for mathematical details. Then we describe the model analysis with respect to the central questions indicated in the previous paragraph.

### *Model description*

As outlined in Fig. 1, the model follows population dynamics in one or two locations, with coral larval exchange between locations. Within each location, one to two species of corals, and potentially macroalgae, compete for space. Each coral has multiple size classes, where the model follows the number of individual coral colonies in each size class based on the rate at which they enter and leave size classes due to growth (extension), shrinkage (fragmentation), mortality, and recruitment. These coral demographic rates depend on the total symbiont densities (irrespective of type) in each size class, where one to two symbiont types compete for resources within the corals. In addition to symbiont population dynamics, the model follows the symbiont thermal tolerance genetic dynamics as they depend on the temperature and coral host.

*Symbiont genetic dynamics.* For the evolutionary dynamics of symbiont thermal tolerance, we use a quantitative genetic model that follows the mean genotype and genetic variance for a clonal, haploid population. This approach reflects available empirical evidence for the genetic makeup of *Symbiodinium* (LaJeunesse, 2001; Santos & Coffroth, 2003) and provides a conservative estimate of the potential rate of evolution (as recombination, ignored here, can lead to more rapid evolution; Lynch & Lande, 1993; Burger, 1999). Depending on the genotype and random environmental effects, the thermal tolerance phenotype is the temperature for which an individual symbiont is optimally adapted. As the actual temperature departs from the phenotype, the fitness, measured as the asymptotic population growth rate, declines, possibly becoming negative. We interpret this fitness function (Fig. 1, lower right-hand corner plots) as reflecting a trade-off of resource investment in thermal tolerance vs. growth: a symbiont is over-investing in thermal tolerance and under-investing in growth for a temperature lower than its phenotype and vice-versa for a temperature greater than its phenotype. Therefore, for two individuals with different phenotypes, the one with the more thermally tolerant phenotype will grow faster at higher temperatures but slower at lower temperatures. The width of the fitness function describing this stabilizing selection for the ambient temperature (i.e., how quickly population growth rates decline as the temperature departs from the phenotype) depends on the coral host species in order to allow for differences in host thermal tolerance.

*Symbiont population dynamics.* While this evolutionary model follows any gradual changes in thermal tolerance



**Fig. 1** Diagram of the size-structured and spatially structured model of coral and symbiont ecological and evolutionary dynamics. The gray boxes along the left indicate the nested dynamics for each organizational level, and the gray boxes with arrows along the right indicate the functions that describe the interactions between these organizational levels. Within these, black boxes indicate state variables, and black arrows with parameter labels indicate dynamics. See Table 1 for an explanation of the symbols.

through time, we model the potential for discrete shifts in thermal tolerance with multiple symbiont ‘types,’ e.g., shifts between *Symbiodinium* from different subclades, which can occur in some but not all coral species (Baker, 2003; Sotka & Thacker, 2005; Stat *et al.*, 2006; van Oppen & Gates, 2006; Baird *et al.*, 2007). These different symbiont types have different mean genotypes, and the tradeoff between growth and thermal tolerance described above drives temperature-dependent population growth rates for each type (similar to empirical observations; Sotka & Thacker, 2005). Symbiont population regulation occurs within the coral host (e.g., as may arise from host regulation; Baghdasarian & Muscatine, 2000); see Baskett *et al.* (2009, Appendix C) for a detailed explanation of the competition mechanism.

In addition to the temperature and density-dependent population growth, symbiont population dynamics in each coral size class are a function of coral host transfer

rates between size classes. Specifically, symbionts follow their coral hosts’ growth into larger size classes and shrinkage into smaller size classes. In new coral recruits, the symbiont composition (i.e., relative densities of each symbiont type) depends on the coral host transmission type. For brooding corals, they depend on the symbiont populations in the reproducing coral colony to represent vertical transmission (following empirical observation; Richmond & Hunter, 1990). For broadcast spawning corals, they either depend on the symbiont populations in all corals in the recruitment location or occur at a set ratio, independent of within-coral symbiont populations, to represent horizontal and open transmission, respectively (Richmond & Hunter, 1990).

*Coral population dynamics.* Assuming that the symbionts contribute energy to coral growth and maintenance (Muscatine *et al.*, 1984), symbiont densities affect coral

growth, mortality, shrinkage, and reproductive rates (Jacques *et al.*, 1983; Szmant & Gassman, 1990; Stimson *et al.*, 2002; Anthony *et al.*, 2007). Specifically, we account for heterotrophic coral energy acquisition supplying a constant (small) proportion of the energy necessary for coral growth and maintenance, and the remaining proportion of the total possible energy available depends on the symbiont densities relative to their maximum capacity (note that this simplification ignores the potential for up-regulation of coral heterotrophy during stressful events possible for some coral species; Grottoli *et al.*, 2006). Coral growth and reproduction increase, and mortality and shrinkage decrease, with the total energy available and therefore with increasing symbiont densities. In order for coral cover to decrease, thermal stress events must be extreme or long-lasting enough to cause symbiont densities to decline to the point where coral mortality and shrinkage exceed growth and recruitment; thus the model accounts for the cumulative stress necessary for a fatal bleaching event (Smith & Buddemeier, 1992; Brown, 1997b; Hoegh-Guldberg, 1999; Donner *et al.*, 2005).

In one-location simulations, we model closed coral dynamics where the recruitment depends on the reproductive (second size class and larger) coral population size. One interpretation of this simplification is that any connected locations to the modeled location experience similar levels of thermal stress and therefore have similar coral dynamics and reproductive output. We relax this assumption in two-location simulations where connectivity between locations occurs through larval exchange in the recruitment dynamics.

*Coral community dynamics.* Within each location, to model coral density-dependent dynamics and a limit to space available for coral cover, we assume that coral growth rates decrease with increasing coral density and recruitment can only occur in unoccupied space (although note that corals rarely reach their carrying capacity in our results). When we model two coral species competing for space, we incorporate a species-level trade-off between coral growth and thermal tolerance (as suggested from empirical evidence; Loya *et al.*, 2001; Bhagooli & Yakovleva, 2004). Specifically, we associate greater thermal stress susceptibility (narrower fitness function for the symbionts it hosts) with the coral species that has parameter values based on the faster-growing coral and, correspondingly, greater thermal stress tolerance (wider fitness function for the symbionts it hosts) with the coral species that has parameter values based on the slower-growing coral (parameterization described in the next subsection below). Rather than a specific coral community, these

corals are intended as representative of different, broad groups of coral species such as branching-type and massive-type corals. In addition to intraspecific and interspecific coral competition for space, we include coral–macroalgal competition in some simulations. In such simulations, macroalgal growth is independent of temperature, and established corals out-compete (overgrow) macroalgae while macroalgae prevents coral recruitment (following empirical observation; McCook *et al.*, 2001; Kuffner *et al.*, 2006).

In summary, the model incorporates a trade-off between growth and thermal tolerance in both coral species and symbiont types, where the temperature and coral host drive the symbiont dynamics and symbiont densities influence coral dynamics. While more biologically detailed than our original model (Baskett *et al.*, 2009), this model formulation necessarily involves a number of simplifying assumptions. Therefore, model results are not appropriate for precise forecasts; rather, comparative trends and sensitivity analysis can indicate the relative importance of different dynamics, processes, parameters, and initial conditions.

#### *Model analysis*

To analyze the model, we numerically integrate the above-described model (equations in Appendix S1) with past and future temperature data from a variety of climate models and locations and with a variety of initial conditions, described below. For the numerical analysis, we base the parameter values for the coral demographic (growth, shrinkage, mortality, and recruitment) rates on values reported in existing coral matrix models. Specifically, for the fast-growing coral we use the parameters values reported in Edmunds (2005) from the branching-type coral Pocilloporidae, and for slow-growing coral species we use the parameter values reported in Hughes & Tanner (2000) and Edmunds & Elahi (2007) from the massive-type coral *Montastraea annularis*. While we use these specific species complexes to calculate the coral demographic parameters, in the model they represent broader functional groups likely to be present in any coral community. In addition, we estimate the macroalgal growth and coral–macroalgal competition parameters from the general empirical information in Mumby *et al.* (2005) and McCook *et al.* (2001). For the symbiont genetic, population, and symbiont–coral interaction parameters, we use the same approach as in our original model (Baskett *et al.*, 2009). See Table 1 for the parameter values and Appendix S2 for a detailed explanation of the model parameterization and numerical analysis.

As in Baskett *et al.* (2009) and similar to Donner *et al.* (2005, 2007), we test model predictions using mean

**Table 1** Parameter values used in the numerical analysis

Parameter and description	Value	Reference(s)	
<i>Macroalgae parameters</i>			
$\gamma_A$	Macroalgal growth rate	237.25 cm <sup>2</sup> yr <sup>-1</sup>	Mumby <i>et al.</i> (2005)
$\alpha_{mA}$	Competitive effect of macroalgae on postsettlement corals	0.2	McCook <i>et al.</i> (2001)
$\alpha_{Am}$	Competitive effect of corals on macroalgae	6	McCook <i>et al.</i> (2001)
<i>Coral parameters</i>			
$\alpha_{mn}$	Interspecific coral competition	1	
$R$	Area available	$6.25 \times 10^6$ cm <sup>2</sup>	Mumby (2006)
$X_{my}$	Average size in each size class	Branching: 3.1416, 28.2743, 78.5398 cm <sup>2</sup> Massive: 25, 125, 250 cm <sup>2</sup>	Edmunds (2005) Hughes & Tanner (2000)
$\gamma_m$	Growth rate ( $\gamma_{mxy} = \gamma_m / (X_{my} - X_{mx})$ )	Branching: 10.1513 cm <sup>2</sup> yr <sup>-1</sup> Massive: 3.3558 cm <sup>2</sup> yr <sup>-1</sup>	Edmunds (2005) Hughes & Tanner (2000)
$\mu_m$	Mortality rate ( $\mu_{my} = \mu_m / X_{my}$ )	Branching: 66.8930 cm <sup>2</sup> yr <sup>-1</sup> Massive: 72.0234 cm <sup>2</sup> yr <sup>-1</sup>	Edmunds (2005) Hughes & Tanner (2000)
$u_m$	Influence of symbionts on mortality	Branching: 28.9855 Massive: 24.5253	Edmunds (2005) Hughes & Tanner (2000)
$\eta_m$	Shrinkage rate ( $\eta_{mxy} = \eta_m / (X_{mx} - X_{my})$ )	Branching: 17.2764 cm <sup>2</sup> yr <sup>-1</sup> Massive: 18.8591 cm <sup>2</sup> yr <sup>-1</sup>	Edmunds (2005) Hughes & Tanner (2000)
$n_m$	Influence of symbionts on shrinkage	Branching: 7.9774 Massive: 1.3487	Edmunds (2005) Hughes & Tanner (2000)
$\beta_m$	Recruitment rate* ( $\beta_{my} = \beta_m X_{my} / \sum_{x=2}^z X_{mx}$ )	Branching: 8.1428 yr <sup>-1</sup> Massive: 6.2166 yr <sup>-1</sup>	Edmunds (2005) Edmunds & Elahi (2007)
$L_{kl}$	Coral connectivity between locations	(number of locations) <sup>-1</sup>	
$c$	Proportion of coral energy gained from heterotrophy	0.28	Grottooli <i>et al.</i> (2006)
<i>Symbiont parameters</i>			
$K_{sm}$	Symbiont carrying capacity†	Branching: $4.92 \times 10^7$ cells cm <sup>-1</sup> Massive: $4.744 \times 10^7$ cells cm <sup>-1</sup>	Fitt <i>et al.</i> (2000), Chancerelle (2000)
$v_m$	Number of symbionts per coral recruit	$0.8 K_{sm} X_{m1}$	
$a$	Symbiont growth rate constant	1.0768 yr <sup>-1</sup>	Muscatine <i>et al.</i> (1984)
$b$	Symbiont growth exponential constant	0.0633 °C <sup>-1</sup>	Eppley (1972), Norberg (2004)
$\sigma_{wm}^2$	Selectional variance	Stress-susceptible coral: $\propto$ initialization temperature variation‡	Noordeloos <i>et al.</i> (2007)
$\sigma_{em}^2$	Environmental variance	Stress-tolerant: $1.25 \cdot$ branching coral $\sigma_{wm}^2$	Mumby <i>et al.</i> (2001) Lynch <i>et al.</i> (1991), Mousseau & Roff (1987), Muscatine <i>et al.</i> (1984)
$\sigma_{Mm}^2$	Rate mutation increases genetic variance	$0.001 \text{ yr}^{-1} \times \sigma_{em}^2$	Lynch (1988)

See Appendix S2 for detailed information on parameterization and the text for initial conditions. We calculate some parameters from combinations of, and conversions based on, published values without rounding; therefore, the number of significant figures does not indicate the accuracy or precision of these parameter values. Also, in one-coral-species simulations we drop all  $m$  subscripts.

\*We increase  $\beta_m$  by a factor of 52 or 12 for southern or northern latitude broadcast spawning corals (which we simulate with a 1-week or 1-month spawning period; Richmond & Hunter, 1990), respectively, to maintain the same total annual recruitment as year-round brooding corals.

†Units reported as per cm of coral projected area, based on combining the expected carrying capacity per cm coral surface area and the expected relationships between coral surface area and coral projected area.

‡Proportionality constant depends on location and equals 0.9 and 0.8 for the Curaçao and Bahamas results presented here (for details, see the Appendix S2 section on Symbiont–coral interaction parameters in this paper and the Model Analysis section in Baskett *et al.*, 2009).

monthly sea surface temperature (SST) data and projections from multiple climate models and locations. For past temperature data we use the Met Office Hadley Centre for Climate Prediction Sea Ice and SST data set (ISST; Rayner *et al.*, 2003). For future temperature we use two climate models: the Hadley Center HadCM3 model, and the National Oceanic and Atmospheric Administration (NOAA) Geophysics Fluid Dynamics Laboratory (GFDL) 2.1 model. For each of these climate models, we compare two future climate scenarios differing in the amount of the greenhouse gas emissions that drive climate change: the 720 ppm stabilization experiment (SRES A1b) and the 550 ppm stabilization experiment (SRES B1). We choose these scenarios as representative (close to, but not at, the extremes) of the range of existing climate scenarios, which vary from expected greenhouse gas emissions given business-as-usual continuation of current practices to those given large-scale greenhouse gas mitigation efforts. To obtain the future temperature data for those climate models and scenarios, we use the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multimodel dataset. For each climate model, we test model predictions with temperature data from a variety of locations spanning the world's tropical oceans, chosen for data availability on coral dynamics (Bak *et al.*, 2005, Brown *et al.*, 2002, Connell *et al.*, 1997, and the Moorea Coral Reef Long Term Ecological Research Site): Moorea, French Polynesia; Curaçao, Netherland Antilles (the location for the sample results presented here); Ko Phuket, Thailand; and Heron Island, the Great Barrier Reef, Australia.

*Initial conditions: overall diversity vs. higher prevalence of stress-tolerant coral species and symbiont types.* We initialize the simulations with 50% of the total area ( $0.5R$ ) covered by coral populations ( $\sum_m \sum_y X_{my} C_{myl}$ ).

We distribute the initial total coral cover for each species across size classes ( $C_{myl}$ ) based on the expected equilibrium size structures (approximated by the eigenvectors corresponding to the leading eigenvalues for the transition matrices in Edmunds (2005) and Hughes & Tanner (2000) used to calculate the coral demographic parameter values). In simulations with macroalgae, we start with 10% macroalgae cover ( $A_l$ ). In one-coral-species simulations, we use parameter values for the slow-growing, massive-type species (*M. annularis*) for Caribbean locations and the fast-growing, branching-type species (Pocilloporidae) for Pacific locations. In both cases, we assume that the one coral species is stress-susceptible. In two-coral-species (stress-susceptible, branching-type and stress-tolerant, massive-type) simulations, we distribute the

initial total cover into 90% of the more common species and 10% of the less common species. The default for the more common species is the branching-type coral. To determine the importance of the initial prevalence of stress-tolerant coral species, we compare this default with the model outcome with the massive-type coral as the initially more common species. To explore the effect of coral community composition in a variety of scenarios, we perform this comparison given one nonevolving symbiont (no symbiont diversity), one evolving symbiont, and two nonevolving symbionts.

We initialize the simulations with total symbiont densities ( $S_{myl}$ ) at 90% of their carrying capacity ( $0.9K_{sm} X_{my} C_{myk}$ ) for each coral size class. As with the two-coral simulations, we initialize two-symbiont-type simulations with 90% of the more common type and 10% of the less common type, where the default more common symbiont type is the more stress-susceptible symbiont. To determine the importance of the initial prevalence of stress-tolerant symbiont types, we compare this default with the outcome with the initially more common type as the more stress-tolerant symbiont. To focus this comparison on initial symbiont community composition, we use one-coral simulations with two nonevolving symbionts.

We initialize the mean genotype ( $\bar{g}_{imk}$ ) at the mean temperature of the initialization temperature series, as the mean is the long-term optimum phenotype. In all cases, we initialize the genetic variance at its expected equilibrium value ( $\sigma_{g_{imyl}}^2 = \sigma_{Mm} \sigma_{wm}$ , Lynch *et al.* 1991; see Baskett *et al.* (2009) Fig. 3 for a test of different initial conditions with respect to genetic variation). In simulations with two symbiont types, we initialize the second (more stress-tolerant) mean genotype as 1°C greater than this first mean genotype. For simulations with past temperature data (ISST), the initialization temperature series is the 1870–1960 temperature data, and then we start simulations in 1960, shortly before regular scientific inquiry of coral bleaching. For simulations with future temperature data (SRES A1b and SRES B1, 2000–2100), we use the simulated past temperature data from the climate models (20C3M simulations, which span 1870–2000) for the initialization temperature series because these runs initialize the SRES climate models.

*Sensitivity analysis: potential effect of additional anthropogenic impacts on coral response to climate change.* In order to analyze the model sensitivity to parameter values, we use elasticity (de Kroon *et al.*, 1986), or the proportional change in each state variable given a proportional change in each parameter. First, we calculate elasticity at each point in time in a one-coral, one-symbiont simulation with genetic and macroalgae dynamics. Then we report



the average over time of the absolute value of each elasticity. We use the relative sensitivity of different parameters to explore which processes may most affect coral response to climate change.

*Multiple locations with varying levels of thermal stress: past selection for stress-tolerance vs. future stress levels.* In order to compare model predictions for multiple locations that differ in past and future thermal stress, we use five sites in the Bahamas and Turks and Caicos Islands: Northern Exuma Cays, San Salvador, Andros Island, and Lee Stocking Island in the Bahamas and South Caicos in Turks and Caicos Islands. We choose these sites due to their spatial variation in past bleaching occurrences (Noordeloos *et al.*, 2007) and projected future temperature stress (Donner *et al.*, 2005) as well as for the availability of coral cover data from the Bahamas Biocomplexity Project. Here we combine the simulated past (20C3M) and future (SRES) temperature series and run simulations over 1960–2100 (using the 1870–1960 20C3M data as the initialization temperature series) to allow the comparison of past (1960–2000) and future (2000–2100) trajectories within the GFDL 2.1 and HadCM3 climate models. In these simulations, we follow one coral species hosting one evolving symbiont type. We run these simulations without connectivity between locations to allow comparison of the dynamics given different temperature trajectories without any confounding factors.

*Multiple locations with connectivity: enhanced recruitment vs. local adaptation.* To explore the role of connectivity between locations with differing levels of thermal stress, we choose San Salvador and South Caicos from the set of locations listed in the paragraph above. Then we compare model predictions with and without coral larval connectivity between these two locations. To determine the potential role of evolution and gene swamping, we explore one-coral simulations with one evolving symbiont type and, for a nonevolutionary comparison, two nonevolving symbiont types.

## Results

Model trends were similar across the different locations and climate models used. Here we present sample results to illustrate those trends using the GFDL 2.1 climate model temperature data from Curaçao, Netherlands Antilles, except in the multiple-location runs based on the Bahamas and Turks and Caicos Islands temperature data.

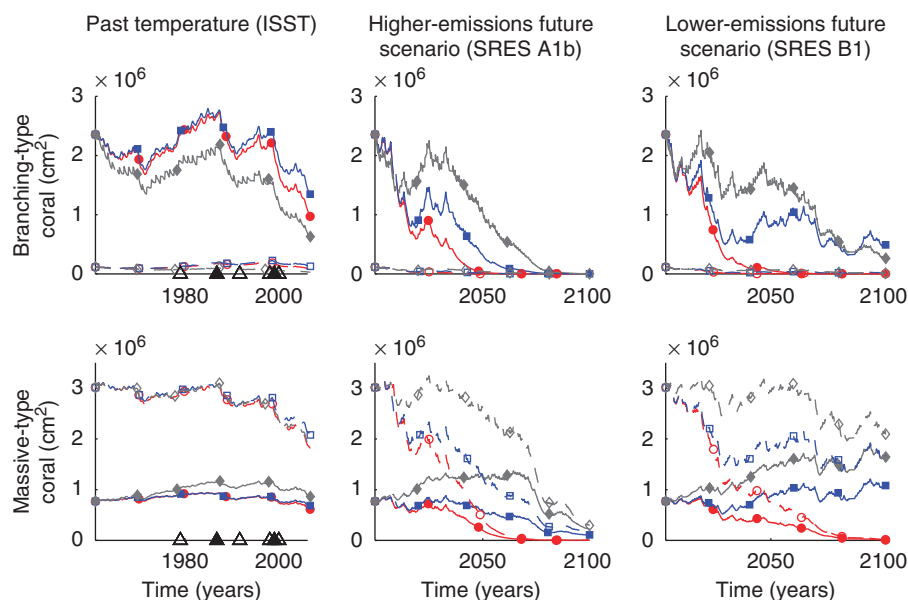
*Initial conditions: overall diversity vs. higher prevalence of stress-tolerant coral species and symbiont types*

In two-coral simulations with a greater initial abundance of the stress-susceptible coral (Fig. 2, solid lines) vs. a greater initial abundance of the stress-tolerant coral (Fig. 2, broken lines), each species' cover differs over decadal times scales. However, over the century simulated in the future climate scenarios, the two sets of simulations (solid and broken lines of each color) eventually approach similar cover for each coral species. In both cases, given future climate scenarios (Fig. 2, middle and right columns) and the demographic parameters used here, the stress-tolerant, massive-type coral (Fig. 2, bottom row) tends to dominate the coral community by the end of the simulations.

Similarly, comparing results starting with a greater abundance of stress-tolerant or stress-susceptible symbiont types (Fig. 3), the densities of each symbiont type approach the same levels within yearly time scales. The more thermal-stress-tolerant (higher-temperature-adapted) symbiont type remains or becomes the dominant type in simulations with future temperature trajectories (Fig. 3, middle and right columns). At first, coral cover (Fig. 3, bottom row) is slightly greater in simulations that start with greater abundances of the symbiont type that has a thermal tolerance closer to the optimal temperature (thermal-stress-susceptible symbiont type given past temperature data and thermal-stress-tolerant symbiont type given future temperature data). However, the simulations with different initial conditions rapidly (within years) approach indistinguishable levels of coral cover.

*Macroalgae dynamics and sensitivity analysis: potential effect of additional anthropogenic impacts on coral response to climate change*

In simulations with macroalgae dynamics (Fig. 4), when coral population sizes fall below a critical threshold, macroalgae population sizes increase due to a release from coral competition (Fig. 4, broken lines). This increase in macroalgae cover and prevention of coral recruitment leads to an increase in average coral size because of a drop in recruits to the smallest size class. Compared with simulations without macroalgae dynamics, macroalgae can cause either a faster coral decline or an unpredicted coral collapse, depending on the future climate scenario (Fig. 4, gray vs. black solid lines). Given the threshold dynamics of the shift from a coral-dominated state to a macroalgae-dominated state and the potential for macroalgae to prevent coral recovery and persistence that would otherwise occur, these results suggest that hysteresis is a part of the



**Fig. 2** Predicted coral cover for each of two coral species with different types of symbiont diversity and varying initial conditions for the corals. Simulations with a greater initial abundance of the stress-susceptible, fast-growing, branching-type coral are in the solid lines (filled symbols), and simulations with a greater initial abundance of the stress-tolerant, slow growing, massive-type coral are in the broken lines (open symbols). Red lines (with circles) represent simulations with one non-evolving symbiont, blue lines (squares) for one evolving symbiont, and gray (diamonds) for two non-evolving symbiont types. In the coral cover past temperature (ISST) plot for all figures, filled and open triangles indicate past major and minor bleaching events, respectively (Noordeloos *et al.*, 2007).

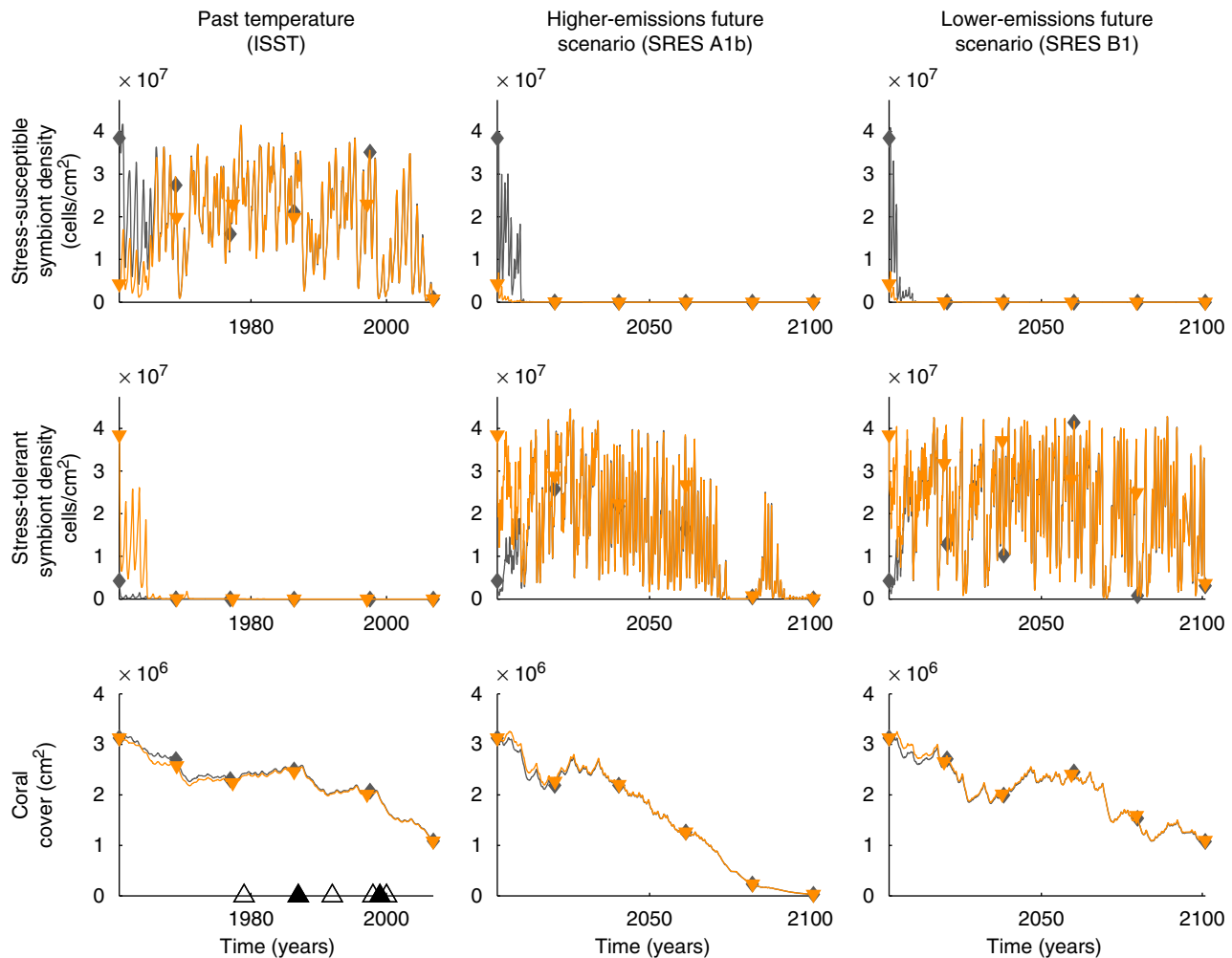
coral-macroalgae dynamics. In support of this hypothesis, a simplified, analytically tractable version of the model presented in Section C.4 of Appendix S3 exhibits alternative stable states under some parameter values. Specifically, both a coral-dominated state and a macroalgae-dominated state are locally stable for a range of temperature-determined symbiont densities (Fig. C.5 in Appendix S3). In this range temporary stressful events can cause the system to cross a threshold and drive switches between these states that are difficult to reverse.

The sensitivity analysis of the model (Fig. 5 and Fig. C.8 in Appendix S3) indicates that the most sensitive coral size class is the smallest one (Fig. C.8 in Appendix S3). In the future climate scenario where accounting for macroalgae dynamics leads to a coral collapse that does not occur without macroalgae dynamics (SRES B1; Fig. 4), both the macroalgae population size and the coral juvenile size class are highly sensitive to the total area available ( $R$ ), the competitive effect of established corals on macroalgae ( $\alpha_{CA}$ ), and macroalgal growth rates ( $\gamma_{Ai}$ ; Fig. 5 and Fig. C.8 in Appendix S3). The sensitivity to the total area available ( $R$ ) likely reflects a sensitivity to initial coral population size, as we define the initial coral population size as a proportion of the area available. Of the symbiont-related parameters, coral population size is most sensi-

tive, on average (Fig. 5), to the proportion of energy obtained from coral heterotrophy ( $c$ ) and the variance in selection on symbiont thermal tolerance ( $\sigma_w^2$ , inversely related to selection strength). With respect to coral demographic parameters (mortality parameters  $\mu$  and  $u$ , recruitment parameter  $\beta$ , growth parameter  $\gamma$ , and shrinkage parameters  $\eta$  and  $n$ ), coral cover is most sensitive to the mortality-related parameters (Fig. 5).

#### *Multiple locations with varying levels of thermal stress: past selection for stress-tolerance vs. future stress levels*

In the simulations of multiple locations that differ in past and future thermal stress, the relative order of coral cover across locations remains constant over time within each temperature scenario: within the ISST, SRES A1b, or SRES B1 scenarios, the coral cover trajectories for each location do not cross one another (Fig. 6). Note that, given future temperature scenarios (SRES A1b or SRES B1), the mean temperature and symbiont genotype are similar across locations, while the variation in temperature differs (Fig. B.1 in Appendix S2). For an independent test of model accuracy, we compare the relative coral cover given past temperature data predicted here to the observed coral cover from the Bahamas Biocomplexity Project in Section C.5 of Appendix S3 (Fig. C.6).



**Fig. 3** Symbiont density and total coral cover with varying initial conditions for the symbionts. Simulations with greater initial density of the more thermal-stress-susceptible (lower-temperature-adapted) symbiont type are in gray (diamonds), and simulations with greater initial density of the thermal-stress-tolerant (higher-temperature-adapted) symbiont type are in orange (triangles). Simulations employ one stress-susceptible coral hosting two nonevolving symbiont types. Note that we report symbiont density per cm of coral projected area, and we calculate coral surface area available to symbionts by multiplying the projected area by a factor of 16.40 (11.86 for the stress-tolerant coral; Chancerelle, 2000); therefore, dividing by this factor gives the symbiont density per cm<sup>2</sup> of coral surface area.

#### *Multiple locations with connectivity: enhanced recruitment vs. local adaptation*

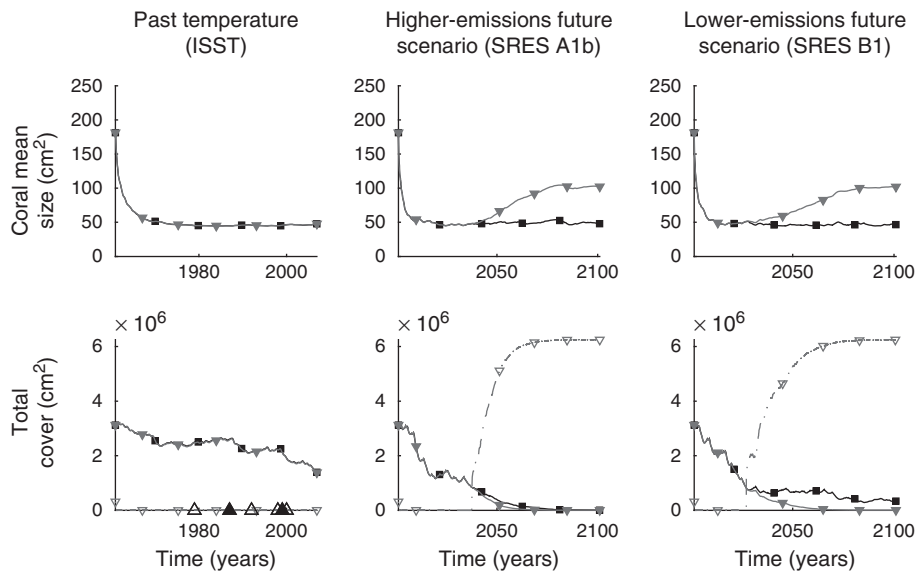
Including connectivity between two locations leads to an increase in coral cover in the higher-thermal-stress location and decrease in coral cover in the lower-thermal-stress location (Fig. 7). This outcome occurs in both simulations with (Fig. 7) and without (Fig. C.7 in Appendix S3) evolution.

#### **Discussion**

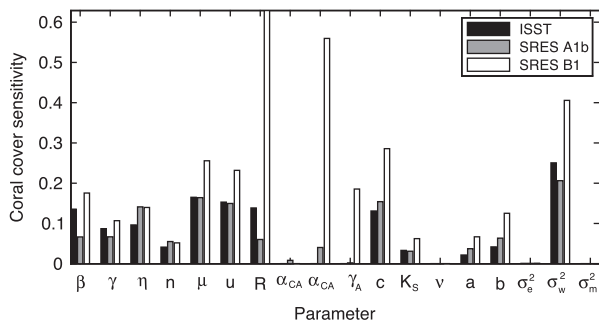
Accounting for coral and symbiont ecological and evolutionary dynamics reveals how the future climate scenario (and thus the rate of climate change) substan-

tially influences the potential for coral reef persistence (Fig. C.1 here; Baskett *et al.*, 2009). Therefore, any reductions in greenhouse gas emissions are likely to be critical to the future of coral reefs (Donner *et al.*, 2007; Baskett *et al.*, 2009). While global greenhouse gas emissions are unlikely to be under the control of local management, local management may mitigate climate change impacts by (1) prioritizing protection of reefs that will most likely survive climate change and (2) protecting against additional anthropogenic impacts that are more likely to impede coral response to climate change (West & Salm, 2003; Marshall & Schuttenberg, 2006; Salm *et al.*, 2006).

Here, we extend our previous model (Baskett *et al.*, 2009) to allow comparative simulation results that can



**Fig. 4** Coral mean size and total cover with and without macroalgal dynamics. Black lines (squares) indicate dynamics in simulations without macroalgae, and gray lines (triangles) indicate dynamics with macroalgae. In the latter, solid lines (filled symbols) indicate coral cover and broken lines (open symbols) indicate macroalgal cover. Simulations employ one stress-susceptible coral hosting one evolving symbiont type.



**Fig. 5** Sensitivity (absolute elasticity, or proportional sensitivity, averaged over time) of coral cover to each parameter in the different climate scenarios: ISST (past temperatures) are the black bars, SRES A1b (higher greenhouse gas emissions future scenario) in gray, and SRES B1 (lower greenhouse gas emissions future scenario) in white. Simulations employ one stress-susceptible coral hosting one evolving symbiont type and macroalgal dynamics. For a description of symbols, see Table 1; see Fig. C.8 in Appendix C.7 for the sensitivity of all state variables.

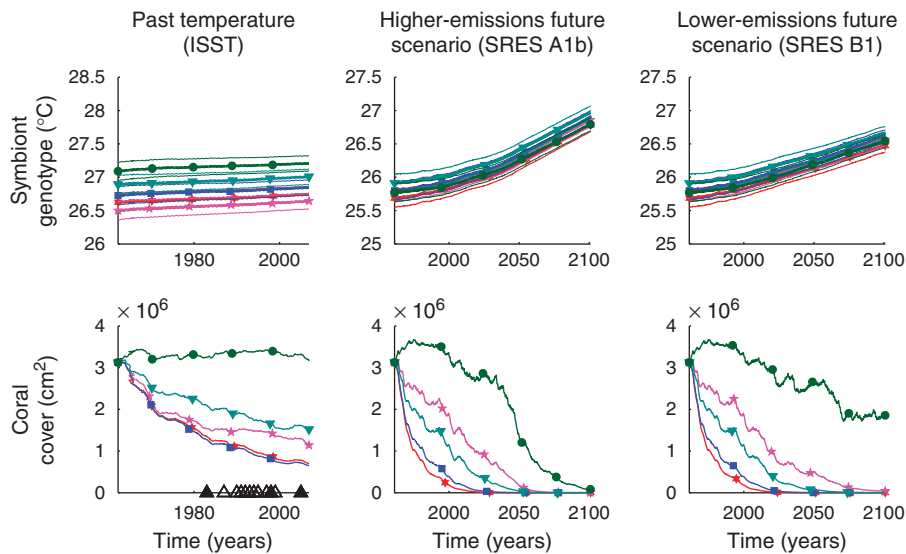
inform possible alternative management approaches and priorities for conserving coral capacity to respond to climate change. Currently, most such management recommendations (e.g., West & Salm, 2003; Obura, 2005) are hypotheses for the best expected approaches given current scientific knowledge; thus they provide a first step toward informing coral reef management while additional empirical investigation into these hypotheses helps to test and refine these recommendations. As an intermediate step, modeling provides a tool

to formalize such hypotheses in a single comparative framework. Our use of modeling in this context of extrapolating to management recommendations inevitably involves speculation. In order to be clear about the uncertainties involved in this approach, we first discuss the simplifying assumptions and robustness of the model developed here. Then we explore management implications in terms of conservation priorities.

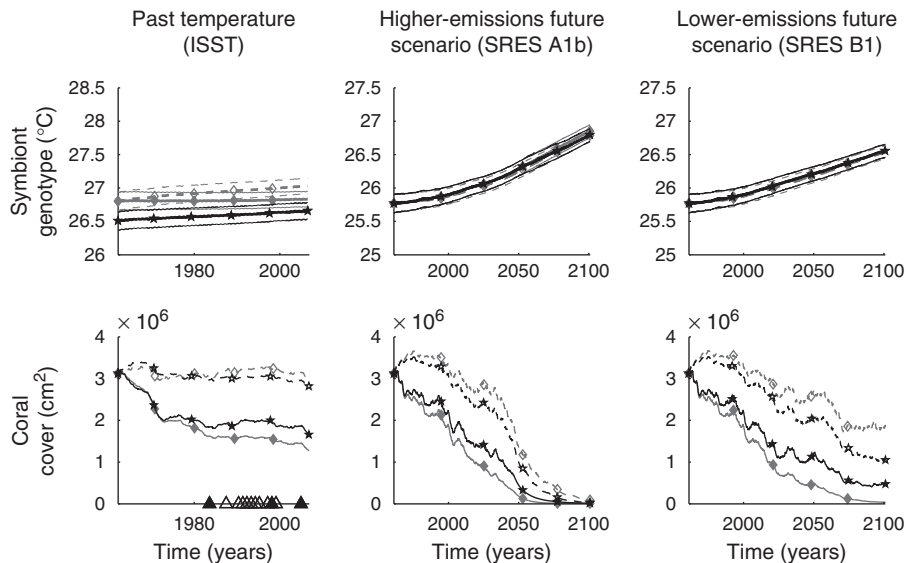
*Model robustness*

Our model is appropriate for comparative trends, rather than precise forecasts, because of the simplifying assumptions necessarily made in the model construction and uncertainty inherent in the parameter values. For example, we ignore the potential for some coral species to up-regulate heterotrophy during bleaching events (Grottoli *et al.*, 2006). High sensitivity to the (constant) coral heterotrophy parameter *c* (Fig. 5) suggests the potential for this assumption to impact the precise predictions for coral response to temperature stress in our model. In addition, the model is highly sensitive to the poorly known selection strength parameter  $\sigma_w^2$  (Fig. 5).

Furthermore, we do not find as strong an effect of thermal stress on size structure (Figs C.1–C.2 in Appendix S3, when ignoring coral–macroalgae competition) as in other matrix models (Fong & Glynn, 2000; Edmunds, 2005). These models use empirically based representations of growth and survivorship in each size class



**Fig. 6** Comparison of symbiont genetics and total coral cover across multiple Caribbean locations (without connectivity). Different color runs and symbols represent different locations (red asterisks: Northern Exuma Cays, Bahamas; magenta stars: San Salvador, Bahamas; blue squares: Andros Island, Bahamas; cyan triangles: Lee Stocking Island, Bahamas; green circles: South Caicos, Turks and Caicos Islands). The genotype plots include 95% confidence intervals for the genetic distribution, where a symbiont ‘genotype’ is its optimal temperature; note the different initial genotypes in past (ISST) and future (SRES) runs because of different initialization temperature series for these runs (see Materials and methods). Simulations employ one stress-susceptible, massive-type coral hosting one evolving symbiont type. For temperature series, see Fig. B.1 in Appendix S2.



**Fig. 7** Predicted symbiont genetics and total coral cover in two locations differing in thermal stress. Simulations with connectivity between locations are in black (stars), and simulations without connectivity between locations are in gray (diamonds). Solid lines (filled symbols) indicate dynamics in the higher-stress location (San Salvador, Bahamas), and broken lines (open symbols) indicate dynamics in the lower-stress location (South Caicos, Turks and Caicos Islands). All simulations employ one stress-susceptible coral hosting one evolving symbiont type.

separately in stressful and normal years and thus may include size-dependent responses to climate change impacts not represented here. However, our simulations that incorporate coral–macroalgae competition

do show increases in coral size with thermal stress due to reductions in the smallest size classes (Fig. 4), as suggested from empirical evidence (Bak & Meesters, 1999).

Finally, the similar model outcomes in simulations with different symbiont transmission types (vertical, horizontal, or open; Fig. C.4 in Appendix S3) suggests that the potential for free-living symbiont input to slow the spread of bleaching resistance is negligible in our simulation predictions. However, Day *et al.* (2008) find that this potential can be significant in their coral-symbiont model. This difference is most likely due to the fact that we do not explore epistasis (a key process in the model by Day *et al.*, 2008) as well as to the high symbiont turnover rates relative to the time scale of coral dynamics in our model.

Despite these simplifications and estimates, we find support for the model's ability to predict accurate comparative trends. In an independent test of model accuracy, given past temperature data the model generally predicts relative coral cover across multiple locations in the Bahamas with different levels of thermal stress (with one exception; Fig. C.6 in Appendix S3). Furthermore, biologically realistic dynamics on multiple time scales readily emerge from the model dynamics (as in Baskett *et al.*, 2009): algal symbiont densities have seasonal sublethal fluctuations similar in magnitude to empirical observation (Fitt *et al.*, 2000), and coral cover declines during previously observed major bleaching events (e.g., Fig. 3; Noordeloos *et al.*, 2007).

#### *Conservation priorities*

Of the many possible approaches to protecting coral capacity to respond to climate change (West & Salm, 2003; Obura, 2005), we focus on the ones related to the coral ecological and evolutionary responses to thermal stress modeled here. First, we explore which biological characteristics may better indicate greater response capacity. Second, we evaluate which demographic processes are most critical to coral response to climate change, and therefore which ones to prioritize protection from additional anthropogenic impacts. Finally, we examine the biological response to past and future variation in thermal stress across, and connectivity between, different locations.

*Initial conditions: is overall diversity or higher prevalence of more stress-tolerant coral species and symbiont types more important to coral response to climate change?* The convergence of long-term coral cover given different initial abundances of stress-tolerant species/types (Figs 2 and 3) suggests that protecting diverse coral communities that include stress-tolerant species/types is more critical than protecting locations with higher abundances of such species/types. Note that the diversity analysis here is limited to two species/types

representative of broad guilds for tractability and generality; more realistic representation of the level of diversity expected in specific coral communities warrants future exploration. However, our previous results indicating the greater potential for coral response to future climate change with greater initial symbiont genetic variation (Fig. 3 in Baskett *et al.*, 2009) reinforce the importance of diversity suggested here. Overall diversity may also indicate general ecosystem health (West & Salm, 2003), including the heterogeneous reef structure necessary for ecosystem function (Bellwood *et al.*, 2004), and possibly greater response capacity to multiple impacts due to functional redundancy (Nyström *et al.*, 2000). Furthermore, specifically targeting sites with greater relative abundances of stress-tolerant species/types may not be an appropriate priority if these greater abundances indicate a high-stress location.

*Coral-macroalgal dynamics and sensitivity analysis: which additional anthropogenic impacts are more likely to impede coral response to climate change?* Two model results indicate that a critical part of any management strategy to protect coral resilience to bleaching events is likely to be the mitigation of additional anthropogenic impacts that affect coral-macroalgal competition (Smith & Buddemeier, 1992; Nyström & Folke, 2001; Pandolfi *et al.*, 2003; West & Salm, 2003). First, macroalgal growth after a bleaching event and the subsequent reduction in coral recruitment can prevent coral recovery that would otherwise occur without macroalgae dynamics in our model (Fig. 4 and Appendix C.4 in Appendix S3, analogous to the coral-algal model by Mumby *et al.*, 2007). Second, in these simulations where macroalgae prevents coral recovery from a bleaching event, the model is highly sensitive to macroalgae-related parameters (Fig. 5, white bars). Management options that may affect coral-macroalgal competition include (1) protecting healthy populations of herbivorous fish from fisheries (Smith & Buddemeier, 1992; Pandolfi *et al.*, 2003; Hughes *et al.*, 2007; Mumby *et al.*, 2007), (2) protecting against runoff of anthropogenic inputs that enhance macroalgal growth (e.g., dissolved inorganic nutrients; Fabricius, 2005), and (3) protecting against runoff that causes decreased herbivorous fish populations due to increased turbidity (Wolanski *et al.*, 2004).

Beyond the importance of coral-macroalgal competition, the sensitivity analysis indicates that protection of early life history stages and survivorship at all stages may more effectively protect coral capacity to respond to climate change. Reinforcing this conclusion, similar analyses in other size-structured coral models (Lasker, 1991; Hughes & Tanner, 2000;

Riegl & Purkis, 2009) parallel the greater sensitivity of the smallest size class (Fig. C.8 in Appendix S3) and greater sensitivity to mortality-related parameters compared with other demographic parameters (Fig. 5) found here. A number of local management options may protect coral early life history stages and overall survivorship. For example, protection against any overfishing or eutrophication (e.g., due to runoff of particulate organic matter; Fabricius, 2005) that may lead to outbreaks of corallivores such as crown-of-thorns seastars would reduce coral mortality (Nyström *et al.*, 2000; Bellwood *et al.*, 2004). Reductions in runoff-related eutrophication, sedimentation, and pollution that tend to increase disease severity in coral reefs would also mitigate disease impacts on coral survivorship (Bruno *et al.*, 2003; Sutherland *et al.*, 2004). Given the impact of sedimentation on coral survivorship at all stages (Fabricius, 2005) and the potential for turbidity and eutrophication to differentially impact smaller coral size classes (Bak & Meesters, 1999), runoff reductions would benefit the most sensitive size class as well.

The greater sensitivity to mortality compared with other demographic processes (Fig. 5) also provides insight into potential synergistic interactions between increased thermal stress and other climate change-related impacts on coral reefs not directly included in our model. For example, the possible increased storm intensity with climate change could impact both coral mortality and fragmentation (Done, 1999); our results suggest that the mortality effects are more likely to impact overall coral response to thermal stress. With respect to ocean acidification with increased carbon dioxide concentrations, the most direct effect is on coral calcification and thus growth (Done, 1999; Gattuso *et al.*, 1999). However, acidification may indirectly affect coral survivorship through resource limitation for recruits as well as through anchor strength and skeletal density reductions and thus susceptibility to storm damage for adults (Kleypas *et al.*, 2006; Hoegh-Guldberg *et al.*, 2007). Given our results, a greater understanding of such possible mortality impacts may be critical to understanding the potential for synergistic interactions between thermal stress and ocean acidification.

*Multiple locations with varying levels of thermal stress: is past stress more likely to indicate selection for stress-tolerance or a location with higher stress overall?* The consistent coral cover across multiple locations with varying thermal stress (Fig. 6) suggests that past thermal stress indicates regions with higher stress and the potential for greater future coral declines on the coarse spatial scales modeled here. In other words, we find more support for

past thermal stress to indicate a location with oceanographic features that lead to higher future stress than corals can respond to through ecological and evolutionary dynamics (Hoegh-Guldberg, 1999) than a location where past selection has led to greater coral and symbiont adaptation to future thermal stress (Cook *et al.*, 1990, West & Salm, 2003, however, note that we do not model coral acclimatization). Therefore, prioritizing protection of regions with lower bleaching occurrences and lower predicted future stress may help management efforts focus on reefs more likely to survive climate change (e.g., Maina *et al.*, 2008; McClanahan *et al.*, 2008). When addressing the relevant broader question of how conservation prioritization depends on the level of threat from disturbances such as bleaching, Game *et al.* (2008) found that protecting the sites that are least threatened makes more sense for systems spending a large amount of time in a degraded state. Given the large-scale coral declines that can occur in our simulations, this analysis further supports the approach of protecting regions with lower past and expected future thermal stress.

In our model, the differences in coral cover across locations are due as much to lower average coral population growth rates in locations with greater temperature variability as to the greater likelihood and severity of mass bleaching events that lead to occasional large declines in coral cover. Therefore, the higher amounts of constant, low-level stress associated with greater temperature variability can lead to lower coral cover on the coarse spatial scales modeled here. Empirical observations support the capacity for nonfatal temperature extremes to cause reductions in coral growth and reproduction (Jokiel & Coles, 1990). However, this predicted negative association between coral population growth and temperature variability does not hold on local spatial scales (e.g., different depths and locations within a reef) because of confounding factors. Specifically, factors such as salinity, light availability, and nutrient flux are locally connected to temperature variability and also affect coral growth and mortality (Potts & Swart, 1984; Leichter & Genovese, 2006).

*Multiple locations with connectivity: is connectivity more likely to be beneficial through enhanced recruitment or detrimental through impeded local adaptation?* When including connectivity between locations with different levels of thermal stress, the increase in coral cover in the higher-stress location suggests that positive effects of recruitment enhancement outweigh the negative effects of an input of recruits poorly adapted to local conditions (Fig. 7). While a decrease in coral

cover occurs in the lower-stress location, it is unlikely to be primarily due to an input of recruits with poorly adapted symbionts because a similar drop also occurs in simulations without evolution (Fig. C.7 in Appendix S3). Instead, the primary driver of this decline is the decrease in recruitment that occurs when relaxing the assumption of closed coral dynamics while adding connectivity. Specifically, with connectivity, corals at the lower-stress location are losing reproductive output sent to the higher-stress location and not receiving as many recruits in return due to the lower coral cover and thus reproductive output at the higher-stress location. The nonevolutionary model of coral community response to climate change by Riegl & Purkis (2009) also indicated this potential for connectivity to enhance persistence in high-stress locations. Therefore, the design of marine reserve networks to promote connectivity may enhance coral resilience to future thermal stress (Salm *et al.*, 2006).

This potential for the demographic benefit of connectivity to outweigh the adaptive drawback is supported by more general theoretical population genetic models of connectivity (gene flow) between locations with differing selection. While most models suggest that gene flow impedes local adaptation and has the potential to negatively affect local population dynamics (e.g., Ronce & Kirkpatrick, 2001; reviewed by Lenormand, 2002; Kawecki & Ebert, 2004), local benefits to gene flow tend to arise from extreme cases such as habitats with a source-sink structure (reviewed by Lenormand, 2002; Garant *et al.*, 2007). Therefore, under certain conditions a source can be more important to maintaining a population than local adaptation (e.g., Holt & Gomulkiewicz, 1997; reviewed by Lenormand, 2002). In fact, gene flow may increase local adaptive potential by enhancing genetic variation in some instances, such as in small populations that experience temporally variable selection (e.g., Gomulkiewicz *et al.*, 1999; Gandon & Michalakis, 2002; Alleaume-Benharira *et al.*, 2006). Such conditions are particularly relevant to corals that experience intermittent extreme temperature stress. Thus, a low-stress location may serve as both a demographic and adaptive source for locations where bleaching or additional anthropogenic impacts dramatically reduce coral populations.

## Conclusions

In summary, to protect coral capacity to respond to climate change, our model results suggest prioritizing (1) protection of diverse coral communities with the presence, but not necessarily higher abundance, of thermally tolerant coral species and symbiont types,

(2) mitigation of additional anthropogenic impacts that affect coral-macroalgal competition, early coral life history stages, and coral survivorship, and (3) protection of, and connectivity to, locations with oceanographic features that lead to lower thermal stress. Achieving these goals requires a comprehensive management approach that incorporates both land-based controls of runoff and fisheries control in and out of marine reserves (Pandolfi *et al.*, 2003; Bellwood *et al.*, 2004).

Because our goal is to compare and resolve conflicts in existing broad management recommendations, our concluding recommendations are very general as well. Actual implementation of conservation decisions such as reserve siting involves a wide array of socioeconomic considerations as well as ecological considerations beyond protecting response capacity to climate change. Furthermore, the appropriate data (e.g., symbiont and coral diversity and abundances, thermal stress history) to follow the recommendations presented here may not be readily available in many locations. In this case, these recommendations can contribute to guidelines for data collection to inform adaptive management and future conservation decision-making. Overall, our conclusions can best serve as information that helps to refine the general scientific guidelines that underly the construction of conservation decision-making tools such as reserve siting algorithms (e.g., Fernandes *et al.*, 2005), decision trees (e.g., Done, 2001), and other analytical decision-making frameworks (e.g., McClanahan *et al.*, 2008).

Finally, the connectivity and diversity priorities can apply beyond coral reefs to more generally inform the protection of ecological communities in a changing climate. In particular, our quantitative framework confirms the intuitive expectation that high diversity can serve as an indicator of adaptive capacity to climate change. In addition, our results demonstrate the potential for connectivity to provide demographic and adaptive sources, rather than a migrational genetic load, for rapid evolutionary responses to climate change.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Model mathematical details.

**Appendix S2.** Model parameterization and analysis details.

**Appendix S3.** Additional model analyses.

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