Title

Symbiont diversity may help coral reefs survive moderate climate change.

Journal

Ecological applications : a publication of the Ecological Society of America, 19(1)

ISSN

1051-0761

Authors

Baskett, Marissa L
Gaines, Steven D
Nisbet, Roger M

Publication Date

2009

DOI

10.1890/08-0139.1

Peer reviewed

Ecological Applications, 19(1), 2009, pp. 3–17

Symbiont diversity may help coral reefs survive moderate climate change

Marissa L. Baskett,[1,4] Steven D. Gaines,[2,3] and Roger M. Nisbet[2]

[1]*National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 320, Santa Barbara, California 93101 USA*
[2]*Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106-9610 USA*
[3]*Marine Science Institute, University of California, Santa Barbara, California 93106-9610 USA*

Abstract. Given climate change, thermal stress-related mass coral-bleaching events present one of the greatest anthropogenic threats to coral reefs. While corals and their symbiotic algae may respond to future temperatures through genetic adaptation and shifts in community compositions, the climate may change too rapidly for coral response. To test this potential for response, here we develop a model of coral and symbiont ecological dynamics and symbiont evolutionary dynamics. Model results without variation in symbiont thermal tolerance predict coral reef collapse within decades under multiple future climate scenarios, consistent with previous threshold-based predictions. However, model results with genetic or community-level variation in symbiont thermal tolerance can predict coral reef persistence into the next century, provided low enough greenhouse gas emissions occur. Therefore, the level of greenhouse gas emissions will have a significant effect on the future of coral reefs, and accounting for biodiversity and biological dynamics is vital to estimating the size of this effect.

Key words: *adaptation; climate change; coral reefs; quantitative genetic model; zooxanthellae.*

Introduction

An understanding of ecological responses to climate change is critical to developing scientifically based ecosystem management in a changing climatic future (McCarty 2001). Responses to climate change include range shifts, shifts in community composition, and genetic adaptation in ecologically relevant traits (Holt 1990, McCarty 2001). Future predictions of ecological responses to climate change tend to focus on range shifts and often ignore the capacity for rapid evolution (Thomas et al. 2004, Araújo and Rahbek 2006), despite demonstrated examples of evolutionary responses to climate change and the potential for evolution to significantly affect ecological dynamics that shape management decisions (Hoffmann and Blows 1993, Frankham and Kingsolver 2004, Bradshaw and Holzapfel 2006, Parmesan 2006, Skelly et al. 2007). As described below, climate change poses a substantial threat to coral reef ecosystems (Wilkinson 1999, Hughes et al. 2003), particularly given their domination by long-lived, and therefore potentially slow-adapting, corals (Hoegh-Guldberg 1999, Hoegh-Guldberg et al. 2007). However, the short generation and turnover times of their algal symbionts makes corals an intriguing example of the need to understand the capacity for, and interaction between, ecological and rapid evolutionary responses to climate change (Ware 1997, Lasker and Coffroth 1999, Parmesan 2006).

Corals, the foundation for some of the most diverse ecosystems on the planet, are declining precipitously due to multiple anthropogenic impacts (Wilkinson 1999, Pandolfi et al. 2003, Bellwood et al. 2004, Hoegh-Guldberg et al. 2007), including coral bleaching. Coral bleaching, the breakdown of the symbiosis between corals and their algal symbionts (zooxanthellae, primarily dinoflagellates from the genus *Symbiodinium*), occurs in response to stressors such as anomalous salinity, solar radiation, and temperature; bleaching is fatal when the stressor is extreme, repeated, or prolonged (Smith and Buddemeier 1992, Brown 1997*b*, Hoegh-Guldberg 1999). Because corals tend to bleach when temperatures exceed the average summer maximum by ~1–2°C, the predicted increases in average temperature as well as the frequency and magnitude of extreme temperatures with global climate change constitute one of the greatest threats to coral reefs worldwide (Hoegh-Guldberg 1999, Wilkinson 1999, Hughes et al. 2003).

Therefore, the persistence of coral reefs depends on the potential for coral communities to respond to climate change. In coral reefs, local adaptation and acclimatization to high average temperatures and recurrent thermal stress have occurred (Cook et al. 1990, Jokiel and Coles 1990, Brown 1997*a*, Rowan et al. 1997, Marshall and Baird 2000, Brown et al. 2002*a*, McClanahan et al. 2007). The high degree of existing variation in coral and symbiont thermal tolerance (Cook et al. 1990, Brown 1997*a*, Rowan et al. 1997, Marshall

Manuscript received 23 January 2008; revised 14 May 2008; accepted 3 June 2008. Corresponding Editor: S. R. Connolly.

[4] Present address: Department of Environmental Science and Policy, University of California, Davis, One Shields Avenue, Davis, California 95616 USA.
E-mail: mlbaskett@ucdavis.edu

and Baird 2000, Hughes et al. 2003, Bhagooli and Yakovleva 2004, Sotka and Thacker 2005) as well as the empirical evidence for symbiont community shifts in response to thermal stress (Baker 2001, Baker et al. 2004, Berkelmans and van Oppen 2006) suggest the potential for response to future climate change in theory (Baker 2004). However, the climate may change too rapidly for coral communities to respond in reality (Jokiel and Coles 1990, Glynn 1993, Hoegh-Guldberg 1999, Wilkinson 1999).

Existing theoretical projections based on realistic future climate scenarios (Ware 1997, Huppert and Stone 1998, Hoegh-Guldberg 1999, Sheppard 2003, Donner et al. 2005, 2007, Wooldridge 2005) predict highly frequent bleaching events or significant coral cover declines within 10–50 years. While they help indicate the total amount (~1–2°C) or rate (~0.1–1°C per decade; <25-yr delay) of thermal acclimatization or adaptation necessary for coral reef persistence in the near future (Ware 1997, Sheppard 2003, Donner et al. 2005, 2007, Wooldridge et al. 2005), these current projections do not account for dynamical changes in thermal tolerance based on biological mechanisms. Therefore, the question remains as to whether biological dynamics such as coral and symbiont community shifts and genetic evolution may allow such a response. In addition, theoretical investigations have explored general ecological and evolutionary factors affecting the genetic dynamics of bleaching resistance (Day et al. 2008) as well as shifts in coral or symbiont community composition (Ware et al. 1996; K. Shiroma, S. Koksal, and R. van Woesik, *unpublished manuscript*) and size structure (Fong and Glynn 2000) given generalized assumptions of climate scenarios (e.g., different amounts of temperature fluctuations, steady increase in mean temperature, set El Niño-Southern Oscillation frequencies), which help identify processes important to predicting future coral dynamics.

In order to explore whether climate change may be too rapid for adequate coral community response, the model presented here incorporates realistic climate change scenarios and biological variation and dynamics. Specifically, it predicts the effect of future temperature changes on coral reefs where thermal tolerance varies with coral and symbiont community dynamics as well as symbiont genetic dynamics. The goal of this model is to use comparative trends to investigate which ecological and evolutionary dynamics are likely to influence the potential for coral reefs to survive future climate change.

Methods

The model

In the model, the temperature and both the symbiont and coral host thermal tolerances drive symbiont population dynamics, and symbiont population densities in turn influence coral growth and mortality (Fig. 1). In particular, the model follows the population size of each of one or two symbiont "types" (for example, but not constrained to, symbionts from different *Symbiodinium* subclades [Baker 2003, Sotka and Thacker 2005, Stat et al. 2006, van Oppen and Gates 2006]) in each of one or two coral species. While the modeled coral species differ in their thermal tolerance (similar to branching *Acropora* and massive *Porites*, for example [Loya et al. 2001]), we ignore evolutionary dynamics in corals and focus on symbiont evolution; this focus provides a reasonable first approximation for understanding potential rates of adaptation because symbiont generation times are much shorter and their evolution may occur at a more rapid rate compared to corals (Ware 1997, Lasker and Coffroth 1999). Specifically, the model includes within-symbiont-type genetic variation in thermal tolerance, and the resulting evolutionary dynamics represent the potential for gradual thermal adaptation within symbiont strains. In comparison, we model the discrete, limited shifts in thermal tolerance potentially associated with shifts between symbiont strains (Hughes et al. 2003, Sotka and Thacker 2005) with the presence of multiple symbiont types that differ in their thermal tolerance. For both symbionts and corals, we assume a trade-off between thermal tolerance and population growth (Loya et al. 2001, Bhagooli and Yakovleva 2004, Little et al. 2004, Sotka and Thacker 2005). Below we provide the model details and assumptions for the coral and symbiont population and evolutionary dynamics.

Symbiont genetic dynamics.—The genetic model follows the dynamics of the thermal tolerance genotype distribution for each symbiont population i in coral m. Here, a "thermal tolerance phenotype," based on the genotype, is the temperature for which a symbiont is optimally adapted. We model thermal tolerance as a quantitative genetic trait in a clonal, haploid population (Fig. 1a); for comparison, we also explore the model without symbiont evolution (no genetic variance or mutation). Empirical evidence supports the assumption that *Symbiodinium* are haploid (Santos and Coffroth 2003). While empirical evidence suggests that recombination occurs in *Symbiodinium* (LaJeunesse 2001), it is unclear whether recombination occurs on a time scale relevant to within-coral dynamics, and within-coral strains of *Symbiodinium* may represent clonal populations. Therefore, we ignore recombination for mathematical simplicity and, as faster rates of adaptation to a changing environment are possible with recombination (Lynch and Lande 1993, Burger 1999), to provide a conservative estimate of the potential for evolutionary response to climate change. Although uncertain, these assumptions allow us to construct a reasonably simple evolutionary model based on the available biological information.

The quantitative genetic model here uses the continuous-time approach of Lynch et al. (1991, originally developed for plankton) to account for overlapping generations. Because this model has been derived elsewhere (Lynch et al. 1991, Lynch and Lande 1993,

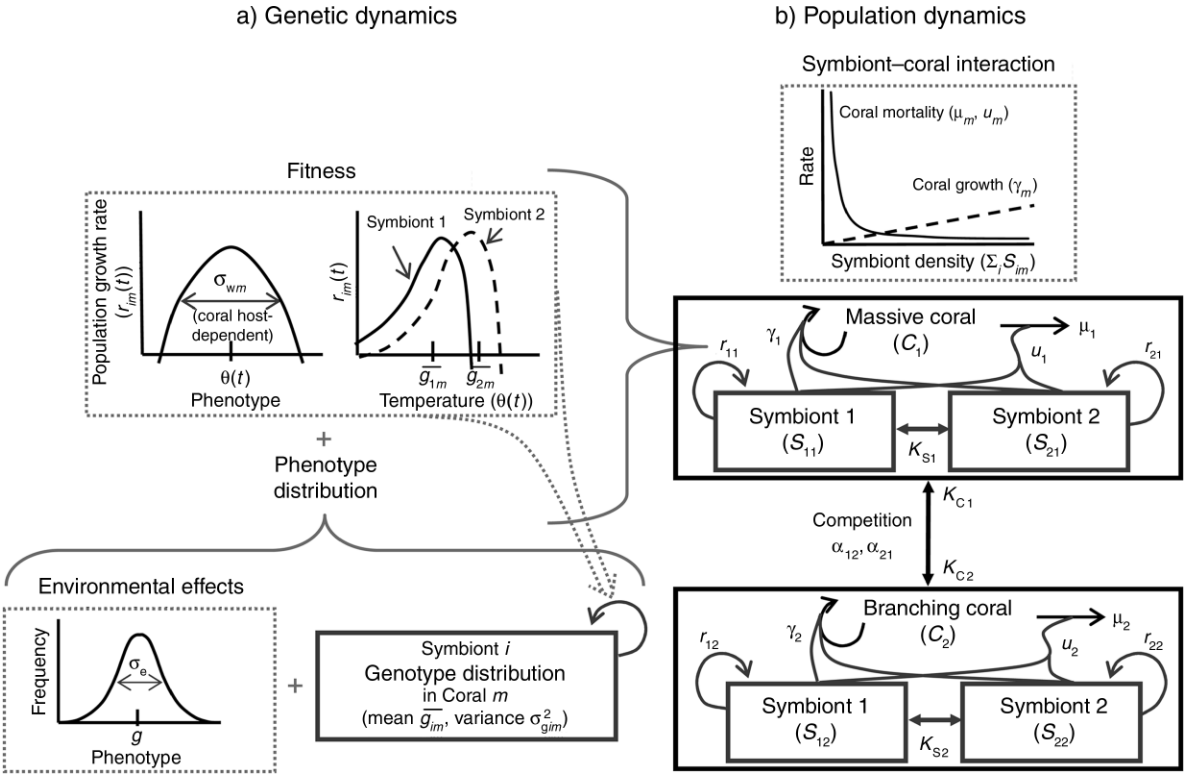

FIG. 1. Outline of the coral–symbiont model: (a) symbiont genetic dynamics (Eqs. 1–3); (b) population dynamics (Eqs. 4 and 5). Solid boxes indicate state variables, and solid arrows indicate dynamics with relevant parameters. The arrow with broken lines in panel (a) indicates the influence of fitness on the genetic dynamics, and the boxes with broken borders indicate functional relationships. Braces indicate state variables and parameters combined to calculate designated values. See Table 1 for an explanation of the symbols.

Lynch 1996), we present the model with an explanation of assumptions. In Appendix A: *Further model derivation: Genetic model derivation*, we provide a recasting of the model derivation in the terms used here. Specifically, we assume the population genotype distribution to be normal, and the model follows the symbiont population's mean genotype $\bar{g}_{im}$ and genetic variance σ^2_{gim} through time. Following a normal genetic distribution is a standard approach to quantitative genetic models based on the assumption that many unlinked loci additively determine a quantitative trait (and it provides a reasonable approximation under a number of circumstances [Turelli and Barton 1994]). We also assume random environmental effects, i.e., an individual's phenotype (temperature for which it is optimally adapted) is a random normal variable with a mean of its genotype and (environmental) variance σ^2_e.

Furthermore, we base the fitness function, or symbiont population growth rate as a function of phenotype and temperature, on the assumption that stabilizing selection occurs for the optimal phenotype, defined as the actual temperature $\theta(t)$, given "selectional variance" σ^2_{wm}, which determines the width of the fitness function ("Fitness" box in Fig. 1a). Our biological interpretation of this formulation is that, if an individual's phenotype is lower than the temperature, it is investing too little in thermal tolerance and too much in reproduction to grow at the maximum rate possible, and if its phenotype is higher than the temperature, it is investing too little in reproduction and too much in thermal tolerance to grow at the maximum rate possible. Therefore, the fitness function reflects the trade-off between symbiont thermal tolerance and growth suggested from empirical evidence (Sotka and Thacker 2005).

Selection strength, which increases with decreasing selectional variance σ^2_{wm}, depends on the host coral species m in order to allow different thermal tolerance in different coral species (which could occur due to coral morphology or physiology) through different susceptibility of each coral's symbionts to thermal stress. While stabilizing selection tends to lead to decreases in genetic variance, we assume that mutation increases genetic variance at a constant rate of σ^2_M. Finally, we use the temperature ($\theta(t)$)-dependent maximum growth rate function $\hat{r}(t) = ae^{b\theta(t)}$ (i.e., the growth rate for an optimally adapted population) from the exponential relationship, where a and b are constants, found for phytoplankton (Eppley 1972, Norberg 2004).

Given these assumptions and following the derivations in Lynch et al. (1991), Lande and Shannon (1996), and Norberg (2004), the mean genotype dynamics are

$$\frac{d\bar{g}_{im}}{dt} = \frac{\sigma^2_{gim}(t)[\theta(t) - \bar{g}_{im}(t)]}{\sigma^2_{wm}} a e^{b\theta(t)} \quad (1)$$

the genetic variance dynamics are

$$\frac{d\sigma^2_{gim}}{dt} = \sigma^2_{M} - \frac{\sigma^4_{gim}(t)}{\sigma^2_{wm}} a e^{b\theta(t)} \quad (2)$$

and the fitness, or population growth rate, for the entire population of each symbiont type is

$$r_{im}(t) = \left\{ 1 - \frac{\sigma^2_{gim}(t) + \sigma^2_{e} + [\bar{g}_{im}(t) - \theta(t)]^2}{2\sigma^2_{wm}} \right\} a e^{b\theta(t)} \quad (3)$$

(Fig. 1a; see Appendix A: *Further model derivation: Genetic model derivation* for detailed derivation). Given this model construction with $\hat{r}(t) = ae^{b\theta(t)}$ (i.e., higher maximum possible population growth rates at greater temperatures) and lags in adaptation (i.e., mean population genotype $\bar{g}_{im}$ differing from the temperature $\theta(t)$), population growth rate declines in response to both warmer and cooler temperatures than the mean genotype (i.e., both heat shock and cold shock) are possible, with a steeper decline in population growth rate for temperatures greater than the mean genotype.

Symbiont population dynamics.—The average fitness $r_{im}(t)$ in Eq. 3 provides the asymptotic population growth rate for each symbiont population, S_{im} (number of cells for symbiont type i in coral species m), in the absence of density dependence. If temperatures deviate greatly enough from the thermal tolerance genotype, negative symbiont population growth rates can occur (i.e., mortality exceeds reproduction). Such declines, if persistent, could drive a breakdown of the symbiosis, either due to symbionts leaving the coral or the coral expelling the symbionts.

Density dependence, both within and between symbiont populations, regulates symbiont density in each coral species at a level proportional to C_m (surface area of the entire three-dimensional structure for coral species m), given total symbiont carrying capacity per unit area K_{Sm}. These terms represent the combined effects of inter- and intra-specific competition for space within the coral tissue, competition for resources supplied by the host, and host expulsion of surplus symbionts (Baghdasarian and Muscatine 2000). While we assume carrying capacity is independent of symbiont type and genotype for simplicity, we scale the density-dependence by the maximum possible population growth rate $\hat{r}(t)$ so that, given two symbiont types, the symbiont type with the greater population growth rate $r_{im}(t)$ is competitively superior; see Appendix A: *Further model derivation: Symbiont density dependence* for an in-depth explanation of this approach. Therefore, the trade-off between growth and thermal tolerance implicit in r_{im} (see *Symbiont genetic dynamics*) causes the competitive outcome of thermal stress tolerant vs. susceptible types to depend on the temperature. Based on these assumptions, the population dynamics of each symbiont type i in coral m are

$$\frac{dS_{im}}{dt} = \frac{S_{im}}{K_{Sm}C_m} \left[r_{im}(t) K_{Sm} C_m - \hat{r}(t) \sum_j S_{jm} \right] \quad (4)$$

(Fig. 1b). Note that we assume closed symbiont dynamics, thus, after a non-fatal bleaching event, symbionts repopulate a coral through the growth of populations within the coral rather than reinfection from populations outside the coral (for empirical support of this assumption, see Berkelmans and van Oppen [2005]; but see Lewis and Coffroth [2004]); we test the importance of this assumption with a model extension that includes open symbiont population dynamics, presented in Appendix C.

Coral population dynamics.—We assume that symbionts provide the energy necessary for coral maintenance and growth (and that the many other factors that influence coral growth and mortality are constant); thus coral population growth and mortality rates depend on the symbiont population densities ("Symbiont–coral interaction" box in Fig. 1b). We test the importance of this assumption with a model extension that includes symbiont-independent coral growth, presented in Appendix C. In the basic model, for the dynamics each coral population C_m, the intrinsic growth rate increases linearly with symbiont density (expressed as a proportion of total symbiont carrying capacity $\Sigma_i S_{im}/K_{Sm}C_m$), with the constant of proportionality γ_m. This growth rate includes both vegetative growth and juvenile recruits, assuming symbiont types infect new recruits with the same frequency in which they occur in existing corals. Corals experience density-independent mortality at a rate μ_m in the absence of symbionts. This mortality rate decreases with increasing symbiont densities through an interaction (incorporated in Eq. 5) whose strength is characterized by the constant u_m.

We chose the linear and inverse relationships between coral growth and mortality, respectively, and symbiont density in order to use the simplest possible functional forms that model the relevant biological dynamics. Specifically, in order to negatively affect coral populations (i.e., coral mortality $>$ growth), temperature anomalies must be extreme or long-lasting enough to cause sufficient symbiont population declines. Consequently, without further assumptions, these biological dynamics may generate the cumulative stress necessary to cause a fatal bleaching event (as reflected by stress metrics currently used to predict bleaching events [Donner et al. 2005]).

We model coral density dependence by assuming that per capita population growth rates decline with increasing coral densities. Considering both intraspecific and interspecific competition for space, we employ Lotka-

TABLE 1. Parameter values used in the numerical analysis of Eqs. 1–5.

Parameter	Description	Value	Reference
Coral parameters			
K_{Cm}	coral carrying capacity	massive: 7.7412×10^7 cm^2, branching: 1.025×10^8 cm^2	Chancerelle (2000), Mumby (2006)
α_{mn}	competition coefficient	massive: 0.75, branching: 0.85	Langmead and Sheppard (2004)
γ_m	growth rate	massive: 1 yr^{-1}, branching: 10 yr^{-1}	Huston (1985)
μ_m	basal mortality	massive: 5.8767×10^3 yr^{-1}, branching: 3.849×10^2 yr^{-1}	Chancerelle (2000), McClanahan et al. (2001)
u_m	symbiont influence on mortality	massive: 30 000, branching: 20 000	Fitt et al. (2000)
Symbiont parameters			
K_{Sm}	symbiont carrying capacity	massive: 3×10^6 cells/cm^2, branching: 4×10^6 cells/cm^2	Fitt et al. (2000)
a	linear growth rate	1.0768 yr^{-1}	Muscatine et al. (1984)
b	exponential growth constant	0.0633°C^{-1}	Norberg (2004), Eppley (1972)
σ_e^2	environmental variance	0.0114°C^2†	Mousseau and Roff (1987)
σ_M^2	mutational variance	1.142×10^{-5}°C^2 yr^{-1}†	Lynch (1988), Muscatine et al. (1984)
σ_{wm}^2	selectional variance	in thermal stress-susceptible coral: 2.7702°C^2 in thermal stress-tolerant coral: 3.4627°C^2	

Notes: See *Methods: Model analysis* for discussion of initial conditions and parameterization details. Some parameters are derived from combinations of published estimates and were not rounded; thus the number of significant figures should not be interpreted as an indicator of either accuracy or precision of a parameter value. Note that we drop all m subscripts for parameters in reference to one-coral-species simulations.

† Note that σ_e^2 and σ_M^2 increase by a factor of 5 in the simulations with greater initial genetic variance and by a factor of 1.25 for the thermally tolerant coral species in order for heritability and variation ratios to remain constant; $\sigma_M^2 = 0$ in simulations without evolution.

Volterra competition for mathematical simplicity and phenomenological generality, where each coral population has its own carrying capacity K_{Cm} and the competitive effect (due to whatever competitive mechanism is at work) of species n on species m is α_{mn}; note that $\alpha_{mm} = 1$ for any m. Therefore, the coral population dynamics are

$$\frac{dC_m}{dt} = C_m \left[\frac{\gamma_m \frac{\sum_i S_{im}}{K_{Sm} C_m}}{K_{Cm}} \left(K_{Cm} - \sum_n \alpha_{mn} C_n \right) - \frac{\mu_m}{1 + u_m \frac{\sum_i S_{im}}{K_{Sm} C_m}} \right] \quad (5)$$

(Fig. 1b). The closed coral dynamics modeled here stem from the assumption that, compared to juvenile recruitment, vegetative growth is the primary contributor to increases in coral cover over the time scales modeled here. When modeling two coral species, we assume one species grows faster but is more susceptible to thermal stress than the other, similar to the observed trade-offs between growth and thermal tolerance in corals with branching or massive morphologies (Fig. 1b; e.g., branching *Acropora* and massive *Porites* [Loya et al. 2001, Bhagooli and Yakovleva 2004]); therefore, the two species represent disparate coral taxa and morphology.

Model analysis

In order to analyze the above model, we numerically integrate Eqs. 1–5 given various climate scenarios, with a varying number of coral and symbiont species, and with or without evolutionary dynamics. For these simulations, we use the numerical integrator based on the Runge-Kutta (4,5) formula with the Dormand-Prince pair in Matlab (version 7.4; MathWorks, Natick, Massachusetts, USA). The parameter values used in the numerical analysis are in Table 1; see below for the model parameterization details and justification. As many of the parameter values are uncertain, we perform a sensitivity analysis of the model, described in *Sensitivity analysis*.

Coral parameters.—We base the slow-growing coral on massive-type corals (e.g., *Montastraea annularis*; species 1) and the fast-growing coral on branching-type corals (e.g., *Acropora palmata*; species 2). The total area available for the corals is 6.25×10^6 cm^2, similar to Mumby (2006). To convert this area to carrying-capacity values (K_{Cm}), we multiply it by the conversion constants from coral projected area to total surface area in Chancerelle (2000): 11.86 for species 1 and 16.40 for species 2. For the competition coefficients between the two coral species, we choose values, $\alpha_{21} = 0.75$ and $\alpha_{12} = 0.85$, that allow coexistence given past climate data and that are consistent with the greater competitive ability for *Montastraea* reported in Langmead and Sheppard (2004). We base the growth rates, $\gamma_1 = 1$ yr^{-1} and $\gamma_2 = 10$ yr^{-1}, on the extension rates reported in Huston (1985); we use extension rates rather than the instantaneous population growth rates that can be estimated from matrix population models (e.g., Hughes 1984, Edmunds and Elahi 2007) because we account for mortality separately from growth. We estimate basal mortality rates (coral mortality in complete absence of symbionts), $\mu_1 = 3.849 \times$

10^2 yr^{-1} and $\mu_2 = 5.8767 \times 10^3$ yr^{-1}, from the crown diameter declines during a bleaching event reported in McClanahan et al. (2001) and the projected area–surface-area conversion coefficients from Chancerelle (2000) mentioned at the beginning of this subsection. Finally, we choose values for the influence of symbionts on coral mortality, $u_1 = 20\,000$ and $u_2 = 30\,000$, such that coral mortality exceeds growth when symbiont densities fall below $\sim 0.5 \times 10^6$ cells/cm^2, the approximate threshold for a bleaching event reported in Fitt et al. (2000).

Symbiont parameters.—We base the total carrying capacity of each coral for symbionts, $K_{S1} = 3 \times 10^6$ cells/cm^2 and $K_{S2} = 4 \times 10^6$ cells/cm^2, on the peak values in Fitt et al. (2000), which are generally in line with other reported values (Szmant and Gassman 1990, Fagoonee et al. 1999, Glynn et al. 2001, Cruz-Piñon et al. 2003); note that carrying capacities represent an upper limit to symbiont population densities, and seasonal fluctuations in growth rates lead to variable symbiont population densities that are often below these limits. For symbiont growth, we use $b = 0.0633°C^{-1}$ based on the general value for phytoplankton from Eppley (1972) and Norberg (2004), and we reduce their reported value for a to 1.0768 yr^{-1} so that the maximum symbiont growth rate is similar to the value reported in Muscatine et al. (1984) based on the mitotic doublet proportion and cell division duration; a lower symbiont growth rate relative to other phytoplankton is reasonable given that ~95% of the energy gained from photosynthesis goes to the coral host (Falkowski et al. 1984, Muscatine et al. 1984).

In order to determine environmental and mutational variance, we use a typical heritability for physiological traits, $h^2 = 0.330$ (Mousseau and Roff 1987). Therefore, given the initial total phenotypic variation σ_p^2 (see *Coral parameters* for initial values), the environmental variance is $\sigma_e^2 = (1 - h^2)\sigma_p^2$. We then calculate the mutational variance $\sigma_M^2 = \sigma_e^2 \times 0.001$ yr^{-1} based on reported values for the ratio σ_M^2:σ_e^2 as 0.0001–0.05 per generation for a variety of model organisms (Lynch 1988) and on the approximate symbiont generation time of 0.2 years (Muscatine et al. 1984). For the selectional variance, we choose the relative values of 1:1.25 for thermal stress-susceptible : thermal stress-tolerant corals (σ_{w1}^2:σ_{w2}^2 in the two-coral-species simulations). We choose the exact value(s) of σ_{wm}^2 in each location such that simulation runs with previous temperature values predict significant population declines for the thermal stress-susceptible species and slight population declines for the thermal stress-tolerant species during previous major bleaching events reported on ReefBase (*available online*).[5] See *Initializations* for more details.

Climate data and locations.—For temperature time series, we use mean monthly sea surface temperature (SST) from a variety of data sets. For past temperature values, we use the Met Office Hadley Centre for Climate Prediction Sea Ice and SST data set (ISST; Rayner et al. 2003). For future temperature values, we use two climate models, the Hadley Center HadCM3 model and National Oceanic and Atmospheric Administration (NOAA) Geophysics Fluid Dynamics Laboratory (GFDL) 2.1 model. With these models, we test our model predictions with two climate scenarios, the 720 ppm stabilization experiment (SRES A1b) and the 550 ppm stabilization experiment (SRES B1). For each of the future models and scenarios, we use one sample realization from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model data set. Note that our use of one realization, along with the simplifying assumptions of the biological model, mean that our results are appropriate for comparing trends rather than producing quantitatively precise forecasts. These models and scenarios represent a range of climate predictions that have been used in previous threshold-based coral bleaching projections (Donner et al. 2005, 2007).

For specific locations in which to test model predictions, we extract temperature data from several coordinates corresponding to the Caribbean (Curaçao, Netherlands Antilles; St. John, U.S. Virgin Islands), the Great Barrier Reef (Heron Island, Australia), Moorea (French Polynesia), and Thailand (Ko Phuket) in order to chose wide-ranging locations where long-term coral data are available to validate model predictions (Connell et al. 1997, Brown et al. 2002*b*, Edmunds 2002, Bak et al. 2005). In addition, to explore the accuracy of symbiont community dynamics in our model, we compare model projections (with one fast-growing, stress susceptible coral and two symbionts with a 1°C difference in thermal tolerance) to a known latitudinal gradient in symbiont community composition for several locations spanning the Great Barrier Reef, Australia (Usltrup et al. 2006; Appendix B).

Initializations.—We initialize coral population sizes to 80% of their total carrying capacity; in the two-species simulations, 80% of this amount initially consists of the branching-type coral and 20% of the massive-type coral. In addition, we initialize symbiont population sizes to 90% of their total carrying capacity, with 10% of that amount in the more thermally tolerant type in two-symbiont simulations (similar to Fabricius et al. [2004] who use 90% as the cutoff for determining which symbiont strain dominates a coral colony). These initial values had little impact on qualitative trends in test model runs.

In order to initialize symbiont genetic values, we use the 1870–1960 data for the simulations with past temperature values (Hadley Centre ISST); we start simulations with past temperature data in 1961 in order to start shortly before coral bleaching became a regular topic of scientific study. For simulations with future temperature values (HadCM3 or GFDL 2.1; 2001–2100), we initialized symbiont genetic values based on the WCRP CMIP3 Climate of the 20th Century

[5] ⟨http://www.reefbase.org/global_database/default.aspx?section=t4⟩

experiment (20C3M; 1861–2000) because these data serve as the initial conditions for the future climate scenarios (SRES A1b and SRES B1) used. We initialize the mean genotype of the first symbiont $\bar{g}_{1m}$ as the mean of the initialization temperature data because that is the optimal genotype averaged over time. In simulations with two symbionts, we test model predictions with the second symbiont having a 1°C or 2°C greater initial mean genotype ($\bar{g}_{2m}$) than the first symbiont. In simulations with evolution, we initialize genetic variance σ^2_{gim} at its expected equilibrium value of $\sigma_M\sigma_{wm}$ (the product of mutational and selectional variances [Lynch et al. 1991]), and we also test the outcome with an initial genetic variance at five times this value (the relationship with the phenotypic variance σ^2_{pim}, $\sigma^2_{gim} = h^2\sigma^2_{pim}$, allows determination of σ^2_M and σ^2_e given the formulas in the *Symbiont parameters* section above). In models without evolution, we set $\sigma^2_{gim} = \sigma^2_M = 0$ (no genetic or mutational variance).

Finally, we set the selection variance of thermal stress-susceptible corals (σ^2_w in the one-coral species simulations and σ^2_{w1} in the two-coral-species simulations, which also sets the selection strength of coral 2 relative to coral 1; see *Symbiont parameters*) as proportional to the variation in the initialization temperature data, with the proportionality constant as: 0.9 for Moorea and Curaçao; 0.8 for St. John, U.S. Virgin Islands; 0.7 for all Australian sites; and 1.3 for Ko Phuket, Thailand. Choosing σ^2_{wm} depending on the initialization temperature data reflects the potential for acclimatization to ambient variation (Brown 2002*a*) to shape how symbiont growth rates depend on phenotype and temperature (i.e., greater past variation may select for greater acclimatization potential for a given genotype, and therefore a wider fitness curve).

Sensitivity analysis.—To analyze the sensitivity of the model output to the parameter values, we numerically determine the derivatives of each state variable (S) with respect to each parameter (P) at each point in time (using the Matlab algorithm by García Mollá and Gómez Padilla [*available online*]).[6] Then we normalize this sensitivity to determine the proportional sensitivity by multiplying by the parameter and dividing by the state variable (i.e., elasticity: $P\partial S/S\partial P$; de Kroon et al. [1986]). A large positive or negative derivative indicates that the changes in a parameter cause rapid changes in the model output; therefore, we present the absolute value of the derivative. In addition, because the relative rank of each parameter in terms of sensitivity was reasonably constant through time, we present the average sensitivities over time.

Results

We test model predictions with one or two coral species, each with one or two symbiont types, with or without genetic diversity. Our model prediction with the various climate models (HadCM3, GFDL 2.1) and locations had qualitatively similar trends; here we present sample results representative of those trends using the GFDL 2.1 climate model in Curaçao. In the sample results of the one-coral species simulations, we use parameter values for a thermal-stress-susceptible, slow-growing coral based on the dominance of such species in the Caribbean (Knowlton and Budd 2001, Pandolfi and Jackson 2006).

In simulations with one coral species, we first compare model predictions with each type of symbiont diversity: none, community diversity (two symbiont types with a 1°C difference in symbiont genotype, or temperature for which they are optimally adapted), and genetic diversity (and therefore potential for evolutionary change in thermal tolerance). Given past temperature data (ISST), all three simulations predict coral persistence with declines in coral cover during previously observed major bleaching events (Fig. 2, first column). Given future temperature data from the more severe (SRES A1b) climate scenario, all three simulations predict coral collapse within the next century, with the earliest collapse in simulations without symbiont diversity and the latest collapse in simulations with symbiont community diversity (Fig. 2, second column). Given future temperature data from the less severe (SRES B1) climate scenario, simulations without symbiont diversity predict coral collapse, while simulations with symbiont diversity predict coral persistence, with greater coral cover in simulations with community diversity compared to genetic diversity (Fig. 2, third column).

Also in simulations with one coral species, we test model predictions with greater amounts of symbiont diversity: two symbiont types with a 2°C difference in symbiont genotype, five times greater initial genetic diversity, and both genetic and community diversity (at the original levels). Given past temperature data, simulations with greater genetic diversity or with both genetic and community diversity predict smaller coral declines during previously observed major bleaching events (Fig. 3, first column). Given temperature data from future climate scenarios, all of the simulations with greater symbiont diversity predict coral persistence (Fig. 3, second and third columns). Note that, in the case of two symbionts with a 2°C difference in thermal tolerance (Fig. 3, magenta lines), greater coral declines in the immediate future occur than in simulations with a 1°C difference in thermal tolerance (Fig. 2, gray lines), most likely because neither symbiont type is well adapted until temperatures increase to a level for which the more thermally tolerant symbiont is well adapted.

In simulations with symbiont genetic diversity and temperature data from future climate scenarios, the mean symbiont genotype gradually increases through time (symbiont genotype rows of Figs. 2 and 3), paralleling the rise in mean temperature. Similarly, in simulations with symbiont community diversity, a shift in dominance

[6] ⟨http://www.mathworks.com/matlabcentral/fileexchange/loadFile.do?objectId=1480&objectType=FILE⟩

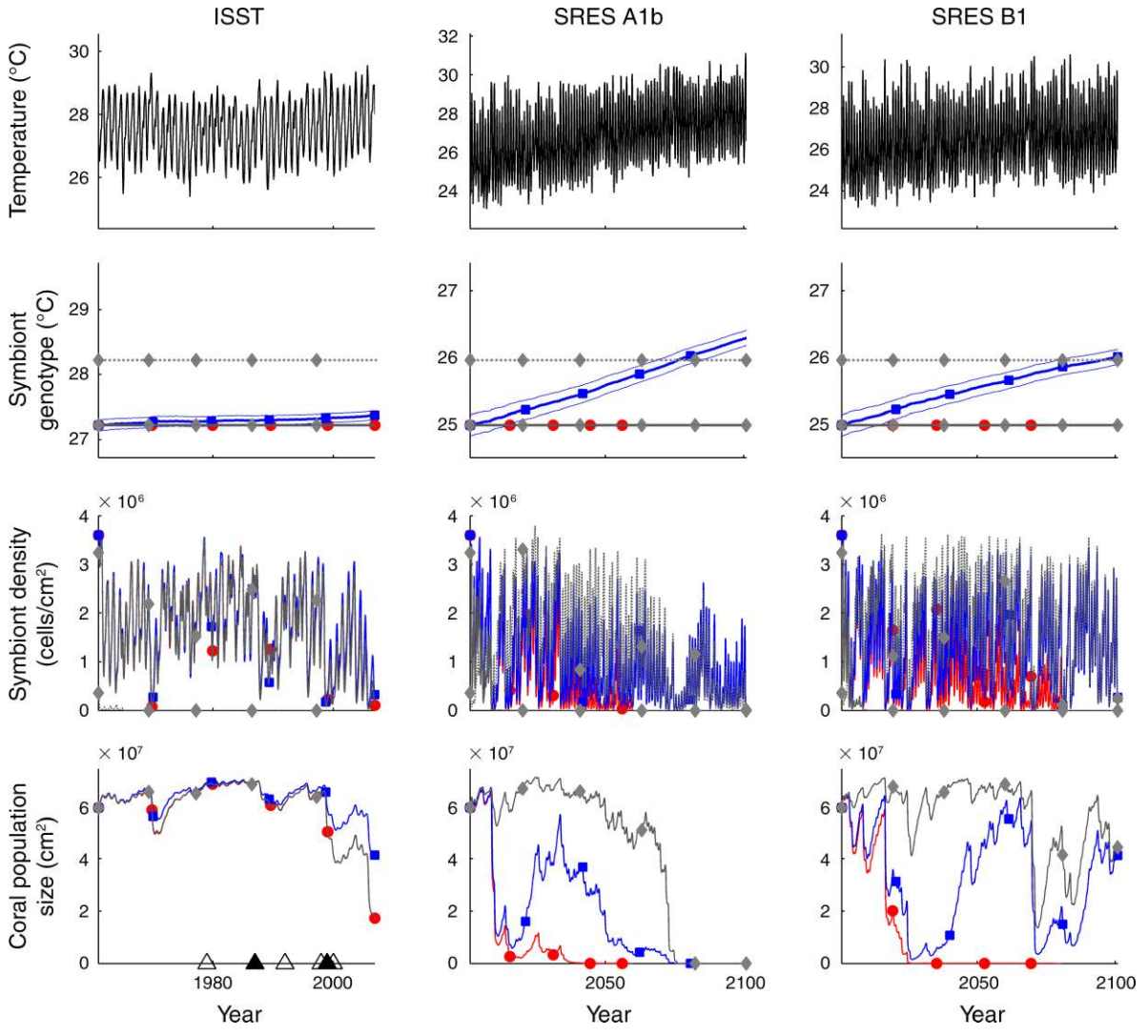

FIG. 2. Simulations with one thermal-stress-susceptible, slow-growing coral (e.g., *Montastraea annularis*). ISST is the past temperature data; SRES A1b and SRES B1 are the future temperature data with greater or lower greenhouse gas emissions, respectively. Simulations with one non-evolving symbiont are in red (circles), with one evolving symbiont in blue (squares), and with two non-evolving symbiont types in gray (diamonds), where solid and broken lines indicate different symbiont types. The genotype plots include genetic distribution 95% confidence intervals, and a symbiont "genotype" is its optimal temperature. The initial genotypes differ in the ISST and SRES plots to account for the different initialization temperature series in these simulations (see *Methods: Initializations*). In the coral ISST plot, solid and open triangles indicate observed major and minor bleaching events, respectively (see footnote 5).

from the less to the more thermal-stress-tolerant symbiont type (greater genotype) occurs over the course of future climate scenarios (e.g., symbiont density row of Fig. 2). Regardless of symbiont type and level of diversity, symbiont densities fluctuate with seasonal temperature fluctuations (see Fig. A.1 in Appendix A for a more detailed illustration of these fluctuations).

In simulations with two coral species and varying levels of symbiont diversity, given past temperature data declines during previously observed bleaching events occur in the fast-growing, thermal-stress-susceptible branching-type coral but not in the slow-growing, thermal-stress-tolerant massive-type coral (Fig. 4, first column). Given future temperature data, trends in simulation results match those of the one-coral simulations: coral collapses in the more severe climate scenario regardless of symbiont diversity and persistence in the less severe climate scenario given symbiont diversity; when collapses occur, the massive-type coral species persists longer than the branching-type coral (Fig. 4, second and third columns). In the simulations with temperature data from future climate scenarios, coral cover for the branching-type or massive-type species is generally greater or less in the simulations with symbiont community diversity compared to those with symbiont genetic diversity, respectively.

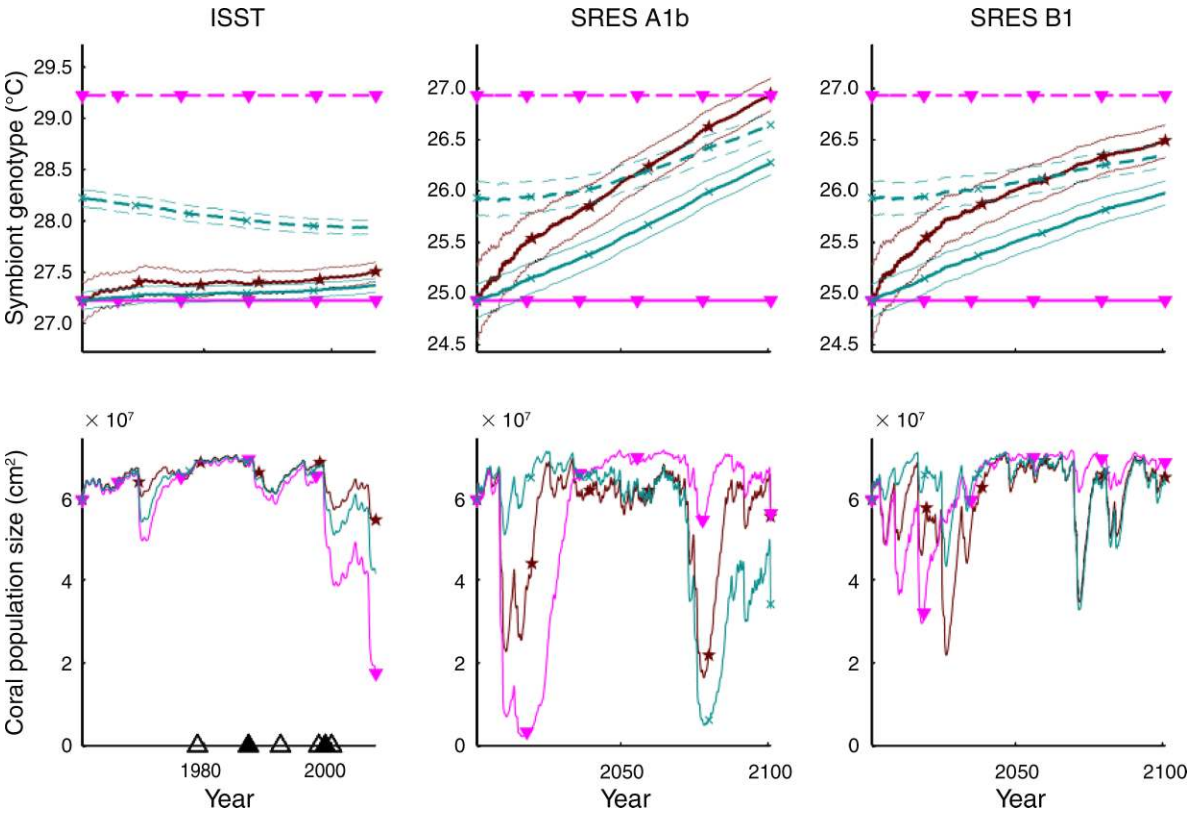

FIG. 3. Simulation predictions with one thermal-stress-susceptible, slow-growing coral and greater symbiont variation. ISST is the past temperature data; SRES A1b and SRES B1 are the future temperature data with greater or lower greenhouse gas emissions, respectively. Simulations with one evolving symbiont and five times greater initial genetic variance than the expected equilibrium value are in brown (stars; i.e., σ_g at start of simulations is $5\sigma_M\sigma_w$ rather than expected equilibrium value of $\sigma_M\sigma_w$), with two non-evolving symbionts with a 2°C difference in thermal tolerance in magenta (down-facing triangles), and with two evolving symbionts with a 1°C difference in thermal tolerance in cyan (x-symbols). Solid and broken lines indicate different symbiont types, and the genotype plots include genetic distribution 95% confidence intervals. In the coral population size plot with past temperature (ISST) data, solid and open up-facing triangles indicate observed major and minor bleaching events, respectively (see footnote 5).

A sensitivity analysis of the model (based on proportional sensitivity, or elasticity) indicates that symbiont and coral population sizes are the most sensitive of the four state variables (Fig. 5). Both symbiont and coral population sizes are the most sensitive to the selectional variance parameter (σ_w^2, which determines selection strength) and second to the symbiont exponential growth constant (b). Sensitivity to these parameters is greater in years and climate scenarios with higher thermal stress because they determine the magnitude of the effect that temperature stress has on symbiont, and consequently coral, population dynamics (results not shown).

DISCUSSION

Although the increased incidence of mass bleaching events associated with climate change threatens the future of coral reefs, corals may have the potential to respond through shifts in community composition and genetic adaptation in terms of thermal tolerance. To test this potential, the model presented here explores the community and genetic dynamics of corals and their symbiotic algae given variation in thermal tolerance and different climate scenarios. This model provides an example approach to exploring the interaction between ecological and evolutionary dynamics in a changing climate (see also Norberg et al. 2001, Hellmann and Pineda-Krch 2007).

Model predictions

Model predictions given past temperature data (first columns of Figs. 2–4) support the potential for our coral-symbiont model to predict qualitative trends. For example, qualitative model trends resemble observed coral declines during previous bleaching events and the overall decline in coral over the past several years in locations such as Curaçao (Bak et al. 2005), the location used in the sample results presented here. On a shorter time scale, the dependency of the symbiont population growth rates on the temperature relative to the symbiont genotype(s) causes sublethal intra-annual variation in symbiont densities (third row of Fig. 2, Fig. A.1) similar

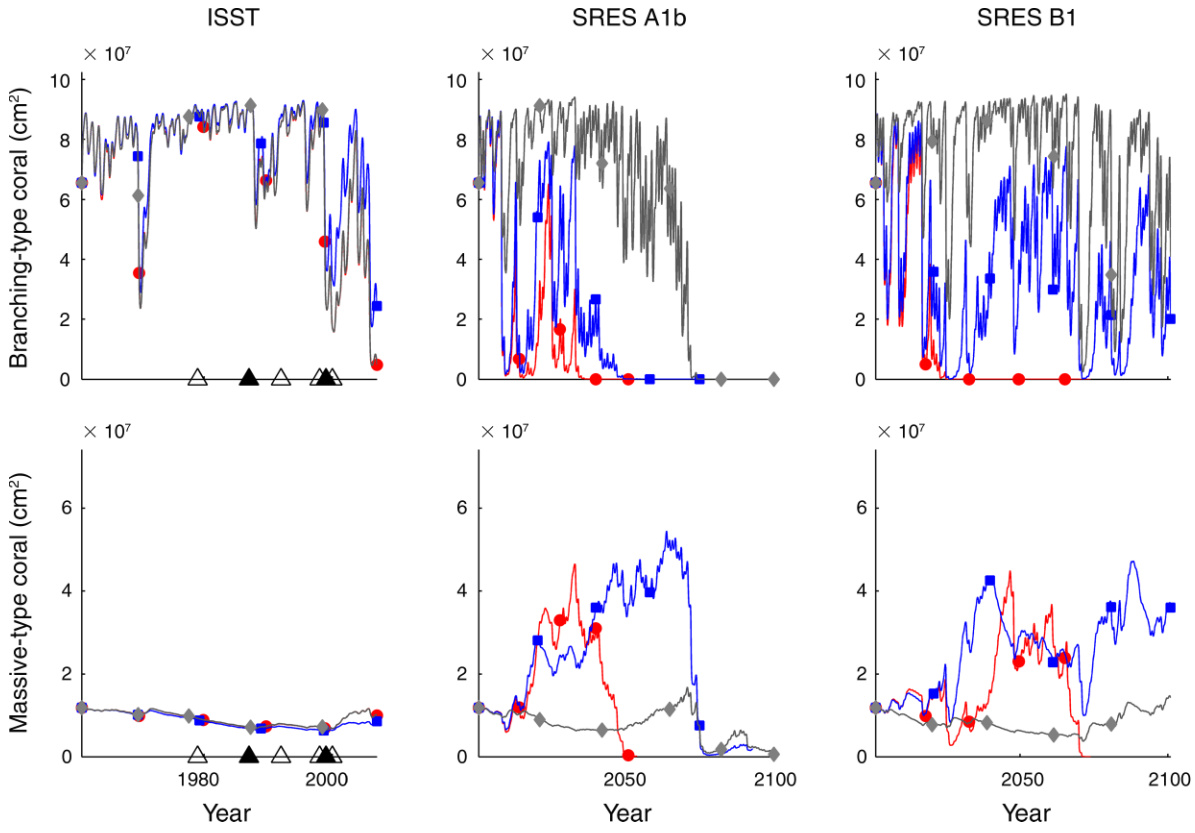

FIG. 4. Simulations with two corals. Population size of the thermal-stress-susceptible, fast-growing (e.g., branching *Acropora*) coral is in the first row; that of the thermal-stress-tolerant, slow-growing (e.g., massive *Porites*) coral is in the second row. ISST is the past temperature data; SRES A1b and SRES B1 are the future temperature data with greater or lower greenhouse gas emissions, respectively. Simulations with one non-evolving symbiont are in red (circles), simulations with one evolving symbiont in blue (squares), and simulations with two non-evolving symbiont types are in gray (diamonds). In the first column (ISST), solid and open triangles indicate observed major and minor bleaching events, respectively (see footnote 5).

in magnitude to empirically observed patterns (Fitt et al. 2000). Finally, the model results (with and without evolutionary dynamics) predict a shift in the dominant symbiont to the more thermally tolerant of the two possible types in the northernmost locations of the Great Barrier Reef (see Appendix B: Figs. B.1 and B.2), in line with the empirically observed latitudinal gradient in symbiont community composition (Ulstrup et al. 2006); this match supports our representation of community-level symbiont diversity. Overall, although this model necessarily involves simplifying assumptions, it provides a first step toward exploring the dynamical processes that link symbiont and coral diversity to future bleaching predictions.

Given future temperature data, simulations with one coral species and symbiont type each and without evolution provide a baseline, similar to previous models, for determining the effect of including coral and symbiont genetic and community diversity. In these simulations without coral or symbiont diversity, the stress-susceptible coral (e.g., *Montastraea annularis*) population collapses between 2020 and 2040 (Fig. 2, red lines); this time frame is consistent with previous predictions based on a static bleaching threshold (Hoegh-Guldberg 1999, Sheppard 2003, Donner et al. 2005, Wooldridge et al. 2005). However, accounting for symbiont diversity through within-type evolution in symbiont thermal tolerance (Fig. 2, blue lines) or the existence of a more thermally tolerant (by 1°C) symbiont type (such as a symbiont from a different *Symbiodinium* subclade; Fig. 2, gray lines) delays coral collapse and may lead to persistence over the next 100 years provided sufficient reductions in greenhouse gas emissions, i.e., climate scenario SRES B1 rather than SRES A1b. Furthermore, greater variation in thermal tolerance, through the existence of both symbiont genetic and community variation (i.e., two symbiont types with evolution), greater initial genetic variation (and therefore adaptive potential), or two symbiont types with a 2°C difference in thermal tolerance, can allow coral persistence over 100 years of climate change under the (higher emission) SRES A1b climate scenario (Fig. 3). However, it is unclear whether such levels of variation may exist, and simulations with this greater variation can predict unrealistically minor bleaching events given past temperature data.

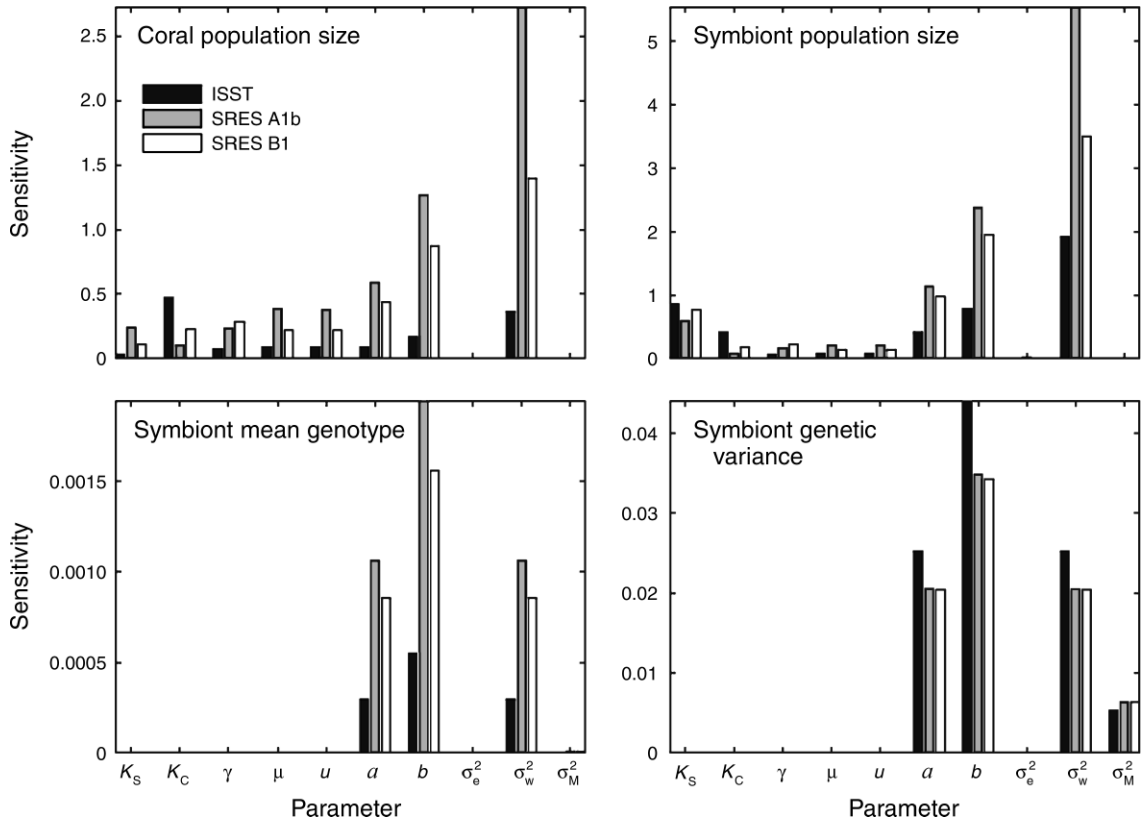

FIG. 5. Proportional sensitivity of the state variables (coral population size, symbiont population size, symbiont mean genotype, symbiont genetic variance) to model parameters (see Table 1 for parameter definitions). Sensitivities for the run (for Curaçao) with past temperature data (ISST) are in black, with the SRES A1b future climate scenario (with the GFDL 2.1 climate model) in gray, and with the SRES B1 future climate scenario in white.

In simulations with two coral species, a community shift in coral composition from the fast-growing, thermal stress-susceptible species (e.g., branching corals from the genus *Acropora*) to the slow-growing, thermal stress-tolerant species (e.g., massive corals from the genus *Porites*) occurs in scenarios that predict the collapse of a stress-susceptible species when considered alone (Fig. 4), similar to previous theoretical predictions (Wooldridge et al. 2005). However, assuming limited thermal tolerance (as suggested by the bleaching mortality in the relatively stress-tolerant massive *Porites* first reported during the 1998 bleaching event [Mumby et al. 2001]), substantial declines in the slow-growing species may, within decades, follow the collapse of the fast-growing species. Therefore, our model results suggest that a shift in the dominant corals to slower-growing, thermal-stress-tolerant species may be a transient indicator of overall coral reef decline provided continued climate change.

Model uncertainties and biases

Due to the general uncertainty of the parameter values and dynamics used in the simulations presented here, our results can only indicate likely trends rather than quantitatively precise forecasts. For example, the model does not include potentially important factors such as the influence of UV irradiance on bleaching events, competition between corals and macroalgae, size-structured coral dynamics, open coral and symbiont dynamics, and heterotrophic coral energy acquisition (Hoegh-Guldberg 1999, Wilkinson 1999, Fong and Glynn 2000). We test the importance of two such factors with model extensions that include open symbiont dynamics (as supported by Lewis and Coffroth [2004]) and coral heterotrophy, or energy acquisition independent of symbionts (as supported by Grottoli et al. 2006). A preliminary exploration of these model extensions indicates that both dynamics do not alter the qualitative trends reported here (see Appendix C: Figs. C.1 and C.2; exploratory results from a size-structured version of this model, not shown, are also consistent with the results here). Overall, the model simplicity allows clearer determination of how the included parameters and dynamics influence the model outcome, and model extensions with additional biological realism can indicate the importance of various simplifying assumptions.

Furthermore, climate-change-related bleaching events are only one of several anthropogenic impacts on coral reefs. Additional impacts include overfishing of herbi-

vores (which affects competition between corals and macroalgae), pollution and sedimentation associated with coastal land use (which affect coral demographics and coral–macroalgal competition), and climate-change-related ocean acidification (which affects coral calcification rates [Wilkinson 1999, Pandolfi et al. 2003, Bellwood et al. 2004, Hoegh-Guldberg et al. 2007]). For example, our model does not predict the shifts in dominant corals to slower-growing species observed in the Caribbean during the past century (Fig. 4, first column [Pandolfi and Jackson 2006]); the most likely causes for these shifts are a combination of climate-unrelated anthropogenic impacts such as sedimentation, eutrophication, fishing, and disease (Pandolfi and Jackson 2006). Therefore, this difference between modeled and observed community composition probably reflects the lack of additional anthropogenic impacts in our model rather than inaccuracy in our model's ability to predict the impact of climate change on coral community dynamics. Constructing quantitative models to explore coral response to each impact alone (thermal stress in the case of this study) is a first step toward comparing the many potentially important anthropogenic impacts.

Additional anthropogenic impacts not accounted for here may interact synergistically with and reduce coral resistance and resilience to stressors such as climate change (Smith and Buddemeier 1992, Hughes and Connell 1999, Nyström et al. 2000, Bellwood et al. 2004, Mumby et al. 2007). The sensitivity analysis here (Fig. 5) can provide initial insight into the potential for such synergistic interactions. For example, model sensitivity to the coral growth rate (γ) indicates the potential for interaction between bleaching and additional anthropogenic impacts that affect coral growth, such as ocean acidification due to carbon dioxide emissions and decreased water quality related to coastal development (Hoegh-Guldberg 1999, Wilkinson 1999). Future research will test the sensitivity of model predictions to more biologically realistic dynamics as well as build on this model to incorporate additional anthropogenic impacts and directly explore the potential for synergy between multiple stressors.

In addition to potential synergistic interactions, model sensitivity to uncertain parameter values can help guide future empirical research. In particular, the parameter to which coral population size is most sensitive, the selectional variance (σ_w^2; Fig. 5), is arguably the most uncertain parameter in the model: it is the only value we chose based on model calibration to past bleaching events rather than based on independent parameterization. Furthermore, the second-ranking parameter for coral cover sensitivity, the symbiont exponential growth constant (b), is one we base on a general value for phytoplankton in the absence of detailed information for *Symbiodinium*. This result suggests model sensitivity not only to this parameter, but also to the exponential functional form, again based on phytoplankton, chosen for maximum symbiont population growth rate (with the realized growth rate depending on both this function and the difference between mean symbiont genotype and temperature). Overall sensitivity to such poorly-known parameters suggests that future empirical research on these parameters and functional responses (e.g., symbiont population growth rates as a function of a range of temperature) may be a necessary component of accurately predicting coral response to climate change.

Conclusions

In summary, symbiont diversity, on both the genetic and community levels, has the potential to allow coral reef persistence over some scenarios for the next 100 years of climate change (Figs. 2–4). While genetic-level diversity generally has a smaller impact on future coral cover than symbiont community-level diversity, some corals may harbor only one symbiont type and thus lack the capacity to respond to future climate change through symbiont community shifts (Goulet 2006). Therefore, provided a conservation goal of protecting coral reefs more likely to be resistant and resilient to future climate change (West and Salm 2003), empirically measuring symbiont genetic variation and community composition may be vital to identifying coral reefs to target for protection from additional anthropogenic impacts.

Furthermore, the climate scenario (SRES A1b or SRES B1) can have a large impact on the potential for future coral reef persistence. The effects of the climate scenario depend on the potential for genetic evolution and/or community composition shifts in symbionts. Without genetic or community variation, the climate scenario has little effect since corals collapse under the time frame that reflects committed climate change from current greenhouse gas emissions (Fig. 2, red lines; see also Donner et al. [2007]). However, much like the climate scenarios differ in rate and amount of change in temperature, incorporating genetic and community variation models the potential rate and amount of change in thermal tolerance. Thus with biological variation, differences between climate scenarios are much more pronounced, with persistence under moderate climate change and collapse under more extreme scenarios. Therefore, our results indicate that greenhouse gas mitigation could have a significant effect on the future of coral reefs, and accounting for biodiversity and biological dynamics is vital to recognizing this effect.

More generally, coral reefs are one of many systems that exist at the edge of their physiological limits and therefore face an immediate threat from climate change; additional examples include polar ecosystems, communities with restricted ranges such as those on mountaintops, and tropical amphibians (Parmesan 2006). The results presented here highlight the importance of incorporating both ecological and evolutionary dynamics in order to understand the potential responses of such ecosystems to climate change (Holt 1990, Frank-

ham and Kingsolver 2004, Skelly et al. 2007). In addition, these results exemplify how the rate of climate change is critical to whether threatened ecosystems can respond through biological dynamics (Lynch et al. 1991, Lynch and Lande 1993).

Acknowledgments

Discussions with and/or feedback on previous versions of this paper from A. Allen, T. Day, S. Donner, R. Gates, A. Hastings, P. Edmunds, N. Knowlton, S. Holbrook, J. Leichter, M. Medina, B. Santer, R. Schmitt, J. Smith, and M. Urban were extremely helpful to the ideas presented here. In addition, comments on a previous version from M. van Oppen and an anonymous reviewer were very helpful to improving this paper. The work by M. L. Baskett was conducted while a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0553768), the University of California–Santa Barbara, and the State of California. R. M. Nisbet acknowledges support from the Moorea Coral Reef LTER, part of the National Science Foundations' Long Term Ecological Research network. Finally, we acknowledge the climate modeling groups for making their simulations available for analysis, the Program for Climate Model Diagnosis and Intercomparison (PCMDI) for collecting and archiving the CMIP3 model output, and the WCRP's Working Group on Coupled Modelling (WGCM) for organizing the model data analysis activity. The WCRP CMIP3 multi-model data set is supported by the Office of Science, U.S. Department of Energy.

Literature Cited

Araújo, M. B., and C. Rahbek. 2006. How does climate change affect biodiversity? Science 313:1396–1397.

Baghdasarian, G., and L. Muscatine. 2000. Preferential expulsion of dividing algal cells as a mechanism for regulating algal–cnidarian symbiosis. Biology Bulletin 199: 278–286.

Bak, R. P., G. Nieuwland, and E. H. Meesters. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curaçao and Bonaire. Coral Reefs 24:475–479.

Baker, A. 2001. Reef corals bleach to survive change. Nature 411:765–766.

Baker, A. 2003. Flexibility and specificity in coral-algal symbiosis: diversity, ecology, and biogeography of *Symbiodinium*. Annual Revue of Ecology, Evolution and Systematics 34:661–689.

Baker, A. 2004. Symbiont diversity on coral reefs and its relationship to bleaching resistance and resilience. Pages 177–194 *in* E. Rosenberg and Y. Loya, editors. Coral health and disease. Springer-Verlag, New York, New York, USA.

Baker, A., C. Starger, T. McClanahan, and P. Glynn. 2004. Corals' adaptive response to climate change. Nature 430:741.

Bellwood, D., T. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. Nature 429:827–833.

Berkelmans, R., and M. J. H. van Oppen. 2006. The role of zooxanthellae in the thermal tolerance of corals: a "nugget of hope" for coral reefs in an era of climate change. Proceedings of the Royal Society B 273:2305–2312.

Bhagooli, R., and I. Yakovleva. 2004. Differential bleaching susceptibility and mortality patterns among four corals in response to thermal stress. Symbiosis 37:121–136.

Bradshaw, W. E., and C. M. Holzapfel. 2006. Climate change: evolutionary response to rapid climate change. Science 312: 1477–1478.

Brown, B. 1997*a*. Adaptations of reef corals to physical environmental stress. Advances in Marine Biology 31:221–299.

Brown, B. 1997*b*. Coral bleaching: causes and consequences. Coral Reefs 16:S129–S138.

Brown, B., R. Dunne, M. Goodson, and A. Douglas. 2002*a*. Experience shapes the susceptibility of a reef coral to bleaching. Coral Reefs 21:119–126.

Brown, B. E., K. R. Clarke, and R. M. Warwick. 2002*b*. Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. Marine Biology 141:21–29.

Burger, R. 1999. Evolution of genetic variability and the advantage of sex and recombination in changing environments. Genetics 153:1055–1069.

Chancerelle, Y. 2000. Methods to estimate actual surface areas of scleractinian coral at the colony- and community-scale. Oceanologica Acta 23:211–219.

Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67:461–488.

Cook, C., A. Logan, J. Ward, B. Luckhurst, and C. Berg, Jr. 1990. Elevated temperatures and bleaching on a high latitude coral reef: the 1988 Bermuda event. Coral Reefs 9:45–49.

Cruz-Piñon, G., J. P. Carricart-Ganivet, and J. Espinoza-Avalos. 2003. Monthly skeletal extension rates of the hermatypic corals *Montastraea annularis* and *Montastraea faveolata*: biological and environmental controls. Marine Biology 143:491–500.

Day, T., L. Nagel, M. van Oppen, and M. Caley. 2008. Factors affecting the evolution of bleaching resistance in corals. American Naturalist 171:E72–E88.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population-growth rate. Ecology 67:1427–1431.

Donner, S. D., T. R. Knutson, and M. Oppenheimer. 2007. Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. Proceeding of the National Academy of Science (USA) 104: 5483–5488.

Donner, S., W. Skirving, C. Little, M. Oppenheimer, and O. Hoegh-Guldberg. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biology 11:2251–2265.

Edmunds, P. J. 2002. Long-term dynamics of coral reefs in St. John, U.S. Virgin Islands. Coral Reefs 21:357–367.

Edmunds, P. J., and R. Elahi. 2007. The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. Ecological Monographs 77:3–18.

Eppley, R. W. 1972. Temperature and phytoplankton growth in sea. Fisheries Bulletin 70:1063–1085.

Fabricius, K. E., J. C. Mieog, P. L. Colin, D. Idip, and M. J. H. van Oppen. 2004. Identity and diversity of coral endosymbionts (zooxanthellae) from three Palauan reefs with contrasting bleaching, temperature and shading histories. Molecular Ecology 13:2445–2458.

Fagoonee, I., H. B. Wilson, M. P. Hassell, and J. R. Turner. 1999. The dynamics of zooxanthellae populations: a long-term study in the field. Science 283:843–845.

Falkowski, P. G., Z. Dubinsky, L. Muscatine, and J. W. Porter. 1984. Light and the bioenergetics of a symbiotic coral. BioScience 34:705–709.

Fitt, W. K., F. K. McFarland, M. E. Warner, and G. C. Chilcoat. 2000. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnology and Oceanography 45:677–685.

Fong, P., and P. Glynn. 2000. A regional model to predict coral population dynamics in response to El Niño–Southern Oscillation. Ecological Applications 10:842–854.

Frankham, R., and J. Kingsolver. 2004. Responses to environmental change: adaptation or extinction. Pages 85–100 *in* R. Ferrière, U. Dieckmann, and D. Couvet, editors, Evolutionary conservation biology. Cambridge University Press, Cambridge, UK.

Glynn, P. 1993. Coral-reef bleaching: ecological perspectives. Coral Reefs 12:1–17.

Glynn, P. W., J. L. Maté, A. C. Baker, and M. O. Calderón. 2001. Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: Spatial/temporal patterns and comparisons with the 1982–1983 event. Bulletin of Marine Science 69:79–109.

Goulet, T. L. 2006. Most corals may not change their symbionts. Marine Ecology Progress Series 321:1–7.

Grottoli, A. G., L. J. Rodrigues, and J. E. Palardy. 2006. Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189.

Hellmann, J. J., and M. Pineda-Krch. 2007. Constraints and reinforcement on adaptation under climate change: selection of genetically correlated traits. Biological Conservation 137: 599–609.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50:839–866.

Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742.

Hoffmann, A., and M. Blows. 1993. Evolutionary genetics and climate change: Will animals adapt to global warming? Pages 165–178 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Holt, R. D. 1990. The microevolutionary consequences of climate change. Trends in Ecology and Evolution 5:311–315.

Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general-model with a reef coral example. American Naturalist 123:778–795.

Hughes, T., et al. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933.

Hughes, T., and J. Connell. 1999. Multiple stressors on coral reefs: a long-term perspective. Limnology and Oceanography 44:932–940.

Huppert, A., and L. Stone. 1998. Chaos in the Pacific's coral reef bleaching cycle. American Naturalist 152:447–459.

Huston, M. 1985. Variation in coral growth-rates with depth at Discovery Bay, Jamaica. Coral Reefs 4:19–25.

Jokiel, P., and S. Coles. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs 8:155–162.

Knowlton, N., and A. Budd. 2001. Recognizing coral species past and present. Pages 97–119 *in* J. Jackson, S. Lidgard, and F. McKinney, editors, Evolutionary patterns: growth, form, and tempo in the fossil record. University of Chicago Press, Chicago, Illinois, USA.

LaJeunesse, T. C. 2001. Investigating the biodiversity, ecology, and phylogeny of endosymbiotic dinoflagellates in the genus *Symbiodinium* using the its region: in search of a "species" level marker. Journal of Phycology 37:866–880.

Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution 50:434–437.

Langmead, O., and C. Sheppard. 2004. Coral reef community dynamics and disturbance: a simulation model. Ecological Modelling 175:271–290.

Lasker, H. R., and M. A. Coffroth. 1999. Responses of clonal reef taxa to environmental change. American Zoologist 39: 92–103.

Lewis, C. L., and M. A. Coffroth. 2004. The acquisition of exogenous algal symbionts by an octocoral after bleaching. Science 304:1490–1492.

Little, A. F., M. J. H. van Oppen, and B. L. Willis. 2004. Flexibility in algal endosymbioses shapes growth in reef corals. Science 304:1492–1494.

Loya, Y., K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, and R. van Woesik. 2001. Coral bleaching: the winners and the losers. Ecology Letters 4:122–131.

Lynch, M. 1988. The rate of polygenic mutation. Genetical Research 51:137–148.

Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. Pages 471–501 *in* J. C. Avise and J. L. Hamrick, editors, Conservation genetics. Chapman and Hall, New York, New York, USA.

Lynch, M., W. Gabriel, and A. M. Wood. 1991. Adaptive and demographic responses of plankton populations to environmental change. Limnology and Oceanography 36:1301–1312.

Lynch, M., and R. Lande. 1993. Evolution and extinction in response to environmental change. Pages 234–250 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors, Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Marshall, P., and A. Baird. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163.

McCarty, J. P. 2001. Ecological consequences of recent climate change. Conservation Biology 15:320–331.

McClanahan, T. R., M. Ateweberhan, C. A. Muhando, J. Maina, and M. S. Mohammed. 2007. Effects of climate and seawater temperature variation on coral bleaching and mortality. Ecological Monographs 77:503–525.

McClanahan, T. R., N. A. Muthiga, and S. Mangi. 2001. Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. Coral Reefs 19:380–391.

Mousseau, T. A., and D. A. Roff. 1987. Natural-selection and the heritability of fitness components. Heredity 59:181–197.

Mumby, P. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecological Applications 16:747–769.

Mumby, P., J. Chisholm, A. Edwards, C. Clark, E. Roark, S. Andrefouet, and J. Jaubert. 2001. Unprecedented bleaching-induced mortality in *Porites* spp. at Rangiroa Atoll, French Polynesia. Marine Biology 139:183–189.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101.

Muscatine, L., P. G. Falkowski, J. W. Porter, and Z. Dubinsky. 1984. Fate of photosynthetic fixed carbon in light-adapted and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. Proceedings of the Royal Society B 222:181–202.

Norberg, J. 2004. Biodiversity and ecosystem functioning: a complex adaptive systems approach. Limnology and Oceanography 49:1269–1277.

Norberg, J., D. P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. A. Levin. 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. Proceedings of the National Academy of Sciences (USA) 98:11376–11381.

Nyström, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology and Evolution 15:413–417.

Pandolfi, J., R. Bradbury, E. Sala, T. Hughes, K. Bjorndal, R. Cooke, D. Mcardle, L. McClenachan, M. Newman, G. Paredes, R. Warner, and J. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301: 955–958.

Pandolfi, J. M., and J. B. C. Jackson. 2006. Ecological persistence interrupted in Caribbean coral reefs. Ecology Letters 9:818–826.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Revue of Ecology, Evolution and Systematics 37:637–669.

Rayner, N. A., D. E. Parker, E. B. Horton, C. K. Folland, L. V. Alexander, D. P. Rowell, E. C. Kent, and A. Kaplan. 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. Journal of Geophysical Research 108:4407.

Rowan, R., N. Knowlton, A. Baker, and J. Jara. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388:265–269.

Santos, S. R., and M. A. Coffroth. 2003. Molecular genetic evidence that dinoflagellates belonging to the genus *Symbiodinium* freudenthal are haploid. Biology Bulletin 204:10–20.

Sheppard, C. 2003. Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 425:294–297.

Skelly, D. K., L. N. Joseph, H. P. Possingham, L. K. Freidenburg, T. J. Farrugia, M. T. Kinnison, and A. P. Hendry. 2007. Evolutionary responses to climate change. Conservation Biology 21:1353–1355.

Smith, S., and R. Buddemeier. 1992. Global change and coral-reef ecosystems. Annual Revue of Ecology and Systematics 23:89–118.

Sotka, E., and R. Thacker. 2005. Do some corals like it hot? Trends in Ecology and Evolution 20:59–62.

Stat, M., D. Carter, and O. Hoegh-Guldberg. 2006. The evolutionary history of *Symbiodinium* and scleractinian hosts: symbiosis, diversity, and the effect of climate change. Perspective in Plant Ecology, Evolution and Systematics 8: 23–43.

Szmant, A. M., and N. J. Gassman. 1990. The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. Coral Reefs 8: 217–224.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Turelli, M., and N. H. Barton. 1994. Genetic and statistical analyses of strong selection on polygenic traits: What, me normal? Genetics 138:913–941.

Ulstrup, K. E., R. Berkelmans, P. J. Ralph, and M. J. H. van Oppen. 2006. Variation in bleaching sensitivity of two coral species across a latitudinal gradient on the Great Barrier Reef: the role of zooxanthellae. Marine Ecology and Progress Series 314:135–148.

van Oppen, M. J. H., and R. D. Gates. 2006. Conservation genetics and the resilience of reef-building corals. Molecular Ecology 15:3863–3883.

Ware, J. 1997. The effect of global warming on coral reefs: acclimate or die. Proceedings of the 8th International Coral Reef Symposium 1:527–532.

Ware, J., D. Fautin, and R. Buddemeier. 1996. Patterns of coral bleaching: modeling the adaptive bleaching hypothesis. Ecological Modelling 84:199–214.

West, J., and R. Salm. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conservation Biology 17:956–967.

Wilkinson, C. 1999. Global and local threats to coral reef functioning and existence: review and predictions. Marine and Freshwater Research 50:867–878.

Wooldridge, S., T. Done, R. Berkelmans, R. Jones, and P. Marshall. 2005. Precursors for resilience in coral communities in a warming climate: a belief network approach. Marine Ecology Progress Series 295:157–169.

APPENDIX A

Further model derivation (*Ecological Archives* A019-001-A1).

APPENDIX B

Symbiont distribution across a latitudinal gradient (*Ecological Archives* A019-001-A2).

APPENDIX C

Test of model assumptions (*Ecological Archives* A019-001-A3).