

Factors Affecting the Evolution of Bleaching Resistance in Corals

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ABSTRACT: We present a mathematical model of coevolutionary interactions between partners in a coral-algae mutualistic symbiosis. Our goal is to better understand factors affecting the potential evolution of bleaching resistance in corals in response to increased average sea temperatures. We explore the evolutionary consequences of four factors: (i) trade-offs among fitness components, (ii) different proximate mechanisms of coral bleaching, (iii) the genetic determination of bleaching resistance, and (iv) the mode of sexual reproduction. We show that traits in mutualistic symbioses, such as thermal tolerance in corals, are potentially subject to novel kinds of evolutionary constraints and that these constraints are mediated by ecological dynamics. We also show that some proximate mechanisms of bleaching yield faster evolutionary responses to temperature stress and that the nature of interspecific control of bleaching resistance and the mode of sexual reproduction interact to strongly influence the rate of spread of resistance alleles. These qualitative theoretical results highlight important future directions for empirical research in order to quantify the potential for coral reefs to evolve resistance to thermal stress.

Keywords: adaptation, *Symbiodinium*, zooxanthellae, thermal stress, climate change, mathematical modeling.

Mutualistic symbioses are symbioses in which two or more interacting species cooperate for mutual benefit. Such associations often involve lifelong interactions between two species and are a common and important component of biodiversity (Bronstein et al. 2003; Moran 2006). Mutualistic interactions are key examples of interspecific cooperation and have been the focus of considerable theoretical and empirical research. Much of this research has been motivated by the perplexing question of why an organism incurs reproductive costs in order to benefit individuals of another species (Herre and West 1997; Bronstein 2001; Ferriere et al. 2002).

While there have been considerable recent advances in our understanding of the formation, maintenance, and breakdown of mutualistic associations (Hamilton 1970; Frank 1994; Doebeli and Knowlton 1998; West et al. 2002*a*, 2002*b*; Ferriere et al. 2002; Sachs and Simms 2006; Ferriere et al. 2007), the dynamics of trait evolution within mutualistic symbioses have received less attention. For example, some traits are emergent properties of interspecific interactions occurring within a symbiosis (Wade 2003, 2007; Whitham et al. 2006) and are determined, in part, by genes in more than one species. It is not well understood how these traits evolve in response to natural selection. The purpose of this article is to address this issue by deriving a simple model for the evolution of such "interspecific traits" in a mutualistic symbiosis. The model we present addresses the potential for the evolution of greater bleaching resistance in corals, in response to increased average sea temperatures. Our primary aim is to use these theoretical results to identify key areas for future empirical research on the evolution of bleaching resistance.

General Coral Biology

Corals are modular marine cnidarians that provide physical protection and certain nutrients for their symbiotic partners, zooxanthellae (genus *Symbiodinium*). The coral host, along with its associated zooxanthellae, is termed a holobiont. The unicellular dinoflagellate algae provide the corals with food in the form of photosynthetic products

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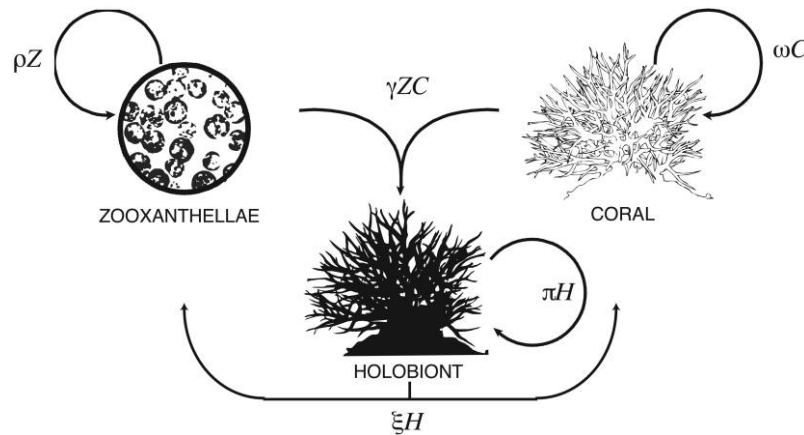


Figure 1: Flow diagram of the ecological model.

(Muscatine 1973; Trench 1979; Muller-Parker and D'Elia 1997). Although some data show that there is typically a single type of zooxanthella that associates with a particular coral species (Goulet 2006), there is some suggestion that these findings are a sampling artifact (Baker and Romanski 2007; but see Goulet 2007). More significantly, the recent use of more sensitive molecular techniques has demonstrated that multiple zooxanthellae genotypes are sometimes present at very low density (Mieog et al. 2007). Thus, more than one type of zooxanthella can associate with a single coral species (Blank and Trench 1985; Rowan 1998; LaJeunesse 2001; Knowlton and Rohwer 2003; Pillay et al. 2005; Berkelmans and van Oppen 2006; Garren et al. 2006) and sometimes even a single holobiont (Rowan and Knowlton 1995; Ulstrup and van Oppen 2003; Little et al. 2004; van Oppen et al. 2005).

Coral reefs are increasingly threatened by many human-induced environmental stresses, including chemical pollution, sedimentation, and increased sea temperatures (Brown 1997; Harvell et al. 1999; Hoegh-Guldberg 1999; Koop et al. 2001; Douglas 2003; Guinotte et al. 2003; Hughes et al. 2003; Bellwood et al. 2004; Jones et al. 2004; Ainsworth et al. 2007). When stressed, the holobiont will often bleach, a process by which zooxanthellae and/or photopigments are lost from the coral tissue, producing a skeletal white appearance (Hoegh-Guldberg and Smith 1989; Brown 1997). If the coral is repopulated by zooxanthellae soon enough after bleaching, it can reform a viable holobiont, but otherwise the coral will usually die (Glynn and D'Croz 1990).

Bleaching risk is not uniformly distributed among coral taxa (Buddemeier and Fautin 1993; Marshall and Baird 2000; Jones et al. 2004; Sotka and Thacker 2005), and variation also occurs at the within-species level (Berkelmans and van Oppen 2006; Ulstrup et al. 2006). Similarly,

some genotypes of zooxanthellae are more tolerant of high temperatures than others (Kinzie et al. 2001; Baker 2003; Tchernov et al. 2004; Berkelmans and van Oppen 2006; Warner et al. 2006). Together these findings suggest that the temperature at which holobionts bleach (i.e., their bleaching threshold) is an emergent property of the interaction between the coral and zooxanthellae genotypes. Evolutionary change in the coral, the zooxanthellae, or both can thereby, in principle, give rise to increased bleaching resistance (Ware et al. 1996).

Given that bleaching resistance is an emergent trait of two interacting species, how do we expect it to evolve in response to increased sea temperature? For example, does the fact that the trait arises from an intimate, mutualistic interaction constrain its evolution? How do various aspects of the coral-zooxanthellae relationship affect the rate and pattern of such adaptation? In this study, we explore these questions theoretically and ask how the spread of bleaching resistance alleles is affected by four aspects of the coral-zooxanthellae interaction: (i) the existence of trade-offs among different components of fitness in zooxanthellae and/or coral; (ii) the proximate mechanism of bleaching; (iii) the nature of the genetic determination of bleaching resistance; and (iv) the mode of sexual reproduction of the holobiont (e.g., reproduction with vertical vs. horizontal transmission of zooxanthellae).

The Model

The model is based on an underlying description of the ecology of coral-zooxanthellae holobiont dynamics (fig. 1). We first describe the ecological model before extending it to allow for multiple genotypes.

Ecological Dynamics

Most holobiont populations grow vegetatively throughout the year, with growth punctuated by an annual bout of sexual reproduction (Harrison et al. 1984; Szmant 1986; Harrison and Wallace 1990; de Graaf et al. 1999). The ecological model presented in this section focuses on the vegetative growth phase only and tracks the population sizes of three things: (i) the coral-zooxanthellae complex (holobiont), denoted H ; (ii) the coral host that is devoid of zooxanthellae (e.g., because of bleaching), denoted C ; and (iii) the free-living zooxanthellae population, denoted Z . Although bleached corals often contain low densities of zooxanthellae (Hoegh-Guldberg and Smith 1989; Jones 1997), we simplify the process by treating bleaching as an all-or-nothing phenomenon.

For mathematical convenience, the holobiont population is assumed to increase in biomass vegetatively in a logistic manner according to $rH(1 - H/K)$. Here r is the per unit growth rate when rare, and K is the biomass at which such vegetative growth ceases because of density-dependent effects. Biomass of the holobiont is also lost through death, and we incorporate this within the parameter r (i.e., r represents the net per unit growth rate). Such death corresponds to one potential mechanism of bleaching: increased sea temperature leads to increased in situ mortality of the zooxanthellae (Brown et al. 1995) and coral within the holobiont (Dunn et al. 2002, 2004) and, thus, to increased bleaching. The holobiont can also dissociate into free-living coral and zooxanthellae, at a per unit rate ξ . This is a second potential mechanism of bleaching: increased sea temperature leads to increased dissociation of holobiont and, thus, bleaching.

Finally, more holobiont can be formed through a reassociation of adult corals and zooxanthellae. The source of zooxanthellae that repopulate coral tissues after bleaching is poorly understood. Repopulation may come either from the residual zooxanthellae inside the host tissues or from an exogenous zooxanthella pool (Jones and Yellowlees 1997; Lewis and Coffroth 2004). In the text, we consider the case where reassociation occurs with free-living zooxanthellae only, but the model in appendix D includes the former process as well. In this case, the dynamics of the holobiont population are

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{K}\right) - \xi H + \gamma CZ. \quad (1a)$$

The coral is formed by dissociation of holobiont, and it is either lost through death or reassociated with zooxanthellae to form new holobiont. We use ω to denote the per unit rate of change of free-living coral (we assume $\omega < 0$), in which case we have

$$\frac{dC}{dt} = \xi H + \omega C - \gamma ZC. \quad (1b)$$

Zooxanthellae are also formed by dissociation of holobiont and are lost through either death or reassociation with coral. We suppose that zooxanthellae reproduce in the free-living state in a logistic manner as $\sigma Z(1 - Z/W)$, where σ is the net per unit growth rate when rare (i.e., it includes mortality) and W is the population size at which such reproduction ceases. This gives

$$\frac{dZ}{dt} = \xi H + \sigma Z\left(1 - \frac{Z}{W}\right) - \gamma ZC. \quad (1c)$$

Provided $r > \xi$, meaning that the holobiont population can increase in size when rare, there is a single nontrivial equilibrium that is biologically feasible.

Evolutionary Dynamics

For simplicity, we assume that each partner in the symbiosis contains a single diallelic locus that is potentially involved in determining the bleaching threshold of the holobiont. We leave the development of more genetically complex models for future work, once the behavior of this simple model is better understood. We also suppose that the coral species is haploid, although relaxing this assumption is unlikely to alter our qualitative conclusions. System (1) is then extended to allow for evolution by incorporating two genotypes for the coral (alleles 1 and 2) and two genotypes of the zooxanthellae (alleles A and B). Thus, there are four holobiont genotypes (A_1, A_2, B_1, B_2), two free-living coral genotypes (1, 2) and two free-living zooxanthellae genotypes (A, B).

We suppose that the mortality rate of coral, ω , depends on its genotype, and we write $\omega_2 = \omega$ and $\omega_1 = \omega + \Delta\omega$, where ω is the baseline mortality rate common to both genotypes and $\Delta\omega$ is the selection coefficient of allele 1 in free-living coral (i.e., the change in mortality rate caused by carrying allele 1 rather than allele 2). Similarly, we suppose that the parameter σ of the zooxanthellae reproduction depends on zooxanthellae genotype, and we write $\sigma_B = \sigma$ and $\sigma_A = \sigma + \Delta\sigma$, where $\Delta\sigma$ is the selection coefficient of allele A in the free-living zooxanthellae. Although there is some genetic evidence suggesting that zooxanthellae can undergo sexual reproduction (Baillie et al. 2000a, 2000b; LaJeunesse 2001; Santos et al. 2003), we ignore this possibility here.

The parameters ξ and r can be affected by the genotype of the coral and/or the zooxanthellae and represent the two different processes corresponding to bleaching. We say that allele 1 confers greater bleaching resistance (relative to allele

2) if it causes a holobiont containing such a coral genotype to have a higher r and/or a lower ξ . Similarly, allele A confers greater bleaching resistance (relative to allele B) if it causes a holobiont containing such a zooxanthellae genotype to have a higher r and/or a lower ξ .

To this end, we allow ξ and r to depend on both coral and zooxanthellae genotypes, and we make the following definitions: $x_{2B} = x$, $x_{1B} = x + \Delta x_1$, $x_{2A} = x + \Delta x_A$, and $x_{1A} = x + \Delta x_1 + \Delta x_A + \Delta x_e$, where x is the baseline value of parameter x for all genotypes, Δx_1 is the change in x due to carrying allele 1 (instead of 2) in the holobiont, Δx_A is the change in x due to carrying allele A (instead of B) in the holobiont, and Δx_e is the extra change in x that is due to interspecific epistatic interactions associated with carrying both alleles 1 and A .

By defining p_h and q_h as the frequency of alleles 1 and A in the holobiont population and q_z and p_c as the frequencies of allele A in the free-living zooxanthellae population and allele 1 in the free-living coral population, the evolutionary dynamics are then given by

$$\begin{aligned} \frac{dp_h}{dt} = & p_h(1 - p_h)s_1 + Ds_A \\ & + (1 - p_h)(D + p_h q_h)s_e + \frac{\gamma CZ}{H}(p_c - p_h), \end{aligned} \quad (2a)$$

$$\begin{aligned} \frac{dq_h}{dt} = & q_h(1 - q_h)s_A + Ds_1 \\ & + (1 - q_h)(D + q_h p_h)s_e + \frac{\gamma CZ}{H}(q_z - q_h), \end{aligned} \quad (2b)$$

$$\frac{dD}{dt} = F_1 D + F_2 s_e - \frac{\gamma CZ}{H}[D - (p_h - p_c)(q_h - q_z)], \quad (2c)$$

$$\frac{dp_c}{dt} = p_c(1 - p_c)\Delta\omega + \frac{H}{C}\phi_{h \rightarrow c}, \quad (2d)$$

$$\frac{dq_z}{dt} = q_z(1 - q_z)\Delta\sigma \left(1 - \frac{Z}{W}\right) + \frac{H}{Z}\phi_{h \rightarrow z} \quad (2e)$$

(eqq. [A2]), where $\phi_{h \rightarrow c}$ and $\phi_{h \rightarrow z}$ represent gene flow from the holobiont to the free-living coral and zooxanthellae populations, respectively (see eqq. [A3]). The variable D represents the interspecific linkage disequilibrium (ILD) between the two loci in the holobiont. It is a measure of the extent to which zooxanthellae and coral alleles are nonrandomly associated within the holobiont population (Wade 2003, 2007). The quantities F_1 and F_2 are defined in appendix A. The parameter S_1 is the selection coefficient for allele 1 in the holobiont and is defined as $s_1 = \Delta r_1(1 - H/K) - \Delta \xi_1$, s_A is the selection coefficient for allele A and is defined as $s_A = \Delta r_A(1 - H/K) - \Delta \xi_A$, and s_e is

the selection coefficient due to interspecific epistatic interactions and is defined as $s_e = \Delta r_e(1 - H/K) - \Delta \xi_e$. The final ingredient for the model is an accounting of how an annual bout of sexual reproduction affects the evolutionary dynamics, and this is detailed in appendix B.

Equations (2) will be used in “Results” to explore the evolutionary dynamics of bleaching resistance; however, each of these equations has a straightforward interpretation that is very helpful for gaining an intuitive understanding of the processes involved in the evolution of any trait in a coral-zooxanthellae symbiosis. Consider equation (2a) for the dynamics of the “resistant allele” 1 (eq. [2b] is analogous for the resistant allele A). In words, this can be written

$$\frac{dp_h}{dt} = \begin{matrix} \text{direct} & + & \text{indirect} & + & \text{epistatic} & + & \text{gene} \\ \text{selection} & & \text{selection} & & \text{selection} & & \text{flow} \end{matrix}. \quad (3)$$

The first term of equation (2a), $p_h(1 - p_h)s_1$, is the effect of direct selection for the 1 allele, and it is the product of the genetic variance in the allele $p_h(1 - p_h)$ and the selection coefficient for this allele, s_1 . Note from the above definition, $s_1 = \Delta r_1(1 - H/K) - \Delta \xi_1$, this selection coefficient is composed of two parts: its effect on dissociation rate $\Delta \xi_1$ and its effect on holobiont death rate $\Delta r_1(1 - H/K)$. The second term of equation (2a), Ds_A , is the effect of indirect selection. The quantity s_A is the selection coefficient of the A allele and is also composed of the above two parts (i.e., $s_A = \Delta r_A[1 - H/K] - \Delta \xi_A$). The 1 allele can change in frequency as a correlated response to selection on this A allele if there is nonzero interspecific linkage disequilibrium, D . For example, if corals containing allele 1 tend to be associated nonrandomly with zooxanthellae containing allele A in the holobiont population, then selection in favor of allele A will indirectly lead to an increased frequency of allele 1 as well. The third term in equation (2a) accounts for epistatic selection (e.g., if selection on allele 1 in the holobiont depends on the allele carried by the associated zooxanthellae). Finally, the fourth term in equation (2a) accounts for gene flow from the free-living coral to the coral in the holobiont population. The effect of this gene flow on the evolutionary dynamics of the 1 allele depends on the difference in allele frequency between these two populations, $p_c - p_h$, as well as the relative sizes of these populations (i.e., $\gamma CZ/H$).

Next, consider equation (2c) for the dynamics of the ILD. This can be interpreted as

$$\frac{dD}{dt} = \begin{matrix} \text{additive} & + & \text{epistatic} & + & \text{gene} \\ \text{selection} & & \text{selection} & & \text{flow} \end{matrix}. \quad (4)$$

The first term of equation (2c), $F_1 D$, describes how the ILD changes as a result of selection acting independently

on each of the two loci in the holobiont population (i.e., additive selection). The second term, $F_2 s_e$, describes how epistatic selection affects the dynamics of ILD. For example, if the dissociation rate of the holobiont is decreased (i.e., higher bleaching threshold) only when it carries both allele 1 in the coral and allele A in the zooxanthellae, then selection is epistatic and will result in the buildup of positive ILD (allele 1 will become statistically associated with allele A in the holobiont population). The third term accounts for the fact that gene flow from the coral and zooxanthellae populations to the holobiont can also affect ILD.

Finally, equation (2d) for the dynamics of allele 1 in the free-living coral population can be interpreted as

$$\frac{dp_c}{dt} = \text{direct selection} + \text{gene flow}. \quad (5)$$

The first term of equation (2d), $p_c(1 - p_c)\Delta\omega$, is the effect of direct selection on allele 1 in the free-living coral population, and it is the product of the genetic variance at this locus, $p_c(1 - p_c)$, and the selection coefficient for this allele, $\Delta\omega$. The second term of equation (2d) accounts for gene flow from the holobiont to free-living coral. Unlike in equation (2a) (and eq. [3]), there is no indirect selection or epistatic selection because the evolutionary dynamics of free-living coral do not depend on zooxanthellae or vice versa.

Results

In all results below, parameter values are chosen arbitrarily. The numerical results serve only to illustrate the general evolutionary processes involved, and these qualitative conclusions are not affected by the specific parameter values.

The Effect of Trade-Offs among Fitness Components

The simplest scenario to examine, and the one that most readily highlights the potential evolutionary consequences of trade-offs among fitness components, is where bleaching resistance is due to either the coral genotype or the zooxanthellae genotype (it suffices to consider only one of these cases since they are analogous). We consider the case where bleaching resistance is due to the zooxanthellae genotype alone (i.e., some zooxanthellae genotypes have a greater temperature tolerance than others). Note, however, that even if the mechanism of bleaching is primarily the dissociation of the holobiont (as opposed to death), this assumption need not imply that the zooxanthellae control the proximate cause of dissociation. For example, dissociation might occur as a result of the coral actively ejecting zooxanthellae that produce high levels of waste

metabolites, but if genotypes of zooxanthellae differ in their production of these metabolites (e.g., Kinzie et al. 2001; Rowan 2004; Tchernov et al. 2004; Berkelmans and van Oppen 2006), then it is still the zooxanthellae genotype that determines whether expulsion occurs.

When bleaching resistance is determined by the genotype of the zooxanthellae, we need to track only the dynamics of q_h and q_z (and $s_1 = 0$, $s_e = 0$). Thus, system (2) reduces to

$$\frac{dq_h}{dt} = q_h(1 - q_h)s_A + \frac{\gamma CZ}{H}(q_z - q_h), \quad (6a)$$

$$\begin{aligned} \frac{dq_z}{dt} = & q_z(1 - q_z)\Delta\sigma\left(1 - \frac{Z}{W}\right) \\ & + \frac{H}{Z}[(q_h - q_z)\xi + q_h(1 - q_z)\Delta\xi_A]. \end{aligned} \quad (6b)$$

Recall that the selection coefficient of the zooxanthellae allele A in the holobiont population is $s_A = \Delta r_A(1 - H/K) - \Delta\xi_A$ where $\Delta\xi_A < 0$ and $\Delta r_A > 0$ (allele A causes reduced dissociation and/or mortality in the holobiont). At ecological equilibrium, it can be shown that $H < K$, and therefore, s_A is always positive. This implies from equation (6a) that the allele causing a higher bleaching threshold (e.g., through a larger r and/or a smaller ξ) is always selectively favored within the holobiont population. An analogous situation holds if bleaching resistance is entirely determined by the coral genotype.

Interestingly, there is some evidence that temperature-resistant zooxanthellae genotypes tend also to result in slower vegetative growth of the holobiont (Little et al. 2004). Such trade-offs are encapsulated by the two terms making up the selection coefficient, s_A . Whether bleaching resistance is selectively favored then depends on the balance between these two components.

Even if bleaching resistance is selectively favored in the holobiont population, equations (6) illustrate that it can nevertheless fail to spread if the resistant allele A suffers a lower growth rate when the zooxanthellae are free living. In particular, if the selection coefficient of allele A is negative in the free-living zooxanthellae population (i.e., $\Delta\sigma[1 - Z/W] < 0$), then allele A will be selectively disfavored when in the free-living state. Gene flow between this state and the holobiont population will then hinder the evolution of bleaching resistance in the holobiont. This represents a novel kind of trade-off unique to such interspecific traits; selectively favored alleles in the interspecific complex can be selected against when the species containing them is on its own. Equations (6) further reveal that this type of trade-off is mediated by the ecological dynamics, because they determine the extent of gene flow

between the two subpopulations. Such trade-offs will hinder the evolution of bleaching resistance in the holobiont most strongly when the zooxanthellae population is relatively large (fig. 2).

The Effect of Different Proximate Mechanisms of Bleaching

The proximate mechanisms by which corals bleach and their relative importance are not well understood. While corals can die as a result of bleaching, not all do (Hoegh-Guldberg 1999). Conversely, zooxanthellae that are ejected from the host can be alive when they leave the host coral (Ralph et al. 2001). Therefore, we modeled two separate extremes for the proximate mechanism of bleaching. The first assumes that bleaching corresponds to the in situ death of the zooxanthellae and coral within the holobiont and does not involve the dissociation of living partners. The second assumes that bleaching corresponds to the dissociation of the living partners (who might subsequently die).

If bleaching-resistance alleles are selectively favored only in the holobiont population, then gene flow between the holobiont and the dissociated populations tends to retard the evolution of resistance because the free-living populations represent a reservoir for the disfavored allele. The magnitude of the evolutionary lag induced by this gene flow is larger when bleaching is due to dissociation than when it is due to death of the holobiont (app. C). Intuitively, when bleaching is due to dissociation, the selectively disfavored allele tends to become overrepresented in the free-living population by the very nature of it causing higher dissociation rates. It is then free to reassociate into the holobiont population, resulting in an evolutionary lag. When bleaching is due to death of the holobiont, the selectively disfavored allele is simply removed from the population.

The Effect of Genetic Determination of Bleaching Resistance

The evolutionary dynamics of bleaching resistance is strongly influenced by the nature of its genetic determination. There are three qualitatively different possibilities (Wade 2003, 2007): (i) Additive interspecific effects—the degree of bleaching resistance is the sum of the bleaching resistance conferred by the genotype of the zooxanthellae and the coral. (ii) Positive interspecific epistasis (IE)—the degree of bleaching resistance is especially strong if the holobiont carries beneficial alleles in both the coral and the zooxanthellae. An extreme case would be one whereby any bleaching resistance at all requires that beneficial alleles are carried in both species of the holobiont. (iii) Negative

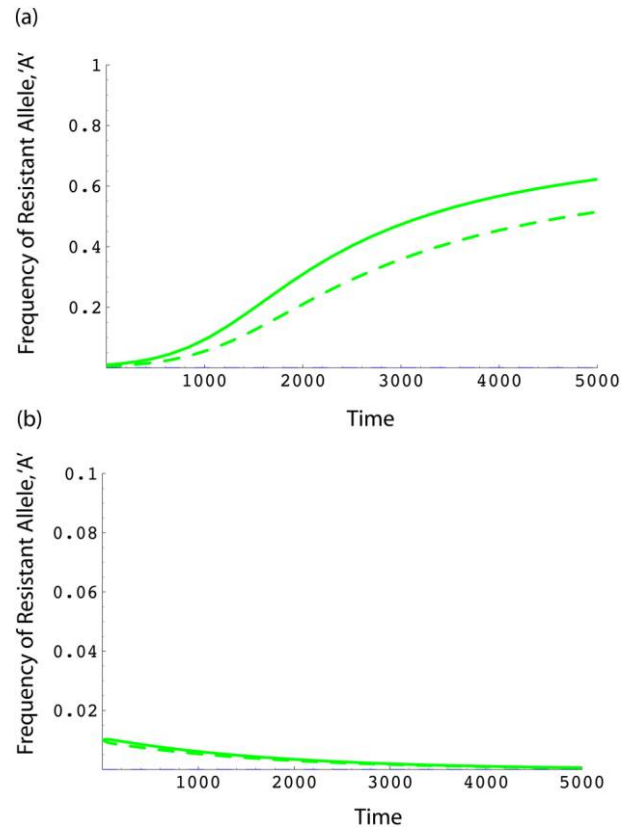


Figure 2: Evolution of bleaching resistance when resistance is conferred solely by the zooxanthellae genotype. Frequency of the resistant allele in the holobiont (*solid lines*) and free-living zooxanthellae (*dashed lines*) populations. Parameter values: $\theta = 0$, $\gamma = 0.01$, $\xi = 0.02$, $r = 0.1$, $\Delta r_A = 0.1$, $\sigma = 0.1$, $\Delta\sigma = 0.2$, $\omega = -1$, $\Delta\omega = 0$, $K = 1,000$. *a*, Free-living zooxanthellae population, and therefore gene flow, is relatively small ($W = 100$); resistance evolves. *b*, Free-living zooxanthellae population, and therefore gene flow, is relatively large ($W = 1,000$); no resistance evolves. Time shown in days.

IE—the degree of bleaching resistance is less than the sum of the effects of each beneficial allele when carried individually. An extreme case would be one whereby bleaching resistance requires a single beneficial allele in either species of the holobiont but where no bleaching resistance is conferred if both species of the holobiont carry the allele.

In the analysis below, we suppose that bleaching results from the death of the holobiont (i.e., $\Delta\xi_A = \Delta\xi_1 = \Delta\xi_e = 0$). At the end of this section we then discuss how the qualitative results are altered if bleaching is instead caused by dissociation. For simplicity, we also ignore any potential trade-offs between resistance and other traits of the free-living coral or zooxanthellae (i.e., $\Delta\omega = 0$, $\Delta\sigma = 0$). Under these assumptions, selection acts only in the holobiont population, with the free-living zooxanthellae and coral evolving solely as a result of gene flow

from the holobiont. Consequently, to further simplify the mathematical analysis, we ignore reverse gene flow from the free-living populations to the holobiont (numerical results are based on the complete model).

With the above assumptions and additive interspecific effects, equations (2) reduce to

$$\frac{dp_h}{dt} = p_h(1 - p_h)s_1 + Ds_A, \quad (7a)$$

$$\frac{dq_h}{dt} = q_h(1 - q_h)s_A + Ds_1, \quad (7b)$$

$$\frac{dD}{dt} = D[(1 - 2p_h)s_1 + (1 - 2q_h)s_A]. \quad (7c)$$

From equations (7) we see that selection is expected to increase the frequency of the beneficial allele in both species of the holobiont population, with the only evolutionary connection between the two arising from interspecific linkage disequilibrium. Equation (7c) reveals that any ILD will decay over time, however, and therefore the two parties in the holobiont will evolve independently of one another. Thus, the fact that the parties are symbiotic does not necessarily hinder the evolution of resistance (figs. 3a, 4). The rate of spread of resistance alleles in the two parties of the holobiont can still differ, however, even if they both confer the same amount of resistance. For example, this can occur if the total population size of one species (including the free-living state) is larger than the other (fig. 3a).

If there is IE, equations (2) reduce to

$$\begin{aligned} \frac{dp_h}{dt} = & p_h(1 - p_h)s_1 + Ds_A \\ & + (1 - p_h)(D + p_hq_h)s_e, \end{aligned} \quad (8a)$$

$$\begin{aligned} \frac{dq_h}{dt} = & q_h(1 - q_h)s_A + Ds_1 \\ & + (1 - q_h)(D + q_hp_h)s_e, \end{aligned} \quad (8b)$$

$$\begin{aligned} \frac{dD}{dt} = & D[(1 - 2p_h)s_1 + (1 - 2q_h)s_A] \\ & + [p_h(1 - p_h)q_h(1 - q_h) \\ & + D(1 - p_h - q_h) - D^2]s_e. \end{aligned} \quad (8c)$$

Assuming that A1 holobionts have the same level of bleaching resistance as A1 holobionts in the case of additive effects, resistant alleles spread more slowly initially but then increase more quickly, as compared to the additive case (fig. 3b vs. 3a). At the beginning of its spread, each allele is only weakly selected for independently be-

cause the main effect of carrying A or 1 comes when both are carried together (i.e., s_1 and s_A are small). Over time, positive IE causes positive ILD to build up (fig. 3b), accelerating the evolution of bleaching resistance due to indirect selection in each species (the second terms in eqq. [8a], [8b]). In other words, once D has built up to positive values, allele 1 will increase in frequency both because of selection in favor of this allele directly and because holobionts carrying this allele also tend to carry allele A in their associated zooxanthellae, and allele A is also favored by selection. Thus, positive IE initially hinders but later enhances the rate of resistance evolution (fig. 4).

Finally, if bleaching resistance is due to negative IE, then the resistant alleles spread more quickly initially but eventually slow down, as compared to the additive case (fig. 3c vs. 3a). At the beginning of its spread, each allele is very strongly selected because the main benefits of resistance occur when the holobiont carries a single beneficial allele (as will be the case when the alleles are rare). Over time, however, negative ILD builds up, eventually hindering the further spread of resistance through a negative indirect component of selection. Thus, all else equal, we expect fast but decelerating evolution of bleaching resistance compared with additive effects (fig. 4).

The Effect of Mode of Sexual Reproduction

The mode of sexual reproduction influences the evolution of bleaching resistance in a way that interacts with the genetic determination. This is easiest to understand by considering the two effects of sex. Sex with vertical transmission simply decreases ILD. Sex with horizontal transmission decreases ILD more strongly (app. B), and it also induces one-way gene flow from the free-living zooxanthellae population to the holobiont. The significance of these processes on the rate of spread of bleaching resistance is greatest when newly recruited holobionts make up a large fraction of the standing holobiont population (i.e., when it is large), as would be the case in species that breed multiple times per year.

When genetic effects are additive, no ILD arises (except for a negligible amount due to gene flow), and therefore, sex with vertical transmission has no effect on the rate of evolution. Sex with horizontal transmission, however, slows the spread of resistance because of gene flow (fig. 5a).

When there is positive IE, positive ILD builds up (fig. 3b), resulting in a statistical overabundance of the most resistant A1 holobiont. Sex with vertical transmission reduces this ILD by breaking down some of these beneficial A1 holobionts, and this slows the spread of resistance. Sex with horizontal transmission has an even stronger effect on decreasing ILD and therefore slows the spread of re-

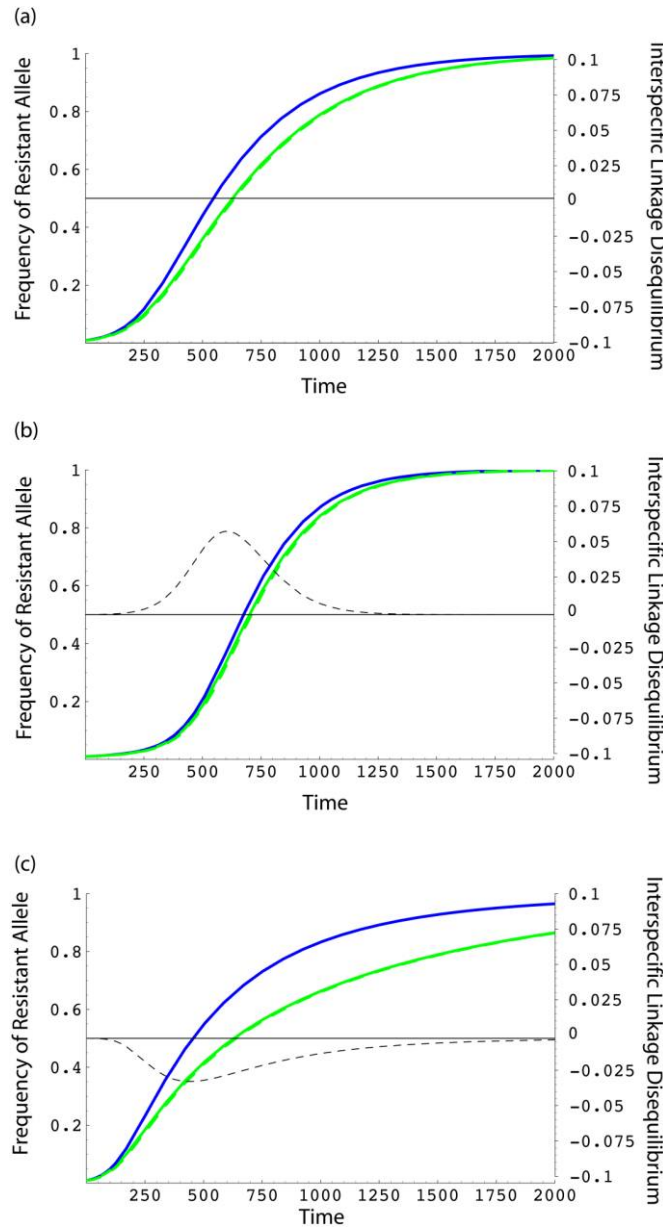


Figure 3: Effect of genetic determination on spread of resistance alleles. Green lines = frequency of allele A in zooxanthellae (solid lines = holobiont, dashed lines = free living). Blue lines = frequency of allele 1 in coral (solid lines = holobiont, dashed lines = free living). Black dashed lines = interspecific linkage disequilibrium. Parameter values: $\theta = 0$, $\gamma = 0.01$, $\xi = 0.02$, $r = 0.1$, $\sigma = 0.1$, $\Delta\sigma = 0$, $\omega = -1$, $\Delta\omega = 0$, $K = 1,000$, $W = 100$. a, Additive genetics effects, $\Delta r_A = 0.15$, $\Delta r_1 = 0.15$, $\Delta r_e = 0$. b, Positive interspecific epistasis, $\Delta r_A = 0.05$, $\Delta r_1 = 0.05$, $\Delta r_e = 0.2$. c, Negative interspecific epistasis, $\Delta r_A = 0.25$, $\Delta r_1 = 0.25$, $\Delta r_e = -0.2$. Time shown in days.

sistance even more. This is further exacerbated by the resulting gene flow from the zooxanthellae to the holobiont population (fig. 5b).

When there is negative IE, negative ILD builds up (fig. 3c), resulting in a statistical rarity of the most resistant A1 holobiont. Sex with vertical transmission reduces the mag-

nitude of this ILD by generating more of these A1 holobionts and thus enhances the rate of spread of resistance (fig. 5c). Sex with horizontal transmission has an even stronger effect on decreasing the magnitude of ILD, but this positive effect on the rate of spread of resistance is counteracted by the negative effect of gene flow. The net

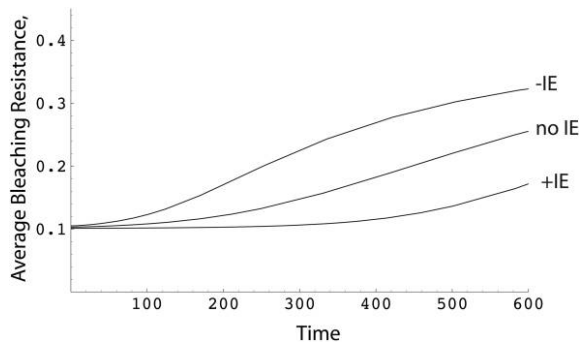


Figure 4: Effect of genetic determination on rate of evolutionary increase of average level of bleaching resistance, as measured by the average value of r in the holobiont population. Parameter values are as in figure 3. Curves represent positive interspecific epistasis, negative interspecific epistasis, and no interspecific epistasis (i.e., additivity). Time shown in days.

effect depends on the relative magnitude of these opposing factors (fig. 5c).

Most of the above results remain qualitatively unchanged if bleaching is due to dissociation rather than death of the holobiont, although there is one important exception. When holobiont genotype affects dissociation rate, allele frequencies in the free and holobiont populations will typically differ substantially, with the free populations tending to be made up of alleles causing the highest dissociation rates. This difference in allele frequency generates positive ILD (third term in eq. [2c]), even with additive interactions. As a result, if bleaching is caused by dissociation, then either type of sex reduces the rate of spread of resistance when there are additive genetic effects.

Discussion

The above model is meant to be a qualitative guide to important factors influencing the evolution of bleaching resistance in corals. We have examined the effects of four factors in isolation in order to better understand their consequences, but in reality these might combine in various ways depending on the species in question. The results presented here can be used to build an intuition for how the spread of resistance alleles is likely to be altered when more than one factor is operating simultaneously.

Perhaps surprisingly, the fact that bleaching resistance is an emergent trait of two intimately interacting, mutualistic species need not, in itself, hinder the evolution of resistance (fig. 3). There is, however, the potential for novel kinds of constraints to arise from the fact that such emergent traits are subject to two different kinds of selection. First, selection acts on the genes in each species that code for the trait when this trait is expressed in the interacting

complex of the two species (i.e., the holobiont). Second, selection can also act on these genes through their effects on other fitness components when each species exists on its own. The extent to which such effects constrain the evolution of holobiont traits depends on the amount of gene flow between the two different contexts in which each species can find itself. This gene flow, in turn, depends on

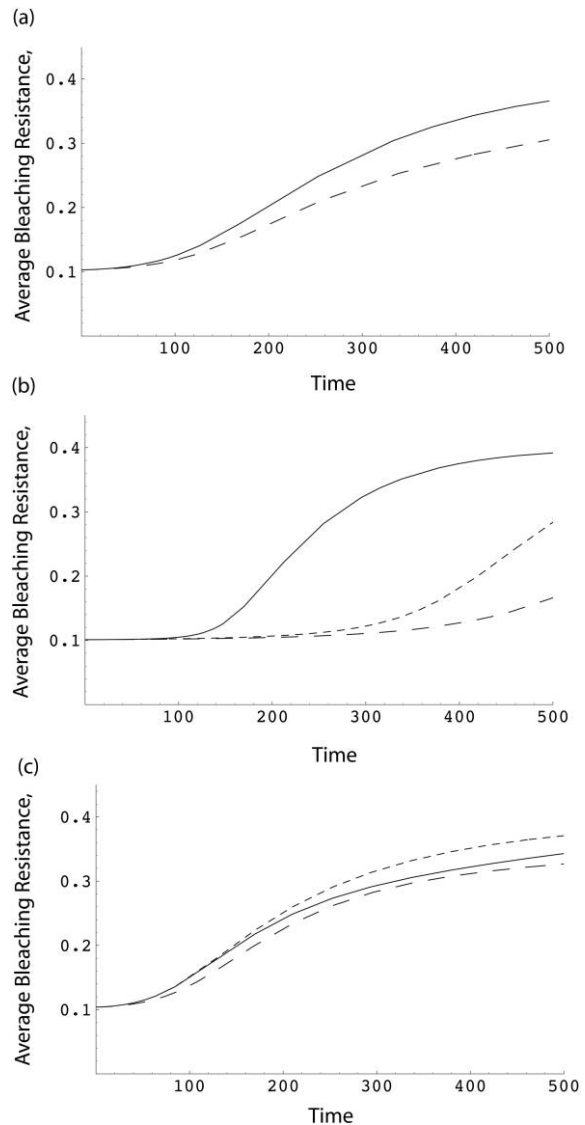


Figure 5: Effect of mode of sexual reproduction on rate of evolutionary increase of average level of bleaching resistance, as measured by the average value of r in the holobiont population. Parameter values as in figure 3 except $W = 1$ and $\theta = 1$ when sexual reproduction is occurring. *Solid line* = no sex. *Short-dashed line* = sex with vertical transmission. *Long-dashed line* = sex with horizontal transmission. *a*, No interspecific epistasis (i.e., additivity); *b*, positive interspecific epistasis; *c*, negative interspecific epistasis. Time shown in days.

the ecological dynamics of both species and how they associate with one another (fig. 2).

We considered two extreme proximate mechanisms of bleaching: bleaching that results from stress-induced death of the holobiont and bleaching that results from stress-induced dissociation. All else equal, we find that bleaching resistance alleles spread more quickly when bleaching results from holobiont death, because the death of the holobiont is more efficient at removing the disfavored allele from the population.

Our results also clearly demonstrate that different qualitative patterns of resistance evolution are expected, depending on how the genotypes of coral and zooxanthellae combine to give rise to resistance. Additive interactions result in both parties of the symbiosis evolving, to a large extent, independently of one another. Positive epistatic interactions between the two genomes yield a delayed and more punctuated pattern of evolution. Conversely, negative epistatic interactions yield a faster but decelerating pattern of allelic spread. Interestingly, under severe negative interspecific epistasis (e.g., having two resistance alleles is worse than having only one), a bistability can occur whereby the holobiont population reaches fixation of either the beneficial coral allele 1 or the beneficial zooxanthellae allele *A* (T. Day, unpublished results). It would be interesting to explore the spatial evolutionary dynamics of such systems, since different spatial locations can fix for different resistance alleles, resulting in “hybrid zones” (in terms of the two genomes making up the holobiont) in which holobionts have low resistance.

The mode of sexual reproduction also interacts with the trait’s genetic determination to influence the spread of resistance alleles. In general, sexual reproduction with either vertical or horizontal transmission tends to reduce the rate of spread of resistance alleles (or leave it unchanged) when genetic effects between species are either additive or display positive epistasis. If there is negative IE, however, sexual reproduction with vertical transmission enhances the rate of spread of resistance. This finding is analogous to results for sexual reproduction in a single species, where sex can be selectively beneficial if there is negative epistasis between loci (Kimura and Maruyama 1966; Kondrashov 1982, 1988, 1993). The results for sex with vertical transmission seen here arise from exactly the same mechanism, but in this case it is acting on two loci in different, associated genomes. Sexual reproduction with horizontal transmission, however, can enhance or retard the rate of spread of resistance. Such reproduction reduces interspecific linkage disequilibrium, which tends to enhance the spread of resistance when there is negative IE, but it also introduces gene flow from free-living zooxanthellae to the holobiont, which tends to retard such spread.

Implications for Future Research

Our modeling has identified some areas that require further empirical study if we are to understand evolutionary adaptation in corals in response to increased temperature. First, it is critical that we determine the extent to which reassociation of coral occurs with free-living zooxanthellae versus zooxanthellae from within the holobiont population. This will determine the kinds of evolutionary trade-offs that are possible, and it will also determine the extent to which different holobiont populations are connected by gene flow. One approach is to set up monitoring programs of the zooxanthella communities harbored by individual coral colonies (e.g., Goulet and Coffroth 2003; Thornhill 2006a, 2006b), using molecular methods with high sensitivity (Ulstrup and van Oppen 2003; Mieog et al. 2007) and resolving power (e.g., Santos et al. 2003; Magalon et al. 2006).

Second, accurate evolutionary predictions require information about the extent to which there are trade-offs among fitness components. Such trade-offs can be species specific (D. Abrego, K. E. Ulstrup, B. L. Willis, and M. J. H. van Oppen, unpublished manuscript) and can occur among fitness components within the holobiont itself (Little et al. 2004) or between the holobiont and each species when living on its own. To date, the latter type of trade-off has received virtually no attention (Ralph et al. 2001; Bhagooli and Hidaka 2003). Similarly, it is not well understood whether bleaching corresponds mainly to the in situ death of zooxanthellae and coral within the holobiont or whether it corresponds to the dissociation of the two living partners (Gates et al. 1992; Brown et al. 1995; Brown 1997; Dunn et al. 2002, 2004). Third, the genetic determination of bleaching resistance plays a critical role in the qualitative evolutionary dynamics. Determining the genetic control of bleaching will require studies of the localization of both host and symbiont gene products associated with cell death and symbiont release mechanisms, as well as cross-infection experiments, where multiple genotypes of coral are cross-infected with multiple genotypes of zooxanthellae and the holobiont’s thermal tolerance is measured. Such experiments would also provide critical information on epistatic interactions between the two partners.

Finally, although the mode of sexual reproduction is known for many species of coral, this information in itself is insufficient to make predictions about the rate of evolution of bleaching resistance. We require more information on the genetics of resistance from the kinds of experiments mentioned above, as well as information about the extent to which sexual reproduction contributes to the recruitment of any given standing holobiont population. Information about where these sexually produced

recruits come from, in terms of their selective environment, would also be very valuable.

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APPENDIX A

Derivation of the Eco-evolutionary Model

Given haploid genetics and two genotypes per species, along with the assumptions in the text, system (1) can be expanded to contain a total of eight equations: an equation for the numbers of each of the two genotypes of each species when free living and an equation for each of the four genotypes of holobiont. Using subscripts A and B for the zooxanthellae genotypes and 1 and 2 for the coral genotypes, we have

$$\begin{aligned}\frac{dH_{ij}}{dt} &= \pi_{ij}H_{ij} - \xi_{ij}H_{ij} + \gamma_{ij}C_iZ_j, \\ \frac{dC_i}{dt} &= \xi_{iA}H_{iA} + \xi_{iB}H_{iB} + \omega_iC_i - \gamma_{iA}C_iZ_A - \gamma_{iB}C_iZ_B, \\ \frac{dZ_j}{dt} &= \rho_jZ_j + \xi_{1j}H_{1j} + \xi_{2j}H_{2j} - \gamma_{1j}C_1Z_j - \gamma_{2j}C_2Z_j,\end{aligned}\tag{A1}$$

where $i \in \{1, 2\}$, $j \in \{A, B\}$, and we have simplified notation by writing $\pi_{ij} \equiv r_{ij}(1 - H/K)$ and $\rho_j \equiv \sigma_j(1 - Z/W)$, where H and Z are taken to be the total numbers $H = \sum_{ij}H_{ij}$ and $Z = \sum_jZ_j$, respectively.

In order to better conceptualize the evolutionary dynamics and how these are tied to the ecological dynamics, it is helpful to rewrite system (A1) in terms of new variables representing the total population size of each the two species and the holobiont (i.e., H , Z , and C , where $C = \sum_iC_i$) and the five variables required to track the evolutionary dynamics (as described in the text). Assuming that the association rates γ_{ij} are independent of genotype, we obtain

$$\frac{dp_h}{dt} = p_h(1 - p_h)(\Delta\pi_1 - \Delta\xi_1) + D(\Delta\pi_A - \Delta\xi_A) + (1 - p_h)(D + p_hq_h)(\Delta\pi_\varepsilon - \Delta\xi_\varepsilon) + \frac{\gamma CZ}{H}(p_c - p_h),\tag{A2a}$$

$$\frac{dq_h}{dt} = q_h(1 - q_h)(\Delta\pi_A - \Delta\xi_A) + D(\Delta\pi_1 - \Delta\xi_1) + (1 - q_h)(D + q_hp_h)(\Delta\pi_\varepsilon - \Delta\xi_\varepsilon) + \frac{\gamma CZ}{H}(q_z - q_h),\tag{A2b}$$

$$\begin{aligned}\frac{dD}{dt} &= D[(1 - 2p_h)(\Delta\pi_1 - \Delta\xi_1) + (1 - 2q_h)(\Delta\pi_A - \Delta\xi_A)] \\ &\quad + [p_h(1 - p_h)q_h(1 - q_h) + D(1 - p_h - q_h) - D^2](\Delta\pi_\varepsilon - \Delta\xi_\varepsilon) - \frac{\gamma CZ}{H}[D - (p_h - p_c)(q_h - q_z)],\end{aligned}\tag{A2c}$$

$$\frac{dp_c}{dt} = p_c(1 - p_c)\Delta\omega + \frac{H}{C}\phi_{h \rightarrow c},\tag{A2d}$$

$$\frac{dq_z}{dt} = q_z(1 - q_z)\Delta\rho + \frac{H}{Z}\phi_{h \rightarrow z},\tag{A2e}$$

where

$$\phi_{h \rightarrow c} = (p_h - p_c)\xi + p_h(1 - p_c)\Delta\xi_1 + [D + q_h(p_h - p_c)]\Delta\xi_A + (1 - p_c)(D + p_h q_h)\Delta\xi_e, \quad (\text{A3a})$$

$$\phi_{h \rightarrow z} = (q_h - q_z)\xi + q_h(1 - q_z)\Delta\xi_A + [D + p_h(q_h - q_z)]\Delta\xi_1 + (1 - q_z)(D + p_h q_h)\Delta\xi_e. \quad (\text{A3b})$$

The ecological equations are given by

$$\frac{dH}{dt} = \bar{r}H \left(1 - \frac{H}{K}\right) - \bar{\xi}H + \gamma CZ, \quad (\text{A4a})$$

$$\frac{dC}{dt} = \bar{\xi}H + \bar{\omega}C - \gamma ZC, \quad (\text{A4b})$$

$$\frac{dZ}{dt} = \bar{\xi}H + \bar{\sigma}Z \left(1 - \frac{Z}{W}\right) - \gamma ZC, \quad (\text{A4c})$$

where an overbar denotes the expectation over the relevant population. Specifically, $\bar{\xi} = \xi + p_h \Delta\xi_1 + q_h \Delta\xi_A + (D + p_h q_h \Delta\xi_e)$, $\bar{r} = r + p_h \Delta r_1 + q_h \Delta r_A + (D + p_h q_h \Delta r_e)$, and $\bar{\sigma} = \sigma + q_z \Delta \sigma$, $\bar{\omega} = \omega + p_c \Delta \omega$.

APPENDIX B

The Effect of Sexual Reproduction

A bout of sexual reproduction causes a reassortment of coral and zooxanthellae genotypes within the holobiont population, and we need to determine how these different modes of reproduction affect this reassortment. Intuitively, we would expect sexual reproduction with horizontal transmission to leave the allele frequency of the coral within the holobiont population unchanged but to reduce the interspecific linkage disequilibrium (ILD) and to potentially change the allele frequency of the zooxanthellae within the holobiont population. On the other hand, a bout of sexual reproduction with vertical transmission should leave both coral and zooxanthellae allele frequencies unchanged and simply reduce the linkage disequilibrium.

Sex with Horizontal Transmission

Haploid coral is assumed to produce male and female gametes, which then unite and undergo meiosis to form haploid coral offspring. A fraction θ of the holobiont population is then replaced by these offspring, but this leaves the allele frequency p_h unchanged. These newly settled offspring then acquire zooxanthellae from the free-living population (in which the frequency of allele A is q_z). Therefore, the frequency of allele A in the holobiont population after the acquisition of zooxanthellae is $(1 - \theta)q_h + \theta q_z$. Similarly, the newly formed holobionts will have an interspecific linkage disequilibrium of zero, resulting in the overall disequilibrium of the holobiont population being $(1 - \theta)D + \theta 0 = (1 - \theta)D$.

Sex with Vertical Transmission

This case is slightly more complex. After the production of gametes there are four types of female gamete ($A1, A2, B1, B2$) and two types of male gametes (1, 2). Thus, there are eight possible matings, each of which then undergoes meiosis to produce haploid holobionts. One can add up the frequency of each of the four genotypes in the newly recruited holobionts and determine the overall frequency of each genotype as $(1 - \theta)x_{\text{old}} + \theta x_{\text{new}}$, where x_{old} and x_{new} are the frequencies of a particular genotype in the standing holobiont population and the newly recruited holobionts, respectively. These frequencies can then be converted back into the variables p_h , q_h , and D to show that sex causes no change in the allele frequencies in the holobiont population, but it reduces interspecific linkage disequilibrium from D to $(1 - \theta/2)D$.

In all numerical results, we simplify the calculations by assuming that there is a small but continuous rate of sexual reproduction over time. Thus, we append the terms $\theta(q_z - q_h)$ and $-\theta D$ to equations (2b) and (2c), respectively, for the change in allele frequency and ILD due to sex with horizontal transmission, or alternatively, we append the term

$-\theta D/2$ to equation (2c) for the case of sex with vertical transmission. This also allows one to use the model for species that breed more often than once per year (e.g., lunar breeders) simply by increasing this value of θ .

APPENDIX C

Analysis of Dissociation versus Death

If bleaching is due to the in situ mortality of the coral and zooxanthellae, without involving dissociation of the live partners, then mathematically we have $\Delta\xi_i = 0$, $s_i = \Delta r_i(1 - H/K)$, $\phi_{h \rightarrow c} = (p_h - p_c)\xi$, and $\phi_{h \rightarrow z} = (q_h - q_z)\xi$ in equations (2). On the other hand, if bleaching is due to dissociation of the zooxanthellae and coral, then mathematically we have $\Delta r_i = 0$, $s_i = -\Delta\xi_i$, $\phi_{h \rightarrow c} = (p_h - p_c)\xi + p_h(1 - p_c)\Delta\xi_1 + [D + q_h(p_h - p_c)]\Delta\xi_A + (1 - p_c)(D + p_h q_h)\Delta\xi_e$, and $\phi_{h \rightarrow z} = (q_h - q_z)\xi + q_h(1 - q_z)\Delta\xi_A + [D + p_h(q_h - q_z)]\Delta\xi_1 + (1 - q_z)(D + p_h q_h)\Delta\xi_e$ in equations (2). Although the form of the selection coefficients differs between these two cases, the only qualitative difference from the standpoint of the evolutionary dynamics is in the terms describing gene flow from the holobiont population to both free-living populations. Specifically, both $\phi_{h \rightarrow z}$ and $\phi_{h \rightarrow c}$ are $\Delta\xi_i$ smaller in the case of dissociation than in the case of mortality (because they are negative). Therefore, the evolutionary increase of the resistant allele in the free-living population will be slower in the case of dissociation (since this gene flow is the only reason it increases at all).

As a simple example, suppose that bleaching resistance is entirely due to the zooxanthellae genotype, so that $\Delta s_1 = 0$. In this case, for death, equations (2) reduce to

$$\frac{dq_h}{dt} = q_h(1 - q_h)s_A + \frac{\gamma CZ}{H}(q_z - q_h), \quad (C1a)$$

$$\frac{dq_z}{dt} = q_z(1 - q_z)\Delta\sigma\left(1 - \frac{Z}{W}\right) + \frac{H}{Z}(q_h - q_z)\xi, \quad (C1b)$$

whereas for dissociation, they reduce to

$$\frac{dq_h}{dt} = q_h(1 - q_h)s_A + \frac{\gamma CZ}{H}(q_z - q_h), \quad (C2a)$$

$$\frac{dq_z}{dt} = q_z(1 - q_z)\Delta\sigma\left(1 - \frac{Z}{W}\right) + \frac{H}{Z}[(q_h - q_z)\xi + q_h(1 - q_z)\Delta\xi_A]. \quad (C2b)$$

As can be seen from a comparison of equations (C1) and (C2), dissociation results in an extra term appearing in the effect of gene flow on the dynamics of the free-living zooxanthellae (eq. [C2b]). This results in the evolutionary response in the free-living zooxanthellae having an increased lag, as it tends to accumulate the nonresistant genotypes from dissociation.

APPENDIX D

An Alternative Model of Reassociation

The model of the text assumes that when a coral reassociates to form more holobiont, it does so with free-living zooxanthellae. More generally, it might reassociate with zooxanthellae already in the holobiont population as well. Model (1) can be extended to allow for this process, yielding

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{K}\right) - \xi H + \gamma CZ + \kappa HC, \quad (D1a)$$

$$\frac{dC}{dt} = \xi H + \omega C - \gamma ZC - \kappa HC, \quad (D1b)$$

$$\frac{dZ}{dt} = \xi H + \sigma Z\left(1 - \frac{Z}{W}\right) - \gamma ZC. \quad (D1c)$$

There parameter κ is the “transmission rate” of zooxanthellae from holobiont to coral. Model (D1) makes the simplifying assumption that transmission of zooxanthellae from the holobiont to a coral does not have a significant effect on the zooxanthellae density in the holobiont. A derivation similar to that in appendix A can then be followed to obtain the following equations analogous to equations (2) for this model:

$$\frac{dp_h}{dt} = p_h(1 - p_h)s_1 + Ds_A + (1 - p_h)(D + p_h q_h)s_e + \frac{\gamma CZ}{H}(p_c - p_h) + \kappa C(p_c - p_h), \quad (D2a)$$

$$\frac{dq_h}{dt} = q_h(1 - q_h)s_A + Ds_1 + (1 - q_h)(D + q_h p_h)s_e + \frac{\gamma CZ}{H}(q_z - q_h), \quad (D2b)$$

$$\frac{dD}{dt} = F_1 D + F_2 s_e - \frac{\gamma CZ}{H}[D - (p_h - p_c)(q_h - q_z)] - \kappa CD, \quad (D2c)$$

$$\frac{dp_c}{dt} = p_c(1 - p_c)\Delta\omega + \frac{H}{C}\phi_{h \rightarrow c}, \quad (D2d)$$

$$\frac{dq_z}{dt} = q_z(1 - q_z)\Delta\sigma\left(1 - \frac{Z}{W}\right) + \frac{H}{Z}\phi_{h \rightarrow z}. \quad (D2e)$$

As a special case of interest, suppose all reassociation occurs from within the holobiont population, in which case $\gamma = 0$. Model (D2) then reduces to

$$\frac{dp_h}{dt} = p_h(1 - p_h)s_1 + Ds_A + (1 - p_h)(D + p_h q_h)s_e + \kappa C(p_c - p_h), \quad (D3a)$$

$$\frac{dq_h}{dt} = q_h(1 - q_h)s_A + Ds_1 + (1 - q_h)(D + q_h p_h)s_e, \quad (D3b)$$

$$\frac{dD}{dt} = F_1 D + F_2 s_e - \kappa CD, \quad (D3c)$$

$$\frac{dp_c}{dt} = p_c(1 - p_c)\Delta\omega + \frac{H}{C}\phi_{h \rightarrow c}, \quad (D3d)$$

$$\frac{dq_z}{dt} = q_z(1 - q_z)\Delta\sigma\left(1 - \frac{Z}{W}\right) + \frac{H}{Z}\phi_{h \rightarrow z}. \quad (D3e)$$

Space constraints prevent a complete analysis of this alternative model here, but the form of equations (D3) allows us to deduce the likely consequences of this alternative assumption about reassociation. In particular, the main qualitative difference between model (2) and model (D3) is that the evolutionary dynamics of the free zooxanthellae population in model (D3) no longer affect the evolutionary dynamics of the zooxanthellae in the holobiont population (cf. eq. [2b], [D3b]). The reason is that there is no longer any gene flow from the free zooxanthellae population to the holobiont (aside from that induced by horizontal sexual reproduction). We leave the more complete analysis of model (D3) to future work, but the following predictions can be deduced for each of the four questions addressed in the main text.

The Effect of Trade-Offs among Fitness Components

The conclusions of this section in the main text should continue to hold if bleaching resistance is due to coral genotype. If bleaching resistance is due to zooxanthellae genotype, however, then we no longer expect a trade-off between holobiont and free-living zooxanthellae to constrain the evolution of bleaching resistance. In such a case, there is no longer any gene flow from the free-living zooxanthellae population to the holobiont (aside from a small amount occurring with horizontal sexual reproduction).

The Effect of Different Proximate Mechanisms of Bleaching

The conclusions of this section in the main text continue to hold provided that bleaching resistance is conferred by the coral genotype. If resistance is due to zooxanthellae genotype, then we no longer expect evolutionary differences between death and dissociation, since there is no longer any gene flow from the free-living zooxanthellae population to the holobiont.

The Effect of Genetic Determination of Bleaching Resistance

Most conclusions of this section in the main text continue to hold, except for the effect of the size of the free-living zooxanthellae on the rate of spread of resistance alleles (it is not expected to have any evolutionary consequence in the case where coral reassociation occurs with zooxanthellae from within the holobiont population).

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