

# Can a thermally tolerant symbiont improve the future of Caribbean coral reefs?

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## Abstract

The detrimental effect of climate change induced bleaching on Caribbean coral reefs has been widely documented in recent decades. Several studies have suggested that increases in the abundance of thermally tolerant endosymbionts may ameliorate the effect of climate change on reefs. Symbionts that confer tolerance to temperature also reduce the growth rate of their coral host. Here, we show, using a spatial ecosystem model, that an increment in the abundance of a thermally tolerant endosymbiont (D1a) is unlikely to ensure the persistence of Caribbean reefs, or to reduce their rate of decline, due to the concomitant reduction in growth rate under current thermal stress predictive scenarios. Furthermore, our results suggest that given the documented vital rates of D1a-dominated corals, increasing dominance of D1a in coral hosts may have a detrimental effect by reducing the resilience of Caribbean reefs, and preventing their long-term recovery. This is because Caribbean ecosystems appear to be highly sensitive to changes in the somatic growth rate of corals. Alternative outcomes might be expected in systems with different community-level dynamics such as reefs in the Indo-Pacific, where the ecological costs of reduced growth rate might be far smaller.

**Keywords:** climate change, coral reefs, symbiosis, thermal tolerance

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## Introduction

Determining the ecosystem response and its ability to adapt to human-driven changes in climate can be challenging, largely because of the complex web of biological and biophysical relationships present in most ecosystems (Bothwell *et al.*, 1994; Portner *et al.*, 2005). In some instances, both ecological and evolutionary mechanisms can ameliorate the potential effect of climate change (Portner *et al.*, 2005; Bennett & Lenski, 2007). Nevertheless, it can be difficult to extrapolate from the acclimatory and adaptative capabilities of organisms to entire ecosystems (Portner *et al.*, 2006). In particular, when the trade-off, or cost associated with the adaptive or acclimatory response, is high, interpreting the ecosystem response becomes more difficult (Stevenson & Bryant, 2000; Portner *et al.*, 2005). Commonly, the trade-off in question refers to the reduction in the efficiency of a particular physiological character as a consequence of the allocation of additional energy for the improvement of the efficiency of a different character (Stevenson & Bryant, 2000; Portner *et al.*, 2006; Jones & Berkelmans, 2010).

Coral reefs are one of the first ecosystems to exhibit effects of climate change (Scavia *et al.*, 2002). Caribbean

reefs, in particular, have shown a dramatic pattern of decline for the last 30 years as a consequence of both natural and anthropogenic disturbances (Gardner *et al.*, 2003; Donner *et al.*, 2007; Edmunds & Elahi, 2007). With rising sea temperature, coral bleaching has been identified as a major threat to Caribbean reefs because it can accelerate the rate of degradation by causing frequent, large-scale coral mortality events (Donner *et al.*, 2007; Rogers, 2009; Eakin *et al.*, 2010; Edwards *et al.*, 2011).

Mass Coral bleaching occurs when prolonged periods of high temperature disrupt the endosymbiosis between corals and their dinoflagellate endosymbionts (zooxanthellae) (Brown, 1997). The performance of a particular coral colony in a given environment is defined by both its intrinsic characteristics and those of its symbiont (Iglesias-Prieto & Trench, 1997). For this reason, the term holobiont has been employed to describe the ecological unit defined by a particular coral-algal symbiosis (Rowan, 1998) and then expanded to include all other possible microbial Eukaryotes (Rohwer *et al.*, 2001). A high diversity of endosymbionts have been identified to date with eight main clades (A–I) (Pochon & Gates, 2010) and more than 100 subclades (LaJeunesse *et al.*, 2009). Some subclades have been characterized as capable of conferring thermal tolerance to the holobiont and these mainly belong to D1a with some exceptions (Toller *et al.*, 2001; Mieog *et al.*, 2007; Mostafavi *et al.*, 2007). These thermally

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tolerant clades are dominant in naturally warm environments but rare (less than 5% of the colonies harbor them) elsewhere (LaJeunesse *et al.*, 2009; Oliver & Palumbi, 2009; Stat & Gates, 2011).

Several studies have concluded that unless CO<sub>2</sub> emissions are reduced, the devastating effects of coral bleaching in the Caribbean will be inevitable (Hoegh-Guldberg 1999; Edwards *et al.*, 2011; Hoegh-Guldberg *et al.* 2007). Nevertheless, It has been suggested that an increase in relative abundance of the thermally tolerant symbiont D1a in Caribbean corals could help ameliorate the potential effect of climate change by reducing the intensity and possibly frequency of future bleaching responses (Baker, 2001; Baker *et al.*, 2004; Berkelmans & van Oppen, 2006; Silverstein *et al.*, 2012). Three mechanisms that could foster an increase in the relative abundance of D1a have been proposed: (i) The replacement of thermally sensitive symbionts by tolerant ones (D1a) through the uptake of D1a symbionts after a bleaching event, defined as switching (Baker, 2001); (ii) The competitive displacement of sensitive clades by cryptic populations of D1a already present in the corals before the thermal disturbance, defined as reshuffling (Berkelmans & van Oppen, 2006; Jones *et al.*, 2008; LaJeunesse *et al.*, 2009); and (iii) An increase in the relative abundance of coral colonies already dominated by D1a as a consequence of selective mortality during bleaching events, where there is no requirement for changes in symbiont composition within colonies (Berkelmans & van Oppen, 2006).

Empirical insight into the mechanisms and generality of changes in symbiont distribution are in their infancy. However, increases in the within-host abundance of D1a have been found after bleaching events in some Caribbean and Pacific systems (Baker *et al.*, 2004; LaJeunesse *et al.*, 2009, 2010). This effect has only been observed in some coral taxa, whereas other taxa appear to develop inflexible partnerships between host and symbiont (Stat *et al.*, 2009). Studies monitoring coral colonies that become dominated by D1a after a bleaching event have found that these colonies eventually revert to the prebleaching symbiont (Berkelmans & van Oppen, 2006; Thornhill *et al.*, 2006; Jones *et al.*, 2008; LaJeunesse *et al.*, 2009).

The potential amelioration of the effect of bleaching as a consequence of an increase in the relative abundance of thermally tolerant symbionts has only been explored conceptually. A reef with a higher abundance of D1a-dominated holobionts is assumed to have a higher tolerance to thermal stress and therefore would be less likely to undergo rapid decline in coral cover (Berkelmans & van Oppen, 2006; Baker *et al.*, 2008). On the other hand, it has been shown in Caribbean and Pacific reefs that corals becoming dominated by

thermally tolerant clades reduced their growth rate significantly in comparison to the rate when dominated by less thermally tolerant clades (Little *et al.*, 2004; Cantin *et al.*, 2009; Smith & Iglesias-Prieto, 2010). Therefore, reefs that become dominated by corals harboring D1a will become more tolerant to thermal stress, but will likely exhibit lower somatic growth rates. However, the degree to which thermally tolerant holobionts are able to ameliorate coral reef decline under future climate change scenarios remains unclear. Furthermore, the impact of thermally tolerant symbionts has largely been documented at the colony scale, and the consequences at the population and community level, within an ecosystem context are unknown. To increase the credibility of future climate change scenarios, it is important to explore the potential consequences of a trade-off between elevated survival and reduced growth of corals at an ecosystem scale.

Here, we study the population-level trade-off between reduced growth and elevated survival of corals using a spatial ecosystem model of a Caribbean fore-reef. We explore the effect of an increase in the dominance of D1a-dominated holobionts on the future trajectory of Caribbean coral reefs under two climate change scenarios. The aims of the study are: (i) to assess the effect of a thermally tolerant symbiont D1a on future Caribbean reef trajectories and (ii) to identify the attributes that an idealized thermally tolerant symbiont would require to facilitate the persistence or reduce the degradation rate of Caribbean coral reefs under contrasting climate change scenarios.

## Materials and methods

### *The basic model*

The simulation model employed in this study was originally designed to represent mid-depth (5–15 m) forereefs in the Caribbean, which typically have the highest biomass and diversity of reef organisms (Mumby, 2006; Mumby *et al.*, 2006; Eakin *et al.*, 2010). Using an individual-based approach, we modeled the dynamics of the main benthic reef components (four massive coral types, algal turf, and two species of macroalgae), including their recruitment, growth, mortality, and competition rates in a spatially explicit framework. The model is structured in a square lattice of 400 cells each of which represents 0.25 m<sup>2</sup> of reef and can be occupied by a combination of living and dead substrata. Individual cells in the model comprise multiple coral colonies and algal patches, so the interactions occur at individual scales as they do *in situ*. Grazing affects all algal classes and grazed patches become algal turf. Corals are subject to size-dependent fecundity and mortality.

Two different climate change scenarios were considered for the calculation of partial and total coral mortality owing to bleaching events (Edwards *et al.*, 2011). The low carbon emissions scenario (Representative Concentration Pathways 2.6)

represents the future trajectory of sea surface temperature anomalies considering an immediate drastic reduction in greenhouse gas emissions. The business-as-usual emissions scenario (Representative Concentration Pathways 8.5) represents a high emissions situation where no action is taken to reduce emissions in the near future. Earth System Model simulation, using the 2nd Hadley Centre Global Environmental Model with earth System Components (Collins *et al.*, 2011), was undertaken following an implementation of the 5th Climate Model Intercomparison Project (CMIP5) protocol as described in Jones *et al.* Climate boundary conditions to the reef ecosystem model were provided from the mean of four parallel climate simulations, each started with different initial conditions, and selected to best sample internal variability in the Earth System Model (Jones *et al.*, 2011). All climate variables were provided as a spatial mean across the Caribbean Sea.

The initial conditions at the start of each simulation are given by the size structure of corals from *in situ* reefs in Belize. Hurricanes and epizootics were not considered in the simulations to avoid potential confounding effects when assessing the effect of changes in the abundance of D1a on the reef as response to bleaching events. Each model simulation was run for 130 time steps (65 years), and 50 simulations were carried out to determine the average population attributes. A more detailed description of the performance of the model and its validation can be found in (Edwards *et al.*, 2011; Mumby, 2006).

#### *Inclusion of symbiont type in the model*

We included two symbiont types, one representing a thermally tolerant symbiont (i.e., zooxanthellae D1a) from here for referred as ToS and the other a thermally sensitive type (e.g., clade C2) from here for referred as SeS. The SeS is conceptualized as the type that a generic Caribbean coral harbors in the absence of coral bleaching. Each coral colony was assigned a set composition of symbionts and four new parameters were added to the model: (i) the initial relative abundance of ToS (proportion of coral colonies that are dominated by the ToS); (ii) growth rate of corals with ToS in comparison to corals with the SeS (proportion of the normal growth rate); (iii) bleaching induced mortality of corals with ToS (proportion of the normal mortality rate due to bleaching); and (iv) probability that individual holobionts will switch or reshuffle from SeS to ToS during a bleaching event. We do not attempt to discriminate whether the mechanism driving the increase in ToS is switching (new infection of the tolerant symbiont from outside the coral colony) or reshuffling (competitive displacement of the SeS population by a cryptic preexisting population of the ToS) and adopt the term switching for either from hereon. We assumed that once a ToS infects a colony it remains dominant overtime, we did not include post bleaching reversal of symbionts to the prebleaching type. Inclusion of post bleaching symbiont reversal in the model would imply having a dynamic community of symbionts in each coral colony. This scenario is extremely difficult to parameterize because it would involve extrapolating the growth of the coral colony as a continuous function of the relative abundance of each of its symbionts. There are no empirical data to characterize such a relationship

at the present time. Therefore, we use scenarios where an infection by a ToS is most beneficial to the host in terms of increased tolerance to bleaching (Berkelmans & van Oppen, 2006).

#### *Parameterization of the model with a holobiont harboring a ToS*

The initial percentage of colonies possessing ToS was set at 5% based on the upper limit observed among reefs of the Caribbean (LaJeunesse *et al.*, 2009). There is broad agreement in the literature that only a small fraction of a coral population is dominated by ToSs, with the exception of areas exposed to constant high temperatures (LaJeunesse *et al.*, 2010). The reduction in growth when switching to ToS was set at 60%, which is the average of the observed range of 40–75% (Little *et al.*, 2004; Jones & Berkelmans, 2010; Smith & Iglesias-Prieto, 2010) and corresponds to the only information available for Caribbean corals (Smith & Iglesias-Prieto, 2010). The reduction in bleaching mortality was set at 30%, calculated from Berkelmans *et al.* (Berkelmans & van Oppen, 2006) and the probability of an individual colony switching symbionts during a bleaching event was set at 0.4 (LaJeunesse *et al.*, 2009).

To identify the characteristics of a holobiont that might ameliorate the overall effect of climate change on the coral assemblage, we created 250 scenarios, representing five levels of symbiont switching, five levels of ToS impacts on coral growth, five levels of ToS impact on coral mortality, and two greenhouse gas emissions scenarios (Business as usual and low emissions).

Three reef-scale response variables were considered for each scenario or model run. The first was simply plots of the trajectory of coral cover over time. The second was the mean difference in final coral cover after a particular time period (usually 65 years). The third was the difference in time taken for coral cover to reach 50% of its initial level (number of years).

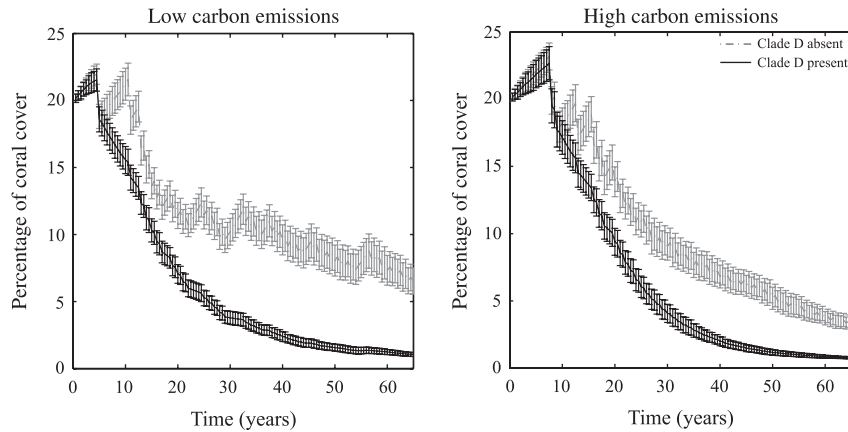
## **Results**

### *Ecosystem response for observed impacts of a ToS*

When using the literature-based empirical parameterization for the effects of a ToS with similar properties to D1a, the ecosystem level effect of this ToS is deleterious. Coral cover declined faster in the presence of D1a than in the absence of a ToS and the final cover was 80–90% lower depending on the climate scenario, with reefs in the low carbon economy faring better (Fig. 1).

### *Systematic analysis of model and idealized holobiont properties*

Most of the combinations of ToS impacts upon growth and mortality (20/25 combinations) resulted in reefs



**Fig. 1** Trajectory of coral cover for two different climate scenarios. Dashed black line is the average cover per time step when corals are dominated by SeS. Blue line is the average cover per time step when a ToS similar to D1a is present and characterized according to published literature: 60% reduction in mortality, 60% reduction in growth, 5% initial abundance of D1a in the population, and 40% probability of switching after a bleaching event.

with either comparably or lower final coral cover than reference reefs dominated by SeS (Fig. 2). In order for a ToS to have a net improvement on reef health after 65 years, the cost of the ToS, in terms of growth reduction, had to be only 20% or less (compared to 60% reported in the literature), and the benefit of the ToS, in terms of reduced bleaching mortality had to exceed 90%, rather than the modest 30% found in empirical studies (Fig. 2). When these idealized conditions were met, the final cover was 3- to 8-fold higher than that without the ToS. Very minor benefits were found just outside this range (Fig. 2) and we do not consider them further here. Moving from high to low greenhouse gas emissions had a barely measurable effect on the impact of ToS to reef health after 65 years (Fig. 2).

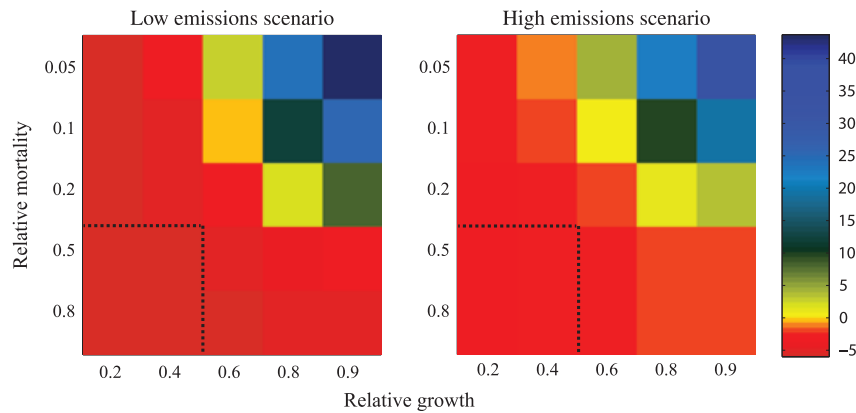
Apart from the five combinations of parameters that presented higher final cover than a reef without ToS, two additional combinations took longer to decline to half the original coral cover (90% reduction in mortality combined with 40% reduction in growth and 80% reduction in mortality combined with 20% reduction in growth, Figs. 3 and 4). The probability of switching had a strong effect in these two combinations. To obtain a 10-year delay in reef decline, a 0.8 switching probability is required, while with a probability of only 0.1 the delay in reef decline is reduced to less than 2 years (Fig. 5). The strongest effect of switching was observed with 90% reduction in mortality and 40% reduction in growth for the high emissions scenario (Fig. 5).

## Discussion

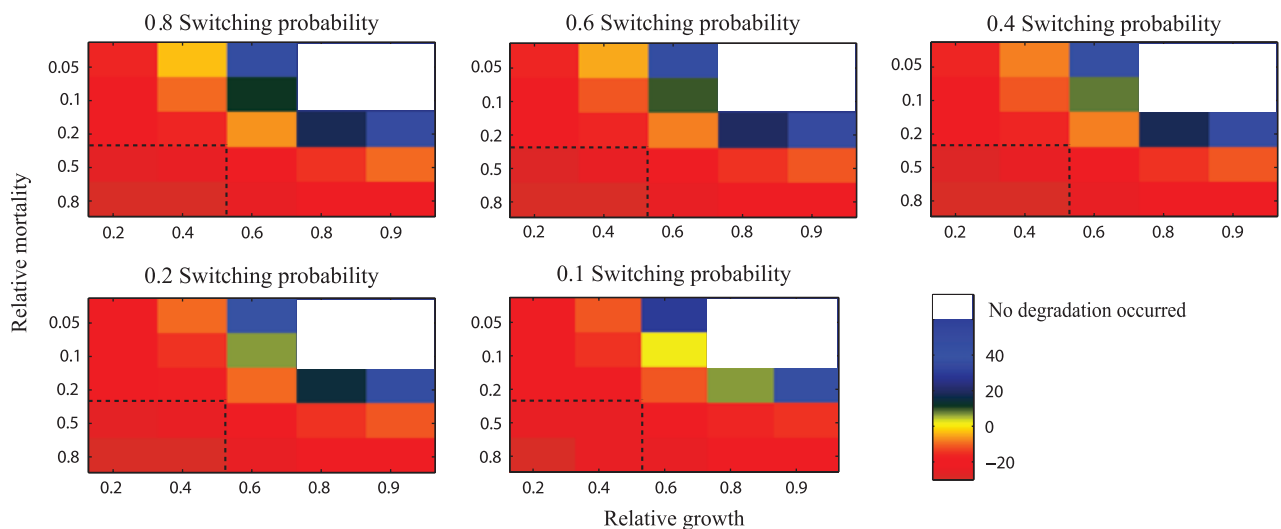
Our results suggest that an increase in the abundance of a ToS with similar properties to D1a might have a detrimental effect on the wider coral assemblage rather

than the hypothesized benefit that accrues from lowering bleaching mortality. The reason for this deleterious outcome is that the Caribbean coral assemblages appear to be highly sensitive to changes in coral growth rate (Mumby *et al.*, 2007a,b) and therefore the cost of a ToS, in terms of growth, outweighs the benefit of reduced mortality. Indeed, the main divergence of coral cover trajectories between reefs dominated by ToS and SeS stems from the ability of reefs to exhibit recovery. In the absence of ToS, recovery periods of coral were evident following bleaching events that compensated for the elevated bleaching mortality. In contrast, reefs with ToS exhibited little recovery because the reduced growth rate of corals implicitly reduced their competitive ability against macroalgae. As thermal stress events became more frequent and intense, the 'recovery advantage' of reefs with SeS progressively weakened, but remained evident in the low emissions scenario. In the high emissions scenario, however, the intensity and frequency of bleaching events was so high in the latest part of the curve that any 'recovery advantage' became moot as there was insufficient opportunity for recovery and the final cover converged between the ToS and SeS scenarios.

Few data are available to parameterize a ToS with similar properties to clade D1a, largely because such data are difficult to acquire. Specifically, there is little information on the proportion of the population that becomes dominated by clade D1a during or after a bleaching event, nor are there many estimates of the bleaching mortality of corals dominated by clade D1a. Of the three studies used to parameterize the reduction in coral growth rate, one focused on juvenile corals in the Pacific Ocean (Little *et al.*, 2004), and only one (Smith & Iglesias-Prieto, 2010) involves Caribbean corals.



**Fig. 2** Effect of ToS on the reef state after 65 years (final cover with ToS – final cover without ToS). Difference in reef state plotted as a function of relative growth (proportion of colony growth relative to the growth of holobionts with ‘normal’ SeS) and relative mortality (proportion of colony bleaching induced mortality relative to the mortality of holobionts with ‘normal’ SeS) under two scenarios of greenhouse gas emissions. Dotted line represents the upper limit of the empirical range for growth and mortality in corals with a ToS similar to D1a.

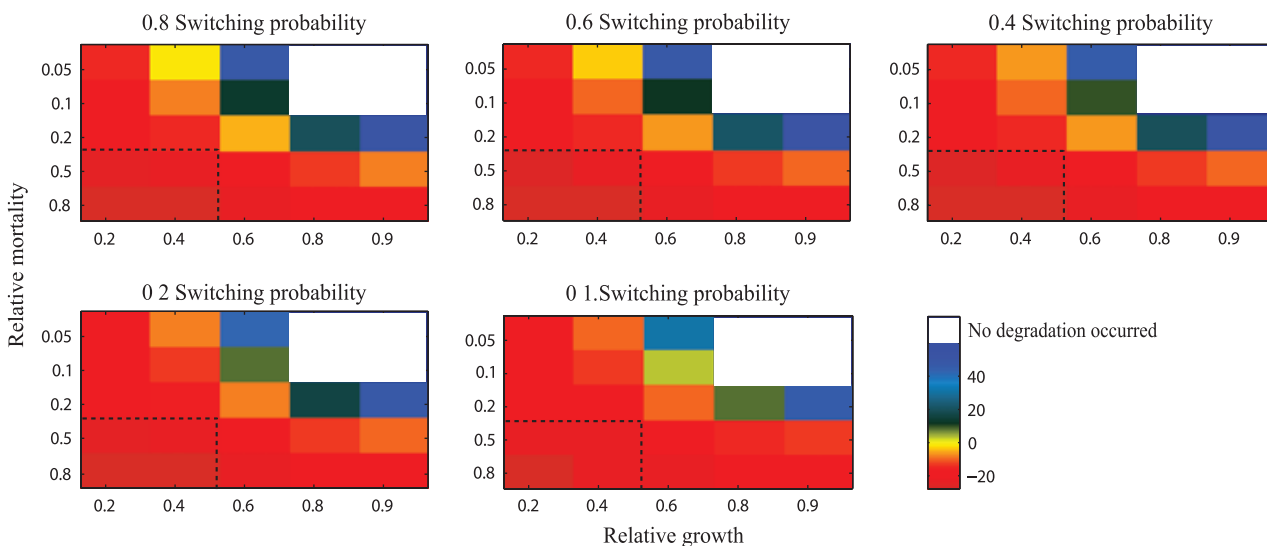


**Fig. 3** Ability of a ToS to reduce the rate of reef degradation, defined as the difference in time required for coral cover to decline from an initial value of 20–10% (time with ToS – time without ToS). A positive value implies that reef degradation takes longer. The difference in degradation rate is plotted as a function of relative growth (proportion of colony growth relative to the growth of holobionts with ‘normal’ SeS), relative mortality (proportion of colony bleaching induced mortality relative to the mortality of holobionts with ‘normal’ SeS), and several probabilities of symbiont switching during a bleaching event. Bleaching events based on the low greenhouse gas emissions scenario. Dotted line represents the upper limit of the empirical range for growth and mortality in corals with D1a.

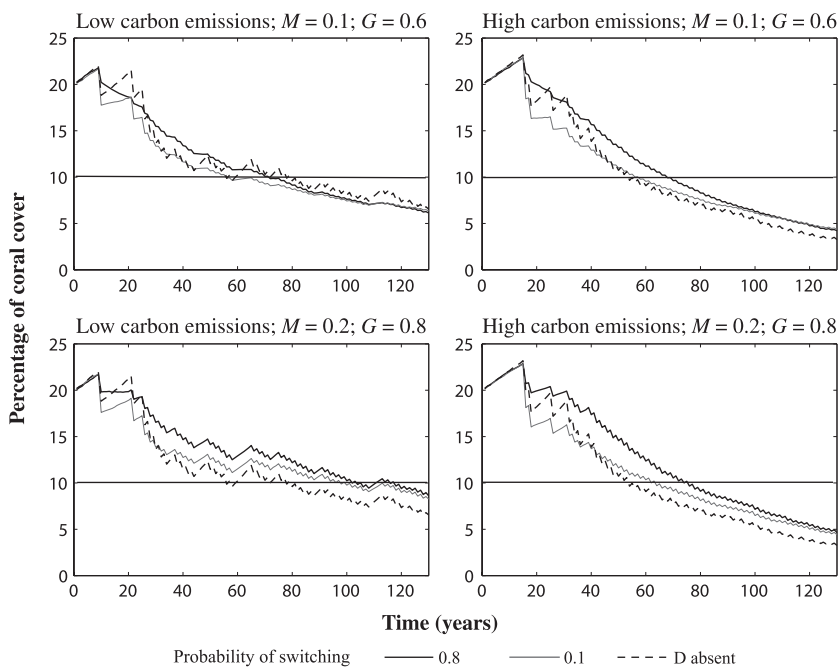
als (although the average of all three datasets was similar to that of the Caribbean based study). Thus, our characterization of a ToS may prove to be quite inaccurate. For this reason, we explored a wider range of parameter space to identify the attributes of ToS that might provide a net benefit to coral reefs under climate change. It appears that the symbiont characteristics required to maintain or improve future trajectories of Caribbean coral cover would involve at least a 90% reduction in present bleaching-related mortality at a cost of only a 20% reduction in growth rate or lower.

There has been no documentation of a symbiont with these or similar characteristics. Furthermore, given the apparent cost of developing thermal tolerance (Little *et al.*, 2004; Abrego *et al.*, 2008; Cantin *et al.*, 2009), it appears unlikely that such an efficient symbiont was to exist, or evolve in the near future.

Even when it appears unlikely that a ToS could significantly ameliorate the effect of climate change in the Caribbean, it has also been suggested that it could buy managers and policymakers some time by delaying the rate of decline (Berkelmans & van Oppen, 2006).



**Fig. 4** Ability of a ToS to reduce the rate of reef degradation, defined as the difference in time required for coral cover to decline from an initial value of 20% to 10% (time with ToS – time without ToS). A positive value implies that reef degradation takes longer. The difference in degradation rate is plotted as a function of relative growth (proportion of colony growth relative to the growth of holobionts with ‘normal’ SeS), relative mortality (proportion of colony bleaching induced mortality relative to the mortality of holobionts with ‘normal’ SeS), and several probabilities of symbiont switching during a bleaching event. Bleaching events based on the high greenhouse gas emissions scenario. Dotted line represents the upper limit of the empirical range for growth and mortality in corals with D1a.



**Fig. 5** Buying time, Trajectory of coral cover for the only two combinations of relative growth and mortality that could delay the time that takes for the reef to reach half its original coral cover under two different climate scenarios. Dashed black line is the average cover per time step when D1a is not present in the community. Blue line is the average cover per time step when the probability of switching is 0.8. Red line is the average cover per time step when the probability of switching or reshuffling is 0.1  $M$  = relative mortality (proportion of colony bleaching induced mortality relative to the mortality of holobionts with ‘normal’ sensitive symbionts).  $G$  = relative growth (proportion of colony growth relative to the growth of holobionts with ‘normal’ sensitive symbionts).

However, when analyzing the time required for a reef to decline to 50% of its original coral cover, most combinations of ToS-dominated holobionts vital rates fail to provide any additional time since most scenarios increase the rate of decline. The only two scenarios that provided some amelioration (10 additional years before reaching half the original cover) require a 10% reduction in growth or a 95% reduction in mortality. Both these values appear even less likely than the previously discussed ones. A 95% reduction in mortality due to bleaching would imply (for the high emissions scenario) an increase in thermal tolerance of about 4.5 °C which is three times higher than what has been found in laboratory experiments with D1a (Berkelmans & van Oppen, 2006) and appears physiologically implausible. In addition, these scenarios would require that at least 80% of the population switched to the ToS after each bleaching event. This rate of change in the abundance of a ToS has not been documented and current estimates lie in the range of 20–50%. Therefore, it seems unlikely that a switch in symbionts will have much benefit, if any, for Caribbean coral communities.

As the focus of this study is to explore whether increases in the abundance of ToSs can help corals naturally overcome the challenges posed by climate change, our model assumes that once the ToS becomes dominant it remains so until the next bleaching event. However, several studies have shown that the SeS can regain dominance once the stressful conditions have ceased (Berkelmans & van Oppen, 2006; Thornhill *et al.*, 2006; Jones *et al.*, 2008; LaJeunesse *et al.*, 2009). If the recovery of SeS was to occur swiftly then it could be argued that corals effectively lose any preparedness to withstand the next bleaching event (Berkelmans & van Oppen, 2006), and the outcome would be indistinguishable from our SeS scenario. By assuming that switches to a ToS are permanent, we allow for the greatest benefits of a ToS in terms of elevated survivorship during bleaching (albeit with associated costs). We anticipate that the model can be refined when empirical data become available to parameterize the dynamics of symbiont switching on continuous time scales, together with the associated costs on growth. We point out that the potential effect of not including post bleaching reversal in the model would only be present in the first 10–20 years of simulations because after this time the incidence of bleaching events reaches almost annual occurrence which exceeds the time necessary for symbiont reversal (Thornhill *et al.*, 2006; LaJeunesse *et al.*, 2009). We also point out that a rapid reversal of symbionts after bleaching is similar to the scenario in which growth costs and survival benefits are low (10% growth cost and 20% mortality benefit). Once again, the net outcome of this scenario was pessimistic (Fig. 2) compared to SeS.

There are some important considerations that should be made when interpreting these results. The approach taken here is conservative with respect to the likely impact of an increase in ToS abundance as it only considers the reduction in growth as a trade-off when thermal tolerance is increased. Given the potential energetic cost of thermal tolerance, it is possible that other physiological traits of the holobiont like fecundity, disease tolerance, or skeletal density could be compromised. Any of these potential additional trade-offs could further reduce the potential ameliorating effect of an increase in ToS. Moreover, this study as well as most of the current literature places most of the responsibility for thermal tolerance on the endosymbiont, with relatively little consideration of the role played by the host. It is possible that there would be limitations in the physiology of the coral host that could compromise the putative thermal tolerance that clade D ToS could provide (Hoegh-Guldberg *et al.*, 2012). Furthermore, we assumed that the ToS will be able to infect all coral types. Although the diversity of corals that already associate with clade D1a is considerable (in LaJeunesse *et al.*, 2009), some coral taxa have inflexible partnerships with symbionts (Stat *et al.*, 2009) and might therefore be unlikely to experience colonization by a ToS. This may represent an additional challenge for new ToS that may evolve in the future (Thornhill *et al.*, 2006). Our results highlight the importance of reducing greenhouse gas emissions. Despite the prediction that coral cover will be low (<10%) later in this century, as, even though, in both climate scenarios the final cover was low (less than 10%) in the low emissions scenario cover was five times higher with SeS than with ToS (Fig. 1). More importantly, the reef without ToS still shows recovery trajectories between bleaching events in the low emissions scenario, although the frequency of events make the periods of recovery very short, suggesting that the reef could potentially recover after the remaining effect of carbon emissions already stored in the atmosphere ceases. In contrast the reduction in growth in the reef dominated by ToS would make the long-term recovery of the reef unlikely.

The main driver of our results is the importance of growth rate for the health of Caribbean reefs, such that even minor costs of the symbiosis to growth rate develop have important ecosystem-wide consequences. Previous studies have shown how the resilience of Caribbean reefs, such as the location of unstable equilibria, is extremely sensitive to changes in coral growth rate (Mumby *et al.*, 2007a,b). As the faster growing acroporids have almost disappeared from Caribbean reefs (Greenstein *et al.*, 1998), a reduction in the growth rate of the remaining – and slower-growing species – has a strong deleterious impact on the competitive



interaction between corals and algae. There are several reasons why coral populations can be so sensitive to somatic growth rate. Slower growth reduces the rate at which coral cover increases. This has a knock on effect in that macroalgae become more persistent and can exert a stronger negative effect on coral recruitment because coral–algal interactions become more frequent and of greater duration (Mumby *et al.*, 2007a,b). As coral recruitment declines, so too does the intrinsic growth rate of individual coral populations. Moreover, rates of whole colony coral mortality are negatively related to coral size (Hughes and Jackson 1985) and there is some evidence that corals achieve an escape in size from predation (Doropoulos *et al.*, 2012). If coral growth rates decline, then corals remain in a vulnerable size class for longer, thereby increasing their mortality rate (Box & Mumby, 2007). It is important to point out, however, that our conclusions do *not* necessarily extend to reefs in the Indian and Pacific Oceans where coral assemblages still possess faster growing corals.

We have shown that it is unlikely that an increment in the abundance of D1a could significantly ameliorate the effect of climate change on Caribbean reefs. In most scenarios, such an increase would accelerate the rate of decline and generate a less resilient reef. Furthermore, it appears that no significant amount of time can be gained as a consequence of an increase in D1a dominance. These results reinforce the need for immediate actions directed to reduce carbon emissions and protect fish stocks to improve the possibility that Caribbean reefs could recover from the inevitable effect of climate change in the long term.

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