Bleaching as a result of coral optimization in a changing environment*

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Abstract

Corals provide important ecosystem services as protective coastal structures and as habitats for coastal biodiversity. Corals depend on their symbiotic relationship with algae, a relationship under threat from rising temperatures. To better understand the nature and resilience of this relationship, we provide a model in which two clades of algae (one efficient, the other resilient) compete over the nitrogen that the coral "chooses" to provide in a changing environment. This model is consistent with a wide range of empirical observations about observed bleaching episodes (when algal populations drop dramatically) and the observed algal composition over time, depending on environmental conditions.

Keywords: Coral reefs, adaptive bleaching hypothesis, symbiosis, zooxanthellae, global warming, modeling

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1 Introduction

Reef-forming corals occur in warmer regions of the world (generally within 30°N and 30°S), where they are valued for their varied ecosystem services. Such services embrace physical protection of coastlines from storms and erosion or their functioning as habitat formers for other forms of marine life. Since this also includes fish, reefs also serve as a nutritional and economic basis for vulnerable human populations around the tropical belt. Unsurprisingly, the estimated economical value of corals is worth of several billions of dollars [Cesar et al., 2003]. It is thus essential to know more about the vulnerability of corals in times of environmental and economic pressure. Unfortunately, the situation of corals throughout the tropical belt has aggravated in recent decades. Due to anthropocentric climate change, corals are at high risk [Pörtner et al., 2019], and the coral cover has already diminished seriously during the last few decades [Bellwood et al., 2019]. Their vulnerability might be associated with the biology of corals as organisms relying on the function of a microbial symbiotic partner.

Corals typically live together with eukaryotic algae in the genus *Symbiodinium* (class Dinophyceae), which are also known as zooxanthellae for their golden-yellow to brown color of their cells. Irrespective of interpreting the living together of corals with their zooxanthellae as mutualism, mild parasitism, or a sort of algal farming, the algae provide carbon products (produced by photosynthesis) to coral hosts in exchange for nitrogen [Yellowlees et al., 2008]. The products of the algae are the main source of energy [Muscatine, 1990] for corals and therefore, the fitness of corals depends on the balance of the symbiosis [de Souza et al., 2022]. Regulation of Zooxanthellae density with environmental conditions is a mechanism used to adjust the symbiotic functionality. If temperature or light intensity exceeds adapted values, corals can expel their zooxanthellae and the symbiosis collapses.

This phenomenon is known as *bleaching* because corals become largely pale without the algae. Since the late 20th century, bleaching has been mainly observed during warmer periods. The first global mass bleaching events were recorded in 1998 and 2010, which correlated with warming induced by the El Niño phenomenon. Subsequently, the 2014–2017 El Niño period was the longest and most damaging harm affecting 70% of all coral reefs. As global change increases the temperature in surface layers of the ocean, this is leading to cascading effects, including a dramatic increase in coral bleaching and subsequent loss of reef structures [Bellwood et al., 2019]. Given the enormous heat capacity of the oceans, which absorb in the top few meters as much heat as the entire atmosphere of the Earth, this worrying development leads to a lasting situation to which organisms need to adapt. Under this scenario, we should better understand whether corals will be lost or survive.

Previous research revealed that corals may host various lineages of zooxanthellae throughout their life, according to analyses of DNA sequence data ([Mieog et al., 2007]). Other studies showed that some of the corals may host several clades of algae simultaneously [Baker, 2003, Little et al., 2004, Quigley et al., 2014]. For most of the time, one of the symbionts dominates while the

others are present in the background [Little et al., 2004]. Nonetheless, certain coral species value the fidelity of fixed partnerships and are not able to switch their symbionts [Goulet, 2006]. Flexibility may however increase the resilience of the whole symbiosis when the different algal types differ in their physiological demands and may be adjusted to different ecological situations [Grégoire et al., 2017]. We may thus envision two situations: Either there is an adjustment under mild stress (so-called "colorful bleaching"; maintaining genuine pigments of the coral), where the change in competing algal populations occurs without complete bleaching, or the corals bleach completely by loosing the entire algal population. It has been proposed by Buddemeier and Fautin [1993] that bleaching facilitates the complete recolonization of the host with a different partner, but it also appears as a risky option [Baker, 2001]. Of course, as such recovery needs to take place before the corals starve to death, corals with thermal stress history are more resilient than others [Guest et al., 2012]. In any case, symbiont changes after bleaching have been observed repeatedly [Silverstein et al., 2015, Baker, 2003, Quigley et al., 2022].

Several models have already been proposed that may predict bleaching frequency in the next decades [Weijerman et al., 2015], yet there is still a need for improved models that connect environmental history with bleaching patterns [Van Woesik et al., 2022]. Ware et al. [1996] modeled the adaptive bleaching hypothesis with competing algae, but did not include active control of the host on the amount of algae by tuning the quantity of nutrients given to the population of algae. Muller et al. [2009] developed a dynamic bioenergetic model (DEB) of the symbiosis between corals and algae. Such an approach was used by Cunning et al. [2017] to describe bleaching as an alternative stable state, and recently by Kaare-Rasmussen et al. [2023], to fit the model with data from the anemone *Exaiptasia pallida*. Brown et al. [2022] developed a model that considers explicitly the shuffling between sensitive and tolerant symbiont and bleaching. Using a particular setting van Woesik et al. [2010] model how corals shuffle between different algal species. Baskett et al. [2009] and later, Logan et al. [2021], compare the importance of symbiont shuffling with symbiont evolution. Different models have considered the evolution of the interaction between corals and algae. In particular, Day et al. [2008] model the evolution of bleaching resistance. Also, Raharinirina et al. [2017] have modeled the evolution of symbiosis investment for corals. Later, Raharinirina et al. [2022] used a similar model to try to predict the consequences of different climate scenarios. To integrate corals in a larger framework, more complex multi-scale models have been developed. Baskett et al. [2010] proposed a 5-layer model of corals (locations, species, coral size structure, symbiont populations, symbiont genetics). Generally, models have been developed to formalize the competition between corals and other organisms, such as macro-algae, notably to predict the consequence of climate change on corals [Fabina et al., 2015, Mumby et al., 2007, Baskett et al., 2014].

As an alternative to the previous approaches, we developed here a simple and analytically solvable model that incorporates also the fact that a coral is in control of the symbiosis. The model could give a better understanding of

the key mechanisms driving symbiotic composition changes and the resulting bleaching susceptibility. Also, the predictions of the model could be tested statistically. As suggested by Weijerman et al. [2015] minimal models can be useful to predict the shape of disturbance response. The proposed model utilizes only a few parameters, yet effectively accounts for various observed features, including dynamic changes in algae within coral symbiosis and the severity of bleaching relative to historical temperatures.

We will first introduce a stylized model and demonstrate its ability to explain several observed empirical features. We will then generalize the model to explain more empirical observations. In addition, we will propose different testable hypotheses. The key principle of the model lies in the ability of the coral to quickly establish symbiosis with various algae, enabling it to adjust rapidly to diverse environments, particularly higher sea temperatures. This adaptability is evolutionarily advantageous. We will show that the competition between the species of algae and the different growth rates associated with each species of algae for each environment could explain how the duration of the warm temperature characterizes a change towards the temperature-tolerant algae. In the same environment, a species of algae will always out-compete the others, the out-competed algae will remain available in the background.

2 The basic model

We consider an individual coral living in a variable temperature environment, engaged in symbiosis with algae. The coral actively controls the quantity of nutrients it provides to the algae, influencing the future population of algae.

The environment Time is discrete and indicated by $t = 0, 1, 2, ...$[1] The state of the environment at time t is given by θ_t, which can take two values $\theta_t = 0$ denoting the bad (warm) environment and $\theta_t = 1$ the good (cool) environment. We relax this simplification to two states in Section 5. All results in the manuscript hold for any sequence of θ_t, except for those in Appendix E. The series of θ_t (a series of zeros and ones) can be generated in any manner. In particular, the series of θ_t can follow a stochastic process, such as a Markov chain transitioning between the two different temperature environments.[2]

Algae dynamics The coral lives in symbiosis with two different clades of Zooxanthellae algae, C (Cladocopium) and D (Durusdinium). The coral provides nutrients to the total population of algae. In exchange, the algae provide carbon products fixed by photosynthesis [Yellowlees et al., 2008]. Clade C is relatively more efficient in doing so [Ezzat et al., 2017, Baker et al., 2013b], while

[1] Discrete time makes it relatively simple to model a coral who makes decisions now (at time t) to affect the future (at time $t + 1$).

[2] This generality is made possible by our assumption that the coral is myopic and not forward looking beyond more than one time step. See Appendix E for the case of a forward looking coral.

clade D is relatively more resilient to warm temperatures [LaJeunesse et al., 2010, Stat and Gates, 2011, Baker et al., 2013b].[3]

The density (or abundance) of clade C, for every time step, is denoted by y_t, and the density of clade D by z_t. The two clades of algae compete for the nutrients that the coral provides. This competition is reflected in their growth rates that depend on the state of the environment. The relevant quantity for this competition is the two clades' relative growth rate (the growth rate of the efficient clade C divided by the growth rate of the resilient clade D). We denote this relative growth rate by $\rho(\theta_t)$ and assume that

$$\rho(\theta_t) = \begin{cases} \eta > 1 & \text{if} \quad \theta_t = 1 \\ \lambda < 1 & \text{if} \quad \theta_t = 0 \end{cases}$$

These assumptions are made to reflect the empirical evidence that the efficient algae growth is relatively faster than the resilient one in a cool environment: $\eta > 1$ [Little et al., 2004] but slower in a warm environment: $\lambda < 1$ [Chen et al., 2005, Fabricius et al., 2004, LaJeunesse et al., 2009].

We here consider a simple model of competition [Krueger et al., 2020, McIlroy et al., 2019, 2020] between the two clades of algae. More precisely, we model only competition between symbionts who are already present (even in very small quantities) with the corals. It has been observed that *shuffling* (a change in the proportion of species of algae already present with the host) is more important than *switching* (an establishment of symbiosis with new species of algae) in coral symbiosis [Berkelmans and Van Oppen, 2006]. Nevertheless, this point is addressed in Appendix D. Also, shuffling has been demonstrated to be more powerful than symbiont evolution [Logan et al., 2021]. The algae dynamics are given by

$$\begin{aligned} y_t &= \tfrac{\rho(\theta_t) y_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t \\ z_t &= \tfrac{z_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t, \end{aligned}$$

where K_t is the amount of nutrients available to the algae at time t. We can verify that the total population of algae at time t is equal to K_t. This serves as the controlled variable for the coral, meaning that the coral can choose the value K_t to maximize its fitness.

We assume that the algae exhibit a growth rate surpassing the coral's ability to adapt its nutrient provision promptly. Thus, at each time step, and even in the presence of changes in the nutrient availability K_t, we posit that algae can adequately approach the equilibrium point.

We opted for this model over a Lotka-Volterra model for its simplicity while retaining the essential features we aim to replicate. In our model, the composition of each algal species is determined by their respective growth rates. For instance, if the growth rate ratio between the efficient and resilient algae is 2, the relative proportion of efficient algae will double compared to the previous

[3] Many different clades have been observed within corals [LaJeunesse et al., 2018, Yorifuji et al., 2021]. The restriction to two key clades, one efficient and the other more resilient, is made for simplicity and tractability as also in, e.g., Logan et al. [2021]. We believe that this restriction is sufficient to capture the main mechanism behind coral bleaching.

time step. Also, with identical growth rates, the proportion of each algal species remains unchanged, even if the total population fluctuates.

Coral strategies It has been shown that corals can control the amount of nutrients given to the population of algae [Morris et al., 2019, Falkowski et al., 1993, Rees, 1991, McIlroy et al., 2022, Yellowlees et al., 2008]; in particular with nitrogen [Thies et al., 2022] in Aiptasia [Cui et al., 2019], Exaiptasia pallida [Xiang et al., 2020], and Stylophora pistillata [Cui et al., 2022, Krueger et al., 2020].[4]

In our model we, thus, assume that the coral can control – at every time step – the amount of nutrients K_t given to the population of algae. When choosing the amount K_t, the coral knows the current state θ_t and the density of the two clades of algae y_{t-1} and z_{t-1} from the previous period. Again, this timing is assumed to capture the idea that the algae grow faster than the coral can adapt its nutrient provision.

Coral payoffs The coral optimizes a tradeoff between receiving benefits (carbon) from the algae and providing costly nutrients (nitrogen) to the algae. Formally, the coral, at every time step t, chooses K_t to maximize its *payoff*

$$u(y_t, z_t, \theta_t, K_t) = b(y_t, z_t, \theta_t) - c(\theta_t, K_t)$$

In the basic model, we choose the following benefit and cost functions. We consider a generalization in Appendix C. More generally, we believe our results would qualitatively hold for any concave benefit and convex cost function. The parameter $\alpha < 1$ is the efficiency trade-off between the two clades of algae.

$$\begin{aligned} b(y_t, z_t, \theta_t) &= b\sqrt{y_t \cdot \theta_t + \alpha \cdot z_t} \\ c(\theta_t, K_t) &= K_t \end{aligned}$$

These functional forms capture some key features for which there is some empirical evidence. In particular, a concave benefit function, as proposed by Cunning and Baker [2014] (at least when the quantity of algae is not too large) and also used by Raharinirina et al. [2017], is consistent with the finding that carbon acquisition and translocation rates per symbiont cell decrease with the symbiont density [Pupier et al., 2019, Rossi et al., 2018].

These functional forms (concavity of the benefit function, with infinite slope at K_t equal zero, and linearity of the cost function) also imply that the coral's optimization problem has a unique and interior solution (i.e. a finite and non-zero value representing the optimal trade-offs where altering the algae population would be possible, but it would lead to a lower payoff for the coral).

For every time step, the temperature of the sea is given by θ_t. Knowing the current state θ_t, the coral chooses the optimal K_t as a function of the previous

[4] Also, Fagoonee et al. [1999] have demonstrated the ability of corals to control the population of algae. Models by Raharinirina et al. [2017, 2022] also utilize that "*corals are in control of the symbiotic relationship*".

density of the two clades of algae from the end of the previous period y_{t-1}, z_{t-1}. Then, after one period of algal growth, the payoff $u(y_t, z_t, \theta_t, K_t)$ is realized at the end of the time step.

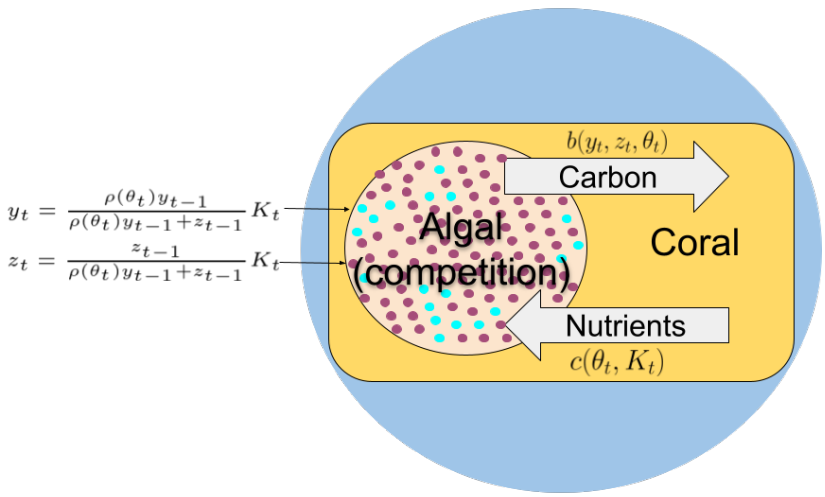

Figure 1: Illustration of the model: Corals live in the sea, where the temperature (θ_t) fluctuates. Inside the coral's cell, algae of a relatively efficient (y_t) and temperature-resilient (z_t) species compete to access nutrients, their amount denoted by K_t, which are provided by the coral $c(\theta_t, K_t) = K_t$. In exchange, the coral receives carbon products from the population of algae $b(y_t, z_t, \theta_t)$. Corals can control the total population of algae with the control variable K_t.

3 Coral optimal nutrient provision

The main idea of this paper is that evolutionary forces have formed coral behavior in such a way that the coral acts as if it maximizes its payoff function subject to the constraints induced by the algae dynamics. The coral's problem, at every point in time t, is then given by

$$\max_{K_t} b\sqrt{y_t \cdot \theta_t + \alpha \cdot z_t} - K_t$$

subject to

$$\begin{aligned} y_t &= \frac{\rho(\theta_t)y_{t-1}}{\rho(\theta_t)y_{t-1}+z_{t-1}} K_t \\ z_t &= \frac{z_{t-1}}{\rho(\theta_t)y_{t-1}+z_{t-1}} K_t. \end{aligned}$$

This can be solved by plugging the constraints into the objective function to obtain the unconstrained problem

$$\max_{K_t} b\sqrt{\frac{\rho(\theta_t)y_{t-1}}{\rho(\theta_t)y_{t-1}+z_{t-1}} K_t \cdot \theta_t + \alpha \cdot \frac{z_{t-1}}{\rho(\theta_t)y_{t-1}+z_{t-1}} K_t} - K_t,$$

Symbol	Description
t	time
y_t	density of the relatively efficient algae species at time t
z_t	density of the temperature-resilient algae species at time t
σ_t	ratio y_t/z_t
K_t	amount of nutrients available to the algae at time t
θ_t	temperature at time t
η	relative growth rate of the efficient alga species to the resilient one in the cold environment
λ	relative growth rate of the efficient alga species to the resilient one in the warm environment
α	efficiency trade-off between the two algae species
$\rho(\theta_t)$	relative growth rate of the efficient species to the resilient one with temperature θ_t
$u(y_t, z_t, \theta_t, K_t)$	coral payoffs at time t
$b(y_t, z_t, \theta_t)$	benefits to the coral at time t
$c(\theta_t, K_t)$	cost to the coral at time t

Table 1: Overview of key notation

which can be simplified to

$$\max_{K_t} b\sqrt{\frac{\rho(\theta_t)y_{t-1}\cdot\theta_t+\alpha\cdot z_{t-1}}{\rho(\theta_t)y_{t-1}+z_{t-1}}K_t}-K_t.$$

We see that only the relative density of the two clades of algae enters this optimization problem. Denoting this by $\sigma_t := \frac{y_t}{z_t}$ for all t, we get

$$\max_{K_t} b\sqrt{\frac{\rho(\theta_t)\sigma_{t-1}\cdot\theta_t+\alpha}{\rho(\theta_t)\sigma_{t-1}+1}K_t}-K_t.$$

The first order condition (and given the function form necessary and sufficient condition for a maximum) are then given by equating the derivative of this objective function to zero. This is given by

$$\frac{\partial u}{\partial K_t}=b\sqrt{\frac{\rho(\theta_t)\sigma_{t-1}\cdot\theta_t+\alpha}{\rho(\theta_t)\sigma_{t-1}+1}}\cdot\frac{1}{2\sqrt{K_t}}-1=0.$$

This can be solved to obtain the optimal quantity of nutrients the coral should provide to the population of algae as a function of the state of the environment θ_t and the last period's relative abundance of the two clades of algae σ_{t-1}. The solution is given by

$$K_t(\theta_t,\sigma_{t-1})=\frac{b^2}{4}\frac{\rho(\theta_t)\sigma_{t-1}\cdot\theta_t+\alpha}{\rho(\theta_t)\sigma_{t-1}+1}.$$

For the two different states, we have

$$K_t(1, \sigma_{t-1}) = \frac{b^2}{4} \frac{\eta\sigma_{t-1} + \alpha}{\eta\sigma_{t-1} + 1} \text{ and } K_t(0, \sigma_{t-1}) = \frac{b^2}{4} \frac{\alpha}{\lambda\sigma_{t-1} + 1}.$$

Since the model is analytically solvable, we can analyze how it responds to changes in parameter variables over time. We can observe notably how K_t, the optimal nutrient provision, reacts to η, the relative growth rate of the efficient algae in the non-warm sea. We notice that K_t increases with η, but this increase gets weaker when η gets higher.

$$\frac{\partial K_t(1, \sigma_{t-1})}{\partial \eta} = \frac{b^2\sigma_{t-1}}{4} \frac{1 - \alpha}{(\eta\sigma_{t-1} + 1)^2}$$

Likewise, we can examine the variations in K_t with α, representing the relative efficiency of the resilient algae compared to the efficient one. In this scenario, as α rises, K_t follows suit, with the change being more significant when the resilient algae is more abundant.

$$\frac{\partial K_t(\theta_t, \sigma_{t-1})}{\partial \alpha} = \frac{b^2}{4} \frac{1}{\rho(\theta_t)\sigma_{t-1} + 1}$$

4 Model consistency with empirical observations

Model validation Figures 2 and 3 compare empirical observations from the literature with the output of the simple model presented earlier. The intention is not to parameterize the model or provide quantitative predictions but to qualitatively reproduce observations. Recall that the model has only very few parameters. As we can observe in the figures below, our model reproduces qualitatively the change of abundance of each algae species, and the corresponding bleaching severity.

In Figure 2, the brown color indicates El Niño which is a warm period for corals. In our simulations (on the right), we introduce a warm period for several time steps, followed by a cold period. The simulation begins with mostly the cladocopium clade (y) which is the relatively more efficient clade. We observe that our model accurately reproduces the decrease in the total density of algae at the onset of the warm period. Another point replicated by the model is the change of symbiont species from C to D during the bleaching. After, during the cold period, the total density of algae is overall stable.

In Figure 3, we attempted to replicate the observations conducted by Chen et al. [2005] (on the left). They measured (on the top) the percentage of phylotype C and phylotype D for a year and a half. They have also provided the corresponding seawater temperature (on the bottom). In our model (on the right), we roughly mimic the temperature trends. This first simple model uses only two temperature categories: cold and warm. We, then, used the following pattern: cold (blue background), warm (red background), cold, warm. We

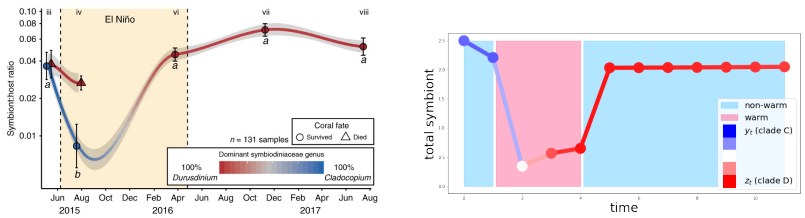

Figure 2: Comparison between observations from Claar et al. [2020] (Figure reproduced unchanged with the kind permission of the authors, CC) and the output of our model. We can see that the model reproduces the shuffling of symbionts during the warm period (El Niño). Specifically, the symbiont composition shifts from a predominance of the clade Cladocopium (depicted in blue) to a predominance of the clade Durusdinium (depicted in red). Additionally, our model presents a decrease in the total symbiont abundance during the warm period.

choose this temperature pattern to roughly mimic the temperature observed by Chen et al. [2005]. The simulations commenced with approximately three times more of phylotype D than phylotype C, mirroring the initial observations made by Chen et al. [2005].

The model predicts a slight shift from the phylotype D to phylotype C during the first stage, followed by a quicker reversal during the second stage, corresponding to the warmer period of the year. After the summer, the composition slowly shifts from phylotype D to phylotype C, but again this shift is quickly reversed during the last warm period of the observations.

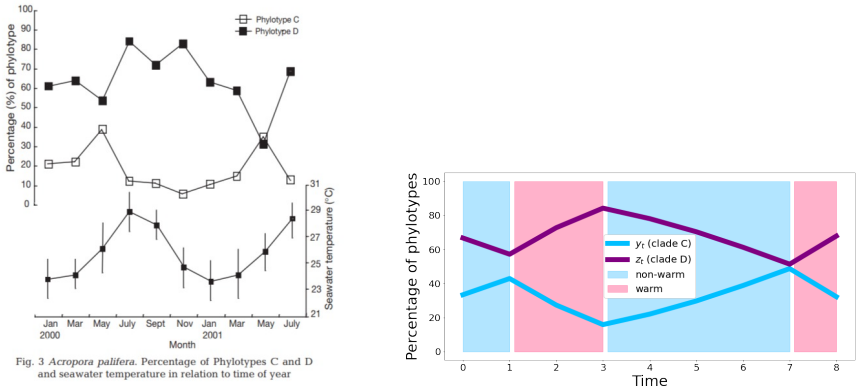

Figure 3: Comparison between observation from Chen et al. [2005] and the output of our model. The value of θ implements the different temperatures: cold for 0 and warm for 1. The percentage of both symbionts changes according to the temperatures.

Distribution of algae species Most of the time, for any specific environment and coral species, one algae species dominates the others [de Souza et al., 2022, LaJeunesse et al., 2010]. Other algal species are still present but at very low densities [Silverstein et al., 2012, Mieog et al., 2007, Ziegler et al., 2018, Quigley et al., 2014, Bay et al., 2016].

In our model the composition of algae is a consequence of the competition between the different clades of algae, and their different growth rates associated with the different temperatures. The ratio of the two algae population at time T is η to the power of the number of time steps where the environment was cold $\theta_t = 1$, multiplied by λ to the power of the number of time steps where the environment was warm $\theta_t = 0$, multiplied by the initial ratio of the two algae population.

$$\sigma_T := \frac{y_T}{z_T} = \eta^{\sum_t 1_{\theta_t=1}} \cdot \lambda^{\sum_t 1_{\theta_t=0}} \cdot \frac{y_0}{z_0}$$

In particular, the composition of symbionts is exponential in the geometric average of growth rates. It means that if we remain long enough in the same environment (i.e. $T_1 > \frac{ln(\frac{z_0}{y_0})}{ln(\eta)}$ in the non-warm environment and $T_0 > \frac{ln(\frac{z_0}{y_0})}{ln(\lambda)}$ in the warm environment) one specie of algae will out-compete the other [Little et al., 2004]. Then, if the environment is not too volatile, most of the time, one alga species will dominate.

Our model can, thus, speak to the influence of the temperature of the environment on the variety of algae species in symbiosis with corals. Indeed, according to the model, a sufficiently prolonged period without change allows a species to out-compete others.

Composition change of algae species It has been observed that the composition of algae changes when temperature increases [Jones et al., 2008, Silverstein et al., 2015, Baker et al., 2004, Hsu et al., 2012]. Warm temperatures can lead the population of algae to move from C to D (i.e. from the relatively efficient to the temperature-resilient clade). Surprisingly, this is not always the case. The population can recover with the same species of algae [de Souza et al., 2022]. This has been referred to as *shuffle back* [Thornhill et al., 2006]. One of the drivers of a change from efficient algae to resilient algae is the duration of warm temperature [Cunning et al., 2015], and the repetition of warm events [Quigley et al., 2022].

Our model offers an interpretation of *shuffle back*, particularly to the environmental regime, including the duration of time spent in the same environment, and the initial composition of algae species. Once more, the symbiont composition follows an exponential pattern with the geometric averages of growth rates.

$$\sigma_T := \frac{y_T}{z_T} = \eta^{\sum_t 1_{\theta_t=1}} \cdot \lambda^{\sum_t 1_{\theta_t=0}} \cdot \frac{y_0}{z_0}$$

The exponential dynamic could explain why for a short warm temperature event, corals do not change their composition of algae (in the formula, the main factor

will be the initial ratio) [Bay et al., 2016] while on the other hand, a longer warmer temperature event implies a shuffle of the composition of algae (the exponential dynamic will be then decisive) [Cunning et al., 2018].

Density population of algae species Observations by Buddemeier and Fautin [1993] indicate that without stress (i.e. in the same cold environment) the total population of algae is notably unchanging.

In the framework of our model, this observation can be visually explained through the time series below and formally addressed with a condition about α, the efficiency trade-off between the two clades of algae.

Firstly, Figure 4 depicts the density of each symbiont, C and D, as well as their sum, representing the total population (in black), which corresponds to K_t, the amount of nutrients provided by corals to the entire algae population. In the absence of stress, within the cold environment when $\theta = 1$ (in blue), the model predicts an almost constant total population. Notably, the total population remains stable even as the composition undergoes changes.

Secondly, this can also be studied formally. Recall that K_t is characterized as the total population of algae and the optimum is given by

$$K_t^* = \frac{b^2}{4} \frac{\rho(\theta_t)\sigma_{t-1} \cdot \theta_t + \alpha}{\rho(\theta_t)\sigma_{t-1} + 1}.$$

In the non-warm environment, we have

$$K_t^* = \frac{b^2}{4} \frac{\eta\sigma_{t-1}+\alpha}{\eta\sigma_{t-1}+1}$$

With $\alpha \approx 1$, the total population of algae K_t^* is approximately constant. In particular, K_t^* no longer depends on the relative density of algal species σ.

$$K_t^*(\sigma_t) \approx \frac{b^2}{4}$$

We can make more precise the statement that the difference $1 - \alpha$ does not dramatically impact K_t.

$$\begin{aligned} K_t^* &= \frac{b^2}{4} \frac{\rho(\theta_t)\sigma_{t-1}+\alpha}{\rho(\theta_t)\sigma_{t-1}+1} \\ K_t^* &= \frac{b^2}{4} \frac{\rho(\theta_t)\sigma_{t-1}+(1-(1-\alpha))}{\rho(\theta_t)\sigma_{t-1}+1} \\ K_t^* &= \frac{b^2}{4} - (1-\alpha)\frac{b^2}{4} \frac{1}{\rho(\theta_t)\sigma_{t-1}+1} \end{aligned}$$

Since, the term $\frac{1}{\rho(\theta_t)\sigma_{t-1}+1}$ is necessarily less than 1, we have that for $\alpha \to 1$, $K_t^* \to \frac{b^2}{4}$.

Venn et al. [2008] explained that the change in the composition of algae clade does not need bleaching. Again, we have in our model that the composition can change without a strong change of K_t (which is defined as bleaching).

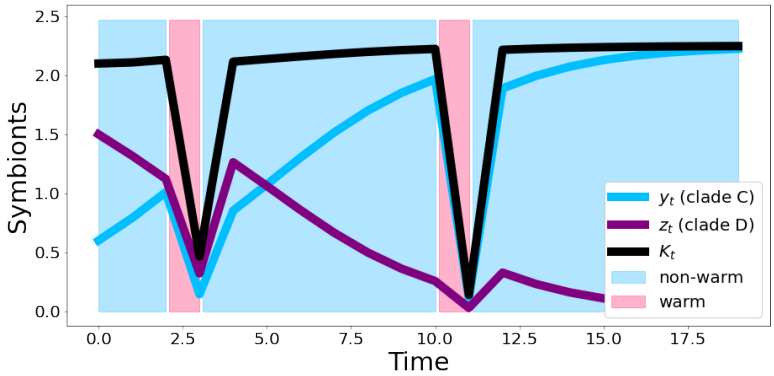

Figure 4: Output of our model. Note that K_t, the total population of algae, is almost constant, as long as the environment is constant.

Bleaching severity It has been observed that bleaching is less severe when the proportion of resilient algae is higher [Palacio-Castro et al., 2023, Fabricius et al., 2004, Douglas, 2003, Quigley et al., 2020]. In particular, Cunning et al. [2015] observed that the severity of bleaching diminished proportionally to the relative abundance of the resilient symbiont.

In our model, we define bleaching as the ratio of the total algae population in non-warm environments to the total population in warm environments. Put differently, this ratio quantifies the reduction factor in the total population when the environment becomes warm. Formally,

$$severity := \frac{K_t^*(\theta=1)}{K_t^*(\theta=0)} \quad \approx \quad 1 + \frac{\eta}{\alpha} \cdot \sigma_{t-1}$$

According to this definition, *severity* is an affine function of the algae species composition at the previous period. Indeed, by assuming that λ and η are not too different, we have that the severity of bleaching is 1 plus $\frac{\eta}{\alpha}$ multiplied by σ_{t-1}, the ratio of the density of y_{t-1} and z_{t-1}. Since $\frac{\eta}{\alpha}$ is strictly positive, increasing the ratio σ_{t-1} will increase severity. This can serve as a rough estimate of how the proportion of each algal species may influence the severity of bleaching.

5 Generalization for any temperatures

In this section, we propose to generalize the model for an arbitrary number of different temperature environments. The dynamic is the following,

$$\begin{cases} y_t &= \frac{\rho(\theta_t)y_{t-1}}{\rho(\theta_t)y_{t-1}+z_{t-1}}K_t \\ z_t &= \frac{z_{t-1}}{\rho(\theta_t)y_{t-1}+z_{t-1}}K_t \end{cases}$$

The instantaneous coral payoff is still $u(y_t, z_t, \theta_t, K_t) = b(y_t, z_t, \theta_t) - c(\theta_t, K_t)$, but with generalized benefit function $b(y_t, z_t, \theta_t) = \sqrt{y_t \cdot b_{\theta_t} + \alpha \cdot z_t}$, and with the feeding cost still the same $c(\theta_t, K_t) = K_t$.

The optimal quantity of nutrients coral should provide to algae – for each environment – is now the following:

$$K_t^{\theta_t} = \frac{1}{4} \frac{\rho(\theta_t)\sigma_{t-1} \cdot b_{\theta_t} + \alpha}{\rho(\theta_t)\sigma_{t-1} + 1}$$

In this generalized model, both the proportion of each algae clade and the total algae densities change continuously with the environment. This is consistent with the observation that the composition of symbionts reacts to small changes in the environment [de Souza et al., 2022].

It has been shown that high-frequency temperature variability has significantly reduced bleaching [Safaie et al., 2018, Sully et al., 2019]. On the other hand, bleaching is more usual where thermal-stress anomalies are more frequent [Sully et al., 2019]. It has also been observed that resilient algae are more present in variable environments [Baker et al., 2013a, Carballo-Bolaños et al., 2019, Oliver and Palumbi, 2011]. Similarly, a bimodal temperature has been shown to decrease bleaching prevalence [McClanahan et al., 2019].

According to this model, it can be demonstrated that temperature variability affects the composition of algae differently than in a stable temperature environment. More precisely, the resilient symbiont can out-compete the efficient one if the temperatures fluctuate enough, while this would not have been possible under the corresponding constant temperature. Mathematically, since the geometric average is always lower than the arithmetic average, we have that variability (in the range of temperature still low enough) gives a relative advantage to the resilient algae species, which, in turn, makes corals more resilient.

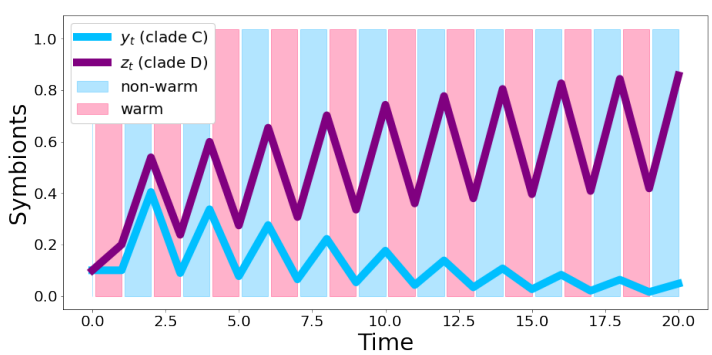

Figure 5: Plot of the model for $\eta = 1.5$ and $\lambda = 0.5$. The resilient algae outcompete the efficient ones over the long term.

However, if the temperature increases too much, (which could correspond, for example to the scenarios *business as usual* from the IPCC [Pörtner et al.,

2019]) even the resilient symbiont will not be able to survive, and corals will face dramatic decreases. We hypothesize that there is a non-linearity between the increase in temperature and coral survival. While a small temperature increase should lower coral survival only a bit [Rowan, 2004] because of the trade-offs between temperature-sensitive and temperature-tolerant algae, warmer temperatures could be significantly more dangerous. Logan et al. [2014] estimate that symbiont shuffling alone will only delay most bleaching events by approximately 10 years (according to most of the lowest emissions scenario).

6 General discussion

Surprisingly, the coral-algae symbiosis lives near its thermal threshold. They do not tolerate a temperature barely higher than their optimal temperature. This threshold can vary with depth [Iglesias-Prieto et al., 2004], location, and other factors [Berkelmans, 2002]. Inhabiting the sea close to this limit may initially seem precarious for corals. However, the capacity of corals to shuffle symbionts provides insight into why it could be a potentially advantageous strategy. The presence of different algal species, specialized for various environments, allows corals to navigate and thrive within dynamic environmental conditions, contributing significantly to their overall resilience. As suggested by Douglas [2003], bleaching may possibly be an advantage in different environments (especially before climate change).

Cunning [2021] argued that the disturbance regime is important to predict future coral reef survival. In our model, we can show that a sufficiently long time (i.e. $T > \frac{ln(\frac{z_0}{y_0})}{ln(\eta)}$) without warm temperatures implies a shuffle back to the relatively less resilient algal species. Corals will, then, be more vulnerable to warm temperatures. Put differently – according to our model – infrequent temperature warming could be more dangerous than frequent temperature warming. In the latter case, corals are better adapted. This characteristic has also been explained in the model of Ware et al. [1996].

According to our model, the effective shuffling of symbionts by corals proves beneficial in enhancing resilience within a specific range of temperature increases. However, this adaptive approach proves advantageous up to the point where the temperature exceeds the threshold of resilience for the algae. Beyond this point, shuffling ceases to provide additional benefits to coral resilience. For a more in-depth exploration of projections regarding coral bleaching, we refer to the work of Logan et al. [2014].

In this study, we focus on the symbiosis between coral and algae for the purpose of clarity. However, we expect that the argument developed in this paper could also be applied to the symbiosis between the coral and the microbiome [Ziegler et al., 2017, Voolstra and Ziegler, 2020]. Just as outlined before, nutrients or signals provided by the coral could control the microbiome population [Rädecker et al., 2015]. The population of microbes also encompasses a diversity of different species, with a variety of functions. Accordingly, it may reasonably be hypothesized that the microbiome also acts as a buffer against

environmental fluctuations. For a model including the coral microbiome, see for example Lima et al. [2020]. Likewise, the sole environmental variable accounted for in the model is sea temperature; nevertheless, a comparable phenomenon may occur with light.

It is tempting to think that acclimation to higher temperatures by symbiont shuffling could lead to lower resistance to other disturbances [Putnam, 2021, Claar et al., 2020]. Indeed, as it has been shown that there is a trade-off between efficiency and resilience, one could speculate that there is also a trade-off between resilience for different disturbances (such as temperature and acidity). The consequence would be that climate change would not only lower the efficiency of the algae symbiosis but also lower their resilience to other disturbances.

7 Conclusion

We developed a model wherein a coral optimizes the quantity of nutrients provided to the total population of algae. Two distinct species of algae (one relatively more efficient, the other relatively more resilient to temperature increases) compete for access to the nutrients supplied by the coral.

The model explains the phenomenon of bleaching as an adaptive process within coral symbiosis. This stylized model allows us to express several key quantities analytically. The severity of bleaching is inferred as a function of the current temperature and the proportion of each algae species but is independent of the density of the algae populations. Also, the future composition of algae species is anticipated to be proportional to the current composition of algae species multiplied by the geometric average of the different growth rates associated with the different environments. With the same result, we can hypothesize the limits of coral adaptation through symbiont change for temperatures too high for the resilient algal species.

This analytical model, with only a few parameters, offers explanations for various previously observed phenomena, including the responses of total population density under constant or variable environmental conditions. Furthermore, the model can explain features noted under different temperature regimes, such as the *shuffle back* phenomenon during short warming periods and the prevalence of resilient algae species amidst highly variable temperatures.

The analytical expressions allow for potential statistical testing, facilitating an assessment of the model's predictions. Additionally, the model could be applied in conjunction with climate change predictions to assess the potential survival of coral reefs in the forthcoming decades. Ultimately, the model could serve as a building block for integrating other interconnected phenomena, such as assessing the impact of acidity or the loss of biodiversity within the coral ecosystem.

A Typical time scale to shuffle back to the efficient clade

We want to prove that the typical time that it takes to achieve a majority of the efficient clade (y) when the environment is always in the non-warm state is $T > \frac{ln(\frac{z_0}{y_0})}{ln(\eta)}$. We here define as the typical time that it takes to achieve a majority of the efficient clade (y) as the first time when $y_t > z_t$, which is equivalent to $\sigma_t > 1$ (by definition). Recall that we have

$$\sigma_T := \frac{y_T}{z_T} = \eta^{\sum_t 1_{\theta_t=1}} \cdot \lambda^{\sum_t 1_{\theta_t=0}} \cdot \frac{y_0}{z_0}$$

Since we consider a succession of only non-warm states, we have

$$\sigma_T = \eta^T \cdot \frac{y_0}{z_0}$$

Then,

$$\begin{array}{rrcl} & \sigma_T & > & 1 \\ \Leftrightarrow & \eta^T \cdot \frac{y_0}{z_0} & > & 1 \\ \Leftrightarrow & T & > & \frac{ln(\frac{z_0}{y_0})}{ln(\eta)} \end{array}$$

Similarly, we can prove that the typical time that it takes to shuffle to the resilient clade when the environment is always in a warm environment is $T > \frac{ln(\frac{z_0}{y_0})}{ln(\lambda)}$.

B Optimum K_t^* for any temperatures

We here generalize previous results for any temperature. The instantaneous coral payoff is still $u(y_t, z_t, \theta_t, K_t) = b(y_t, z_t, \theta_t) - c(\theta_t, K_t)$,
with benefit function different as before $b(y_t, z_t, \theta_t) = \sqrt{y_t \cdot b_{\theta_t} + \alpha \cdot z_t}$,
and the feeding cost is still the same $c(\theta_t, K_t) = K_t$.

$$u(y_t, z_t, \theta_t, K_t) = \sqrt{y_t \cdot b_{\theta_t} + \alpha \cdot z_t} - K_t$$

The dynamics of algae are still,

$$\begin{array}{rcl} y_t & = & \frac{\rho(\theta_t) y_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t \\ z_t & = & \frac{1 z_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t \end{array}$$

We can rewrite, again, the expression of the payoff, as a function of θ_t and K_t. Again, recall that by definition, $\sigma_t := \frac{y_t}{z_t}$.

$$\begin{array}{rcl} u(\theta_t, K_t) & = & \sqrt{\frac{\rho(\theta_t) y_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t \cdot b_{\theta_t} + \alpha \cdot \frac{z_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t} - K_t \\ & = & \sqrt{\frac{\rho(\theta_t) \sigma_{t-1}}{\rho(\theta_t) \sigma_{t-1} + 1} K_t \cdot b_{\theta_t} + \alpha \cdot \frac{1}{\rho(\theta_t) \sigma_{t-1} + 1} K_t} - K_t \\ & = & \sqrt{\frac{\rho(\theta_t) \sigma_{t-1} \cdot b_{\theta_t} + \alpha}{\rho(\theta_t) \sigma_{t-1} + 1} K_t} - K_t \end{array}$$

Consider the derivative with respect to the control parameter K_t.

$$\frac{\partial u}{\partial K_t} = \sqrt{\frac{\rho(\theta_t)\sigma_{t-1} \cdot b_{\theta_t} + \alpha}{\rho(\theta_t)\sigma_{t-1} + 1}} \frac{1}{2\sqrt{K_t}} - 1$$

The derivative is null only at one point,

$$\begin{array}{rrcl} & \frac{\partial u}{\partial K_t} & = & 0 \\ \Leftrightarrow & K_t^{\theta_t} & = & \frac{1}{4} \frac{\rho(\theta_t)\sigma_{t-1} \cdot b_{\theta_t} + \alpha}{\rho(\theta_t)\sigma_{t-1} + 1} \end{array}$$

The optimum quantity of nutrients the coral should provide to the population of algae is then:

$$\begin{array}{rcl} K_t^{\theta_t} & = & \frac{1}{4} \frac{\rho(\theta_t)\sigma_{t-1} \cdot b_{\theta_t} + \alpha}{\rho(\theta_t)\sigma_{t-1} + 1} \\ K_t^{\theta_t} & = & \frac{1}{4} \frac{\rho(\theta_t)\sigma_{t-1} \cdot b_{\theta_t} + \alpha}{\rho(\theta_t)\sigma_{t-1} + 1} \end{array}$$

C Payoff generalization

In this section, we want to show that there is exactly one optimum for a broader definition of benefit and cost function. We use the following definition of benefit and cost.

$$u(y_t, z_t, \theta_t, K_t) = b(y_t, z_t, \theta_t) - c(\theta_t, K_t),$$

with

$$\begin{array}{rcl} b(y_t, z_t, \theta_t) & = & b(y_t \cdot \theta_t + \alpha \cdot z_t)^\beta \\ c(\theta_t, K_t) & = & K_t^\gamma \end{array}$$

The dynamic of algae is still the same,

$$\left\{ \begin{array}{rcl} y_t & = & \frac{\rho(\theta_t) y_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t \\ z_t & = & \frac{z_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t \end{array} \right.$$

We can rewrite, again, the expression of the payoff, as a function of θ_t and K_t.

$$\begin{array}{rcl} u(\theta_t, K_t) & = & b\left(\frac{\rho(\theta_t) y_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t \cdot \theta_t + \alpha \cdot \frac{z_{t-1}}{\rho(\theta_t) y_{t-1} + z_{t-1}} K_t\right)^\beta - K_t^\gamma \\ & = & b\left(\frac{\rho(\theta_t)\sigma_{t-1}}{\rho(\theta_t)\sigma_{t-1} + 1} K_t \cdot \theta_t + \alpha \cdot \frac{1}{\rho(\theta_t)\sigma_{t-1} + 1} K_t\right)^\beta - K_t^\gamma \\ & = & b\left(\frac{\rho(\theta_t)\sigma_{t-1} \cdot \theta_t + \alpha}{\rho(\theta_t)\sigma_{t-1} + 1} K_t\right)^\beta - K_t^\gamma \end{array}$$

The first derivative,

$$\frac{\partial u}{\partial K_t} = b\left(\frac{\rho(\theta_t)\sigma_{t-1} \cdot \theta_t + \alpha}{\rho(\theta_t)\sigma_{t-1} + 1}\right)^\beta \cdot \beta K_t^{\beta-1} - \gamma K_t^{\gamma-1},$$

is null only at one point in the interior, i.e., in $(0, \infty)$, for $\beta < \gamma$.

$$\begin{aligned}
& & \frac{\partial u}{\partial K_t} &= 0 \\
\Leftrightarrow & & b\left(\frac{\rho(\theta_t)\sigma_{t-1}\cdot\theta_t+\alpha}{\rho(\theta_t)\sigma_{t-1}+1}\right)^{\beta}\cdot\beta K_t^{\beta-1} - \gamma K_t^{\gamma-1} &= 0 \\
\Leftrightarrow & & b\left(\frac{\rho(\theta_t)\sigma_{t-1}\cdot\theta_t+\alpha}{\rho(\theta_t)\sigma_{t-1}+1}\right)^{\beta}\cdot\beta - \gamma K_t^{\gamma-\beta} &= 0 \\
\Leftrightarrow & & b\left(\frac{\rho(\theta_t)\sigma_{t-1}\cdot\theta_t+\alpha}{\rho(\theta_t)\sigma_{t-1}+1}\right)^{\beta}\cdot\beta &= \gamma K_t^{\gamma-\beta} \\
\Leftrightarrow & & K_t &= \left(\frac{\beta}{\gamma} b\left(\frac{\rho(\theta_t)\sigma_{t-1}\cdot\theta_t+\alpha}{\rho(\theta_t)\sigma_{t-1}+1}\right)^{\beta}\right)^{\frac{1}{\gamma-\beta}}
\end{aligned}$$

D Shuffling and switching

In this appendix, we want to show that, in general, the dynamic of alga is driven by the growth of alga already present in the symbiosis. While it has been shown that shuffling (a change in the proportion of species of algae already present with the host) is more significant than switching (the establishment of symbiosis with new species of algae) [Berkelmans and Van Oppen, 2006, Jones et al., 2008], corals have still the possibility to establish new symbiosis [Boulotte et al., 2016]. According to Sampayo et al. [2008] the main driver of composition change is the differential mortality of algae. We propose a variation of the model described earlier to consider the possibility for the coral to establish new symbiosis. We note τ the quantity of new symbiont.

$$\begin{cases} y_{t+1} &= \frac{\rho(\theta_t)y_t+\tau}{\rho(\theta_t)y_t+z_t+2\tau}K_t \\ z_{t+1} &= \frac{z_t+\tau}{\rho(\theta_t)y_t+z_t+2\tau}K_t \end{cases}$$

We can show that:

$$\begin{aligned}
\frac{y_{t+1}}{z_{t+1}} &= \frac{\rho(\theta_t)y_t+\tau}{z_t+\tau} \\
&= \rho(\theta_t)\frac{y_t}{z_t} + \frac{-\rho(\theta_t)\frac{y_t}{z_t}(z_t+\tau)+\rho(\theta_t)y_t+\tau}{z_t+\tau} \\
&= \rho(\theta_t)\frac{y_t}{z_t} + \frac{-\rho(\theta_t)\frac{y_t}{z_t}\tau+\tau}{z_t+\tau} \\
\frac{y_{t+1}}{z_{t+1}} &= \rho(\theta_t)\frac{y_t}{z_t} + \frac{1-\rho(\theta_t)\frac{y_t}{z_t}}{\frac{z_t}{\tau}+1}
\end{aligned}$$

For $\tau < \frac{\rho(\theta_t)y_t}{1-2\rho(\theta_t)\frac{y_t}{z_t}}$, we have that shuffling as a larger influence than switching. In particular, if τ the quantity of new symbiosis is small enough, the dynamic of algae will not be significantly affected.

This means that if we relax the assumption to allow both *shuffling* and *switching*, as long as the influx of new symbionts is sufficiently small (a quantity we can characterize), the dynamics of the algae are not dramatically impacted, and the previously observed results remain valid.

E Non-myopic corals

In this section, we assume corals optimize their fitness in the long term and not only for the present time. We consider again two states of the environment $\theta \in \{0, 1\}$ with 0 the *bad* state and 1 the *good* state. However, now the two states occur according to a Markov model, with transition probabilities p_{00}, p_{01}, p_{10}, and p_{11}, where p_{ij} is the probality of a switch from state $i \in \{0, 1\}$ to state $j \in \{0, 1\}$. The dynamics of the algae are given by

$$\begin{cases} y_{t+1} &= \frac{\rho(\theta_t)y_t}{\rho(\theta_t)y_t+z_t}K_t \\ z_{t+1} &= \frac{z_t}{\rho(\theta_t)y_t+z_t}K_t \end{cases}$$

The overall payoff function is now

$$U = \sum_{t=0}^{\infty} \delta^t u(y_t, z_t, \theta_t, K_t)$$

Both the benefit and cost functions are maintained. The optimal nutrient quantity for the two states is as follows. The solution has now become slightly more complicated.

$$\begin{cases} K_t(1, \sigma_t) &= \frac{(\delta b)^2}{4(\eta\sigma_t+1)}(p_{11}\sqrt{\eta\sigma_t + \alpha} + p_{10}\sqrt{\alpha})^2 \\ K_t(0, \sigma_t) &= \frac{(\delta b)^2}{4(\lambda\sigma_t+1)}(p_{01}\sqrt{\lambda\sigma_t + \alpha} + p_{00}\sqrt{\alpha})^2 \end{cases}$$

Notice that for $\sigma_t \to 0$ the influence of the stochastic process is negligible on the optimum $K_t(1, .)$ and $K_t(0, .)$. If we have almost only the resilient algae, then the optimum quantity of the population of algae will be the same, for all expected future states (since the resilient algae will perform equally well).

Note also that the generalized solution here embeds the previous solution. Indeed, for $\delta \to 1, p_{11} \to 1$ and $p_{00} \to 1$ we have the same optimum (for the next step). Consider the relative change between the two different model results (m refers as the myopic –basic– model, and nm as the non-myopic model, presented here):

$$\begin{aligned} \frac{K_t^{nm}(1,\sigma_t)}{K_t^{m}(1,\sigma_{t+1})} &= \frac{\frac{(\delta b)^2}{4(\eta\sigma_t+1)}(p_{11}\sqrt{\eta\sigma_t+\alpha}+p_{10}\sqrt{\alpha})^2}{\frac{b^2}{4}\frac{\eta\sigma_t+\alpha}{\eta\sigma_t+1}} \\ &= \delta^2\left(p_{11} + (1-p_{11})\sqrt{\frac{1}{1+\frac{\eta\sigma_t}{\alpha}}}\right)^2 \end{aligned}$$

$$\begin{aligned} \frac{K_t^{nm}(0,\sigma_t)}{K_t^{m}(0,\sigma_{t+1})} &= \frac{\frac{(\delta b)^2}{4(\lambda\sigma_t+1)}(p_{01}\sqrt{\lambda\sigma_t+\alpha}+p_{00}\sqrt{\alpha})^2}{\frac{b^2}{4}\frac{\alpha}{\lambda\sigma_t+1}} \\ &= \delta^2\left(p_{00} + (1-p_{00})\sqrt{1+\frac{\lambda\sigma_t}{\alpha}}\right)^2 \end{aligned}$$

With this model, we find that the optimal K_t^* depends on the stochastic regime (i.e., p_{ij}).

If corals are indeed adapted to a specific stochastic regime (i.e., a specific value of p), transferring corals from one sea associated with one regime to another could lead to their maladaptation in the new stochastic environment. The translocation of corals between seas may necessitate further investigation of the various environmental factors, particularly the temperature conditions, to ensure the well-being of the corals.

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