Modelling Bacteria-enhanced Thermal Tolerance in Marine Phytoplankton

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Introduction

Phytoplankton (or algae) fuel marine food webs, regulate major nutrient cycles, and produce about 50% of Earth's oxygen. Warming oceans will affect algal growth, productivity, and geographic ranges. However, few predictive models consider effects of species interactions, especially mutualisms. Recent lab studies show algae-bacteria interactions enhance algal thermal tolerance.[1,2] We modeled this mutualism to study:

1. How stable is this ecological interaction across temperatures?
2. What mechanisms protect this mutualism from collapse via the evolution of cheaters?

Algae-Bacteria Model

Changes in algae (A) and bacteria (B) biomass depend on their temperature (T) dependent growth and death rates. The mutualists (A & B) synthesize photosynthate (C) and cobalamin (B_{12}) for their partner's benefit, yet compete for nitrogen (N).

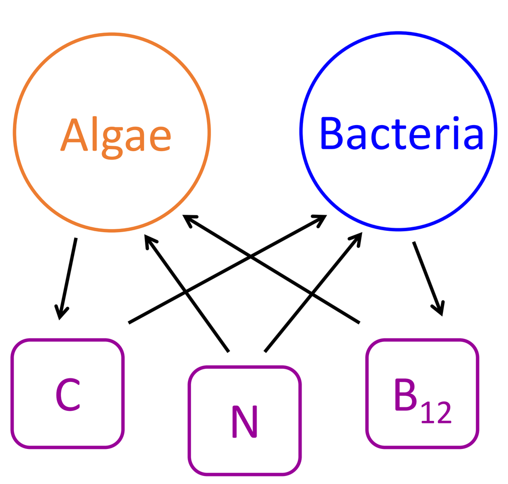
$$A' = A(\underset{\text{Growth (METH)}}{\mu_H[B_{12}, N, T]} + \underset{\text{Growth (METE)}}{\mu_E[N,T]} - \underset{\text{Death}}{m_A[T]})$$

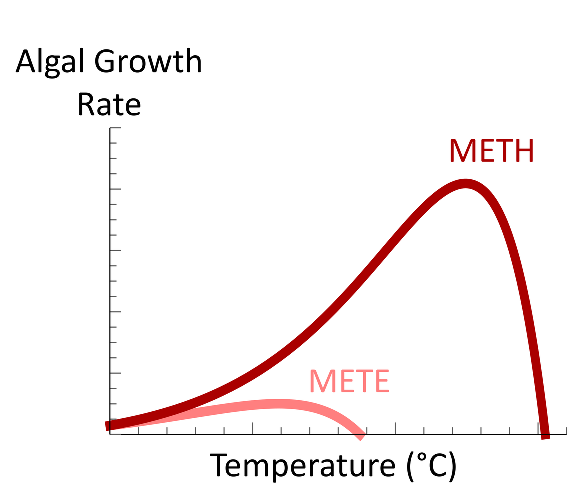
$$B' = B(\underset{\text{Growth}}{\mu_B[C, N, T]} - \underset{\text{Death}}{m_B[T]})$$

$$N' = \rho(\underset{\text{Inflow}}{N_{in}} - \underset{\text{Outflow}}{N}) - \underset{\text{Algal uptake}}{(\mu_E A + \mu_H A)} - \underset{\text{Bacterial uptake}}{\mu_B B}$$

$$B_{12}' = \rho(\underset{\text{Inflow}}{B_{12in}} - \underset{\text{Outflow}}{B_{12}}) - \underset{\text{Algal uptake}}{\mu_H A} + \underset{\text{Synthesis}}{s_{B12} B}$$

$$C' = \rho(\underset{\text{Inflow}}{C_{in}} - \underset{\text{Outflow}}{C}) - \underset{\text{Bacterial uptake}}{\mu_B B} + \underset{\text{Synthesis}}{s_C A}$$

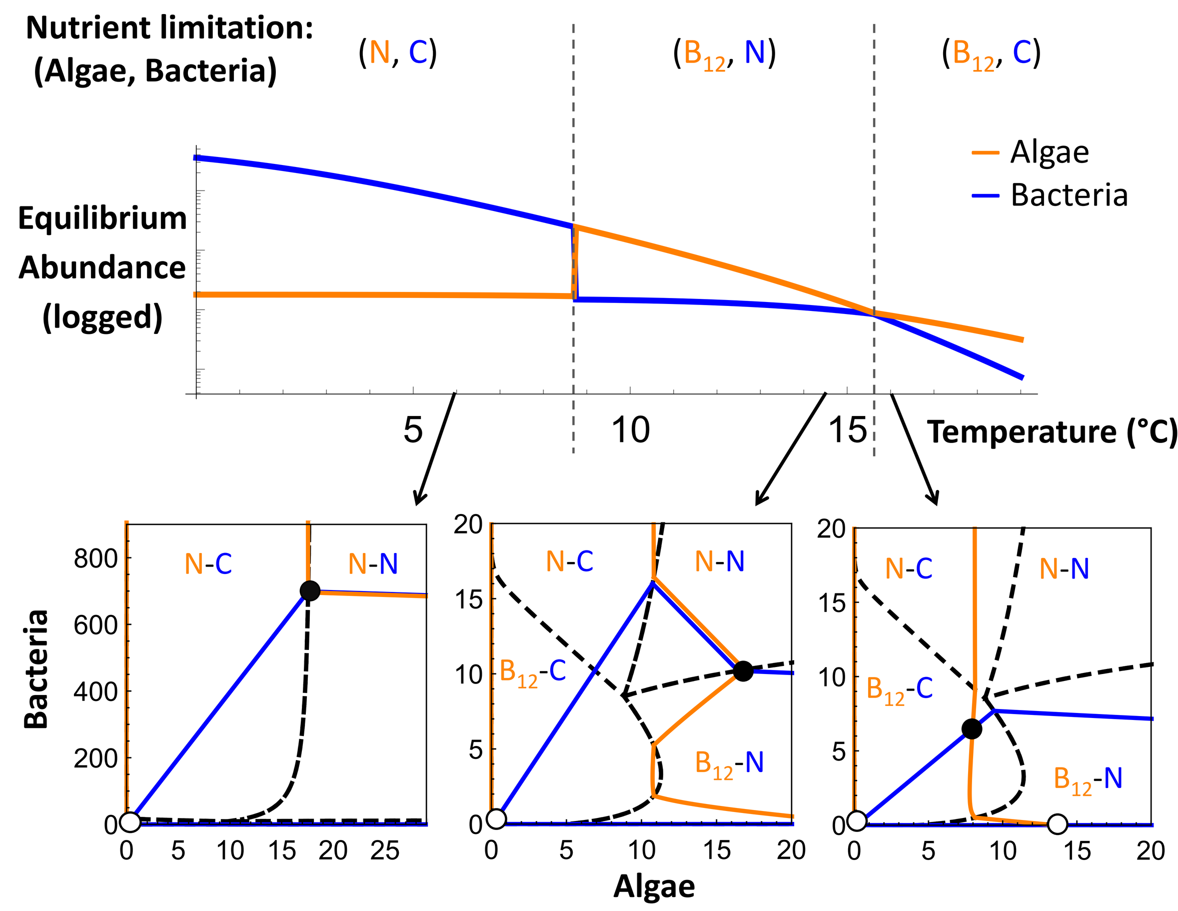




Bacteria depend obligately on carbon from algae. However, many algae rely facultatively on B_{12}. With B12, they can use the METH pathway to make methionine, a process that works well at high temperatures. Without B12, they use an alternate pathway, METE, that is less efficient.

Temperature Dependence

We analyzed this ODE model using a quasi-equilibrium framework[3] to investigate how temperature changes equilibrium abundances and which nutrients limit each mutualist.



At high temperatures, both species were limited by the nutrients provided by their partner, highlighting mutualism's importance in warming oceans.

Evolutionary Instability

Prior models[3] ignore the costs of mutualism. We explored two trade-offs linking growth μ to substrate synthesis s, governed by ϕ which ranged between 0 (only growth) and 1 (only synthesis).

Then we studied the effects of selection on optimal ϕ using a quantitative genetics approach[5]:

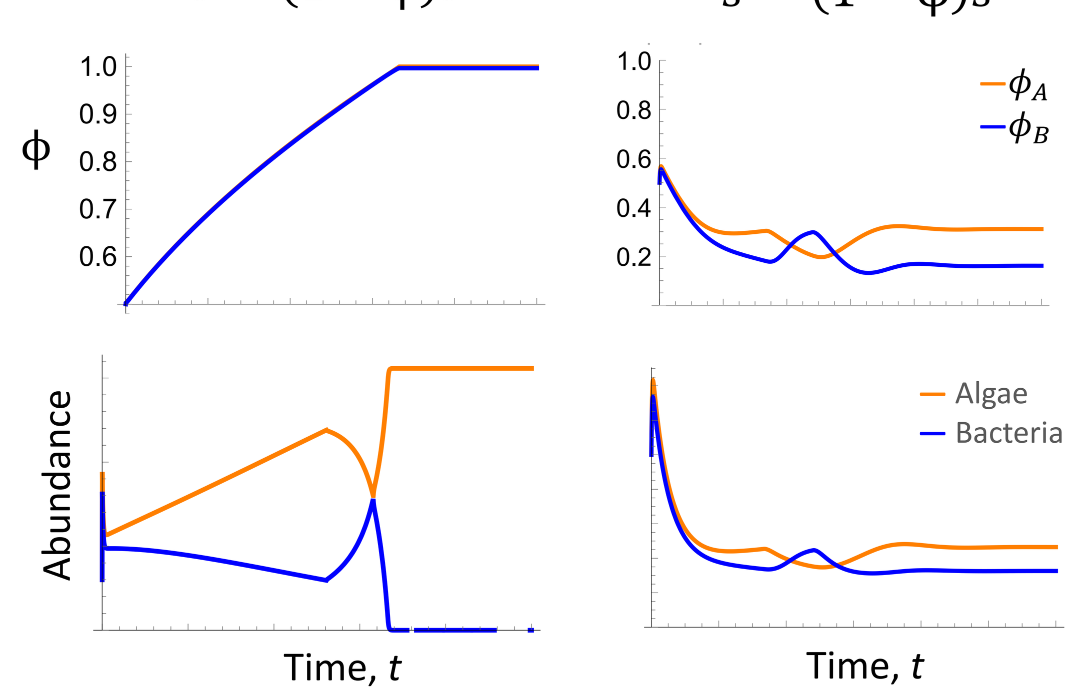
$$\frac{d\phi}{dt} = V \frac{\partial}{\partial \phi}\left(\frac{A'}{A}\right)$$

<u>s linked to μ</u>

$$\hat{\mu} = \phi\mu$$
$$\hat{s} = (1-\phi)s$$

<u>s linked to $\mu - m$</u>

$$\widehat{(\mu - m)} = \phi(\mu - m)$$
$$\hat{s} = (1-\phi)s$$



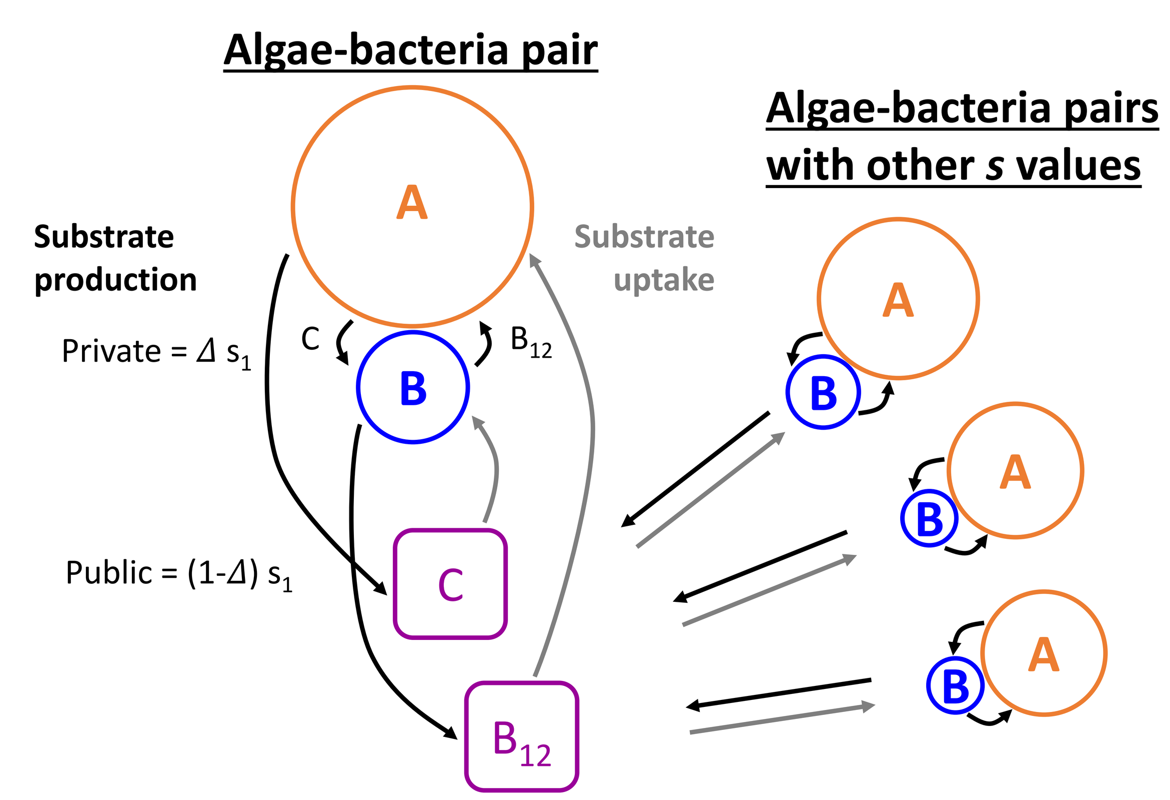
Loss of Cooperation | **Loss of Selection**

Private substrate exchange

Addressing limitations of our initial work, we built a second model of this interaction, where:

- Costs of substrate production and sharing are explicit (and tied to internal nutrient stores)
- Substrates can be exchanged privately and/or publicly between algae and bacteria

We predicted this would stabilize the evolutionary dynamics of the mutualism. Key relationships in the new model are shown here:



Pairs of algae and bacteria produce C and B_{12} at rate s, share a fraction Δ privately with their partner, and excrete the rest. Different pairs can have different synthesis rates. All individuals also compete for N (not shown), and we track per-cell contents (or quotas, Q) of N, C, and B_{12} for A and B. For simplicity, we neglect temperature effects.

$$A' = A\,(\underset{\text{Growth}}{\mu f[\dot{Q}^A]} - \underset{\text{Outflow}}{\rho})$$

$$Q_C^{A\prime} = \underset{\text{Production}}{p_C} - \underset{\text{Growth}}{\mu f[\dot{Q}^A]\, Q_C^A} - \underset{\text{Sharing}}{s_C\,(Q_C^A - Q_{Cmin}^A)}$$

$$Q_{B12}^{A\;\prime} = \underset{\text{Uptake}}{v_{B12}\, B_{12}} + \underset{B_{12}\text{ shared by B}}{\Delta_B\, s_{B12}(Q_{B12}^B - Q_{B12min}^B)\, B/A} - \underset{\text{Growth}}{\mu f[\dot{Q}^A]\, Q_{B12}^A}$$

$$Q_N^{A\prime} = \underset{\text{Uptake}}{v_N\, N} - \underset{\text{Growth}}{\mu f[\dot{Q}^A]\, Q_N^A}$$

$$B' = B\,(\underset{\text{Growth}}{\mu f[\dot{Q}^B]} - \underset{\text{Outflow}}{\rho})$$

$\left(Q_C^{B\prime}, Q_{B12}^{B\;\prime}, Q_N^{B\prime}\right)$ = follow the same structure as algal quotas

$$N' = \rho(\underset{\text{Inflow}}{N_{in}} - \underset{\text{Outflow}}{N}) - \underset{\text{A Uptake}}{v_N\, N\, A} - \underset{\text{B Uptake}}{v_N\, N\, B}$$

$$B_{12}' = \rho(\underset{\text{Inflow}}{B_{12in}} - \underset{\text{Outflow}}{B_{12}}) + \underset{\text{Synthesis}}{(1-\Delta_B) s_{B12}(Q_{B12}^B - Q_{B12min}^B)} B - \underset{\text{A Uptake}}{v_{B12}\, B_{12}\, A}$$

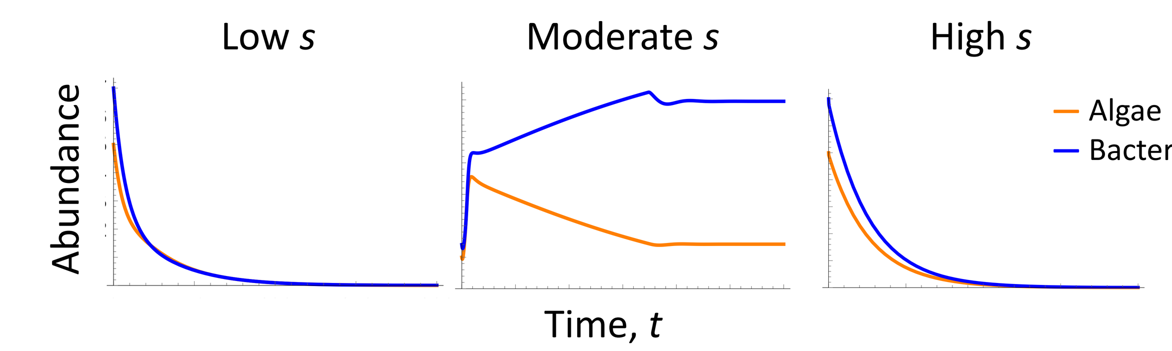
$$C' = \rho(\underset{\text{Inflow}}{C_{in}} - \underset{\text{Outflow}}{C}) + \underset{\text{Synthesis}}{(1-\Delta_A) s_C(Q_C^A - Q_{Cmin}^A)} A - \underset{\text{B Uptake}}{v_C\, C\, B}$$

$$f\left[\dot{Q}^i\right] = Min\left[1 - \frac{Q_{Nmin}^i}{Q_N^i}, 1 - \frac{Q_{B12min}^i}{Q_{B12}^i}, 1 - \frac{Q_{Cmin}^i}{Q_C^i}\right] \text{ where } i \in \{A, B\}$$

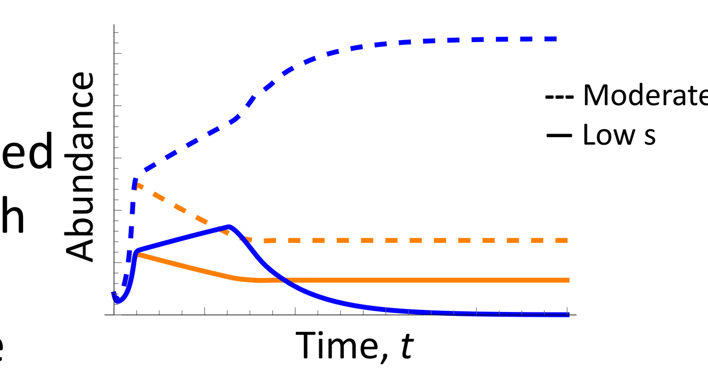
Protection from Cheaters

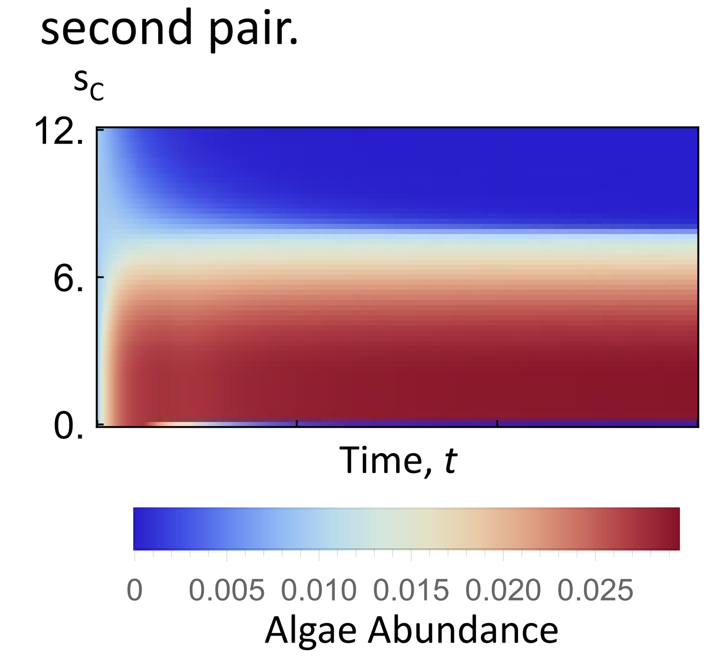
Private substrate exchange prevents non-participating members from accessing nutrients shared by mutualists[4]. We explored how the degree of coupling, governed by Δ, affected the evolution of nutrient sharing (s).

Irrespective of Δ, only A-B pairs with moderate s survived. Low s led to unmet nutrient requirements whereas high s resulted in overinvestment in mutualism at the cost of growth.



At low Δ, two A-B pairs with low and high s_C were allowed to compete[5]. A with low s_C survived on B_{12} released by the second pair.





At high Δ, sixty A-B pairs with different s_C values were allowed to compete[5]. A range of strains with low, but non-zero, s_C coexisted stably.

Conclusions

- Algae species that depend on METH should rely on close associations with bacteria, especially at high temperatures.
- Typical models of microbial mutualisms neglect costs and are evolutionarily unstable.
- Tracking costs and allowing partners to exchange substrate privately stabilizes these interactions.

[1]Xie, B., et al. 2013. *Chlamydomonas reinhardtii* thermal tolerance enhancement mediated by a mutualistic interaction with vitamin B12-producing bacteria. *The ISME Journal*, *7*(8), 1544-1555.

[2]Grant, M. A., et al. 2014. Direct exchange of vitamin B12 is demonstrated by modelling the growth dynamics of algal–bacterial cocultures. *The ISME journal*, *8*(7), 1418-1427.

[3]Sun, Z., et al. 2019. Microbial cross-feeding promotes multiple stable states and species coexistence, but also susceptibility to cheaters. *Journal of Theoretical Biology*, *465*, 63-77.

[4]Stump, S. M., et al. 2018. Local interactions and self-organized spatial patterns stabilize microbial cross-feeding against cheaters. *Journal of the Royal Society Interface*, *15*(140), 20170822.

[5]Klausmeier, C.A., 2022. https://github.com/cklausme/EcoEvo.