## What Causes Spatial Gradients in the Diversity of Marine Phytoplankton?



## Andrew D Barton\*, Mick Follows, Stephanie Dutkiewicz, & Jason Bragg Massachusetts Institute of Technology, Cambridge, MA, USA



INTRODUCTION Many terrestrial and marine taxa show a pronounced equator-to-pole increase in biodiversity<sup>1,2</sup>. It is unknown if this pattern exists in marine phytoplankton. We present here the results of a global ecosystem model<sup>3</sup>, which represents many tens of potential phytoplankton types, that shows an equator-to-pole increase in phytoplankton diversity. Using resource competition theory, we hypothesize that the spatial diversity gradients are linked closely to the timescales of environmental variability in the ocean.

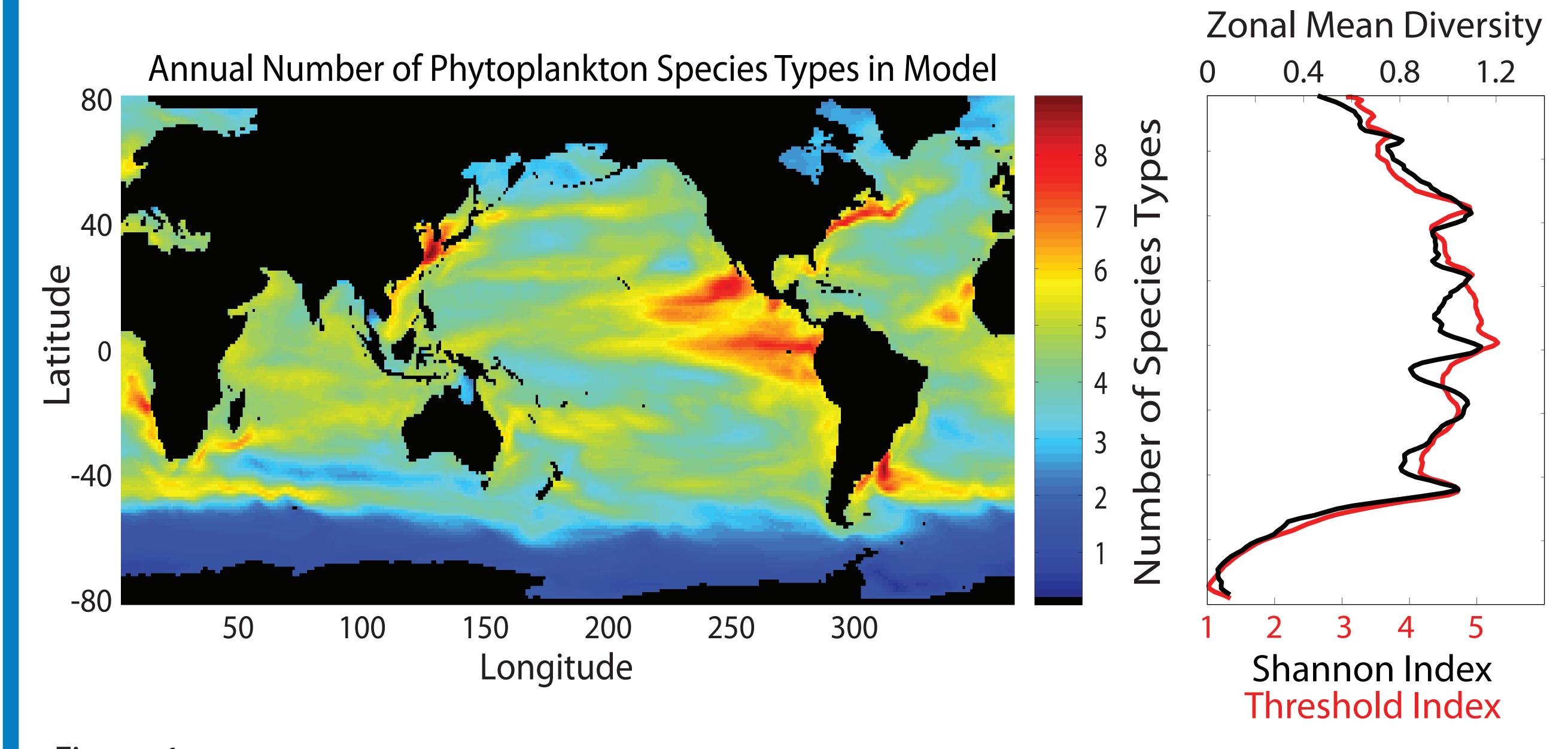


Figure 1 Global map of the diversity of modeled phytoplankton species types (left), defined as the number of species comprising greater than 0.1% of the total biomass at that location. The diversity includes species that are present at any point during the year. The right panel shows the zonal mean of the figure on the left. There are local diversity hotspots in energetic regions of the ocean such as the Gulf Stream, but here we focus on the hemispheric-scale pattern seen in the zonal mean plot on the right. These data are the average of ten unique model runs.

HEMISPHERE-SCALE DIVERSITY GRADIENTS We interpret the hemisphere-scale diversity gradients by using numerical experiments with an idealized, zero-dimensional model of phytoplankton growth with one nutrient<sup>4</sup>:

$$\frac{\partial N}{\partial t} = -\sum_{j} \left[\mu_{j} P_{j} \frac{N}{N+k_{j}}\right] + S_{N}(t) \qquad \frac{\partial P_{j}}{\partial t} = \mu_{j} P_{j} \frac{N}{N+k_{j}} - m_{j} P_{j}$$

where  $P_j$  is the concentration of phytoplankton j, N is the nutrient concentration,  $S_N(t)$  is the time varying source of nutrients (idealized as a sine function),  $\mu_j$  is the growth rate of phytoplankton j,  $k_j$  is the half saturation constant for phytoplankton j, and  $m_j$  is the mortality for phytoplankton j.

In the global model we note that the dominant species in lower latitudes tend also to have the lowest R\* values. R\* is the nutrient concentration at which growth equals mortality:

$$R^* = \frac{m_j k_j}{\mu_j - m_j}$$

We conduct a series of numerical experiments where all phytoplankton have equal R\* values in order to understand the diversity patterns.

## References

<sup>1</sup>Huston, M.A. (1994), Biological Diversity: The Coexistence of Species on Changing Landscape, Cambridge U. Press, Cambridge, UK, 708 pp. <sup>2</sup>Angel, M.V. (1993), Biodiversity of the pelagic ocean, Conservation Biology, 7(4), 760-772. <sup>3</sup>Follows, M.J, et al. (2007), Emergent biogeography of microbial communities in a model ocean, Science, 315, 1843-1846. <sup>4</sup>Tilman, D. (1977), Resource competition between planktonic algae: An experimental and theoretical approach, Ecology, 58, 338-348.

\*Contact adbarton@mit.edu for more information

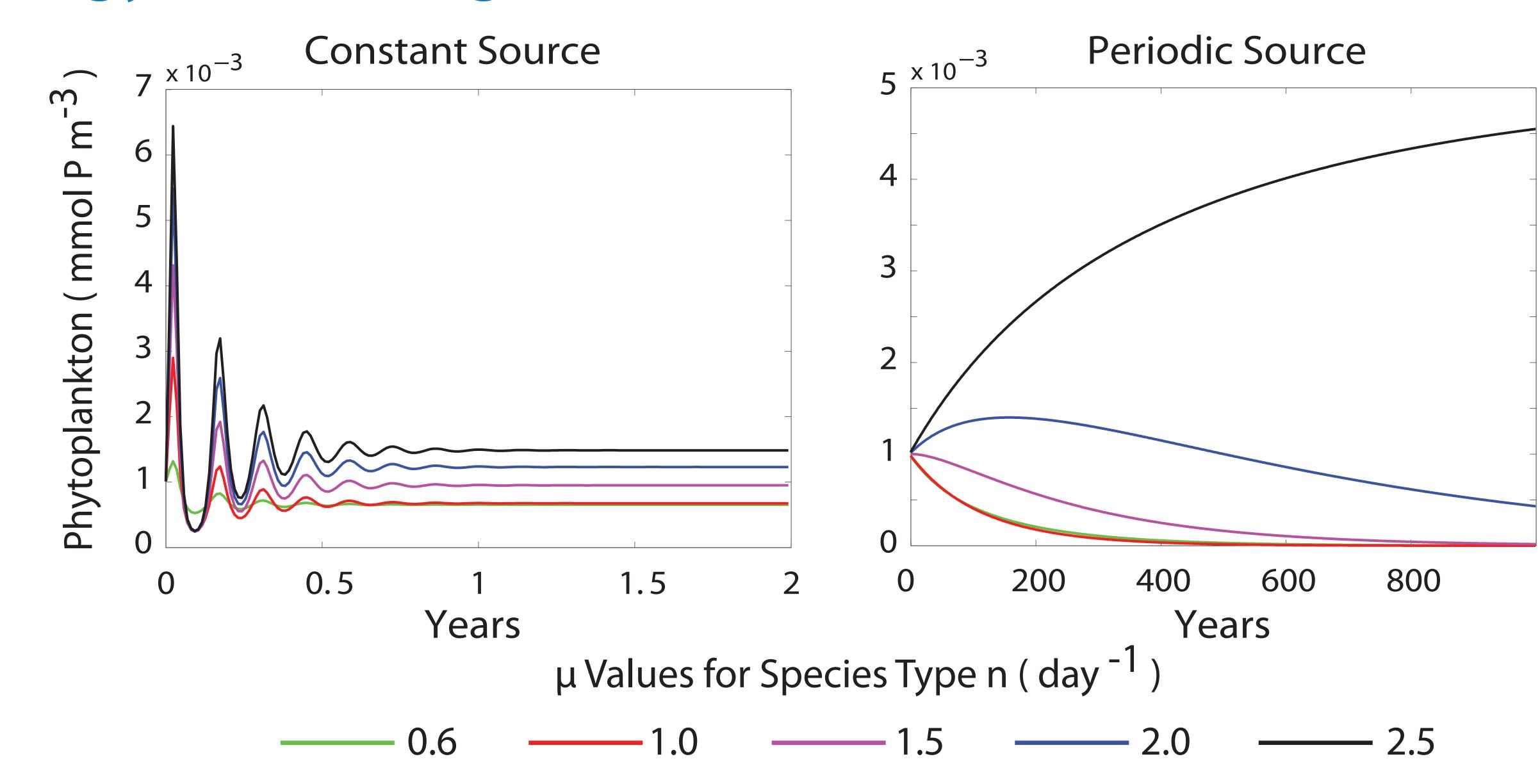
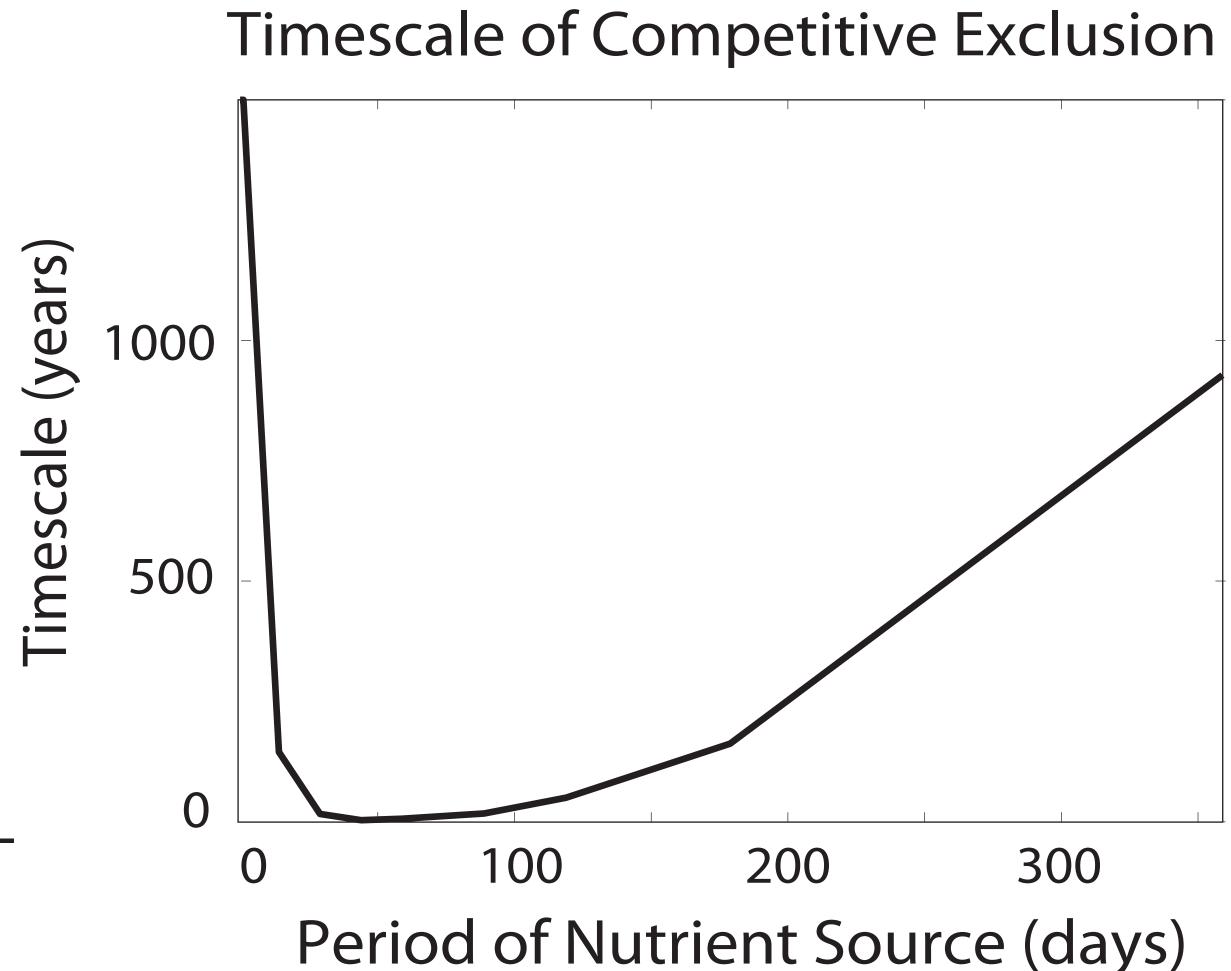


Figure 2 Species with equal R\* can coexist in a stable environment (left). When the environment varies (here, on an annual cycle), the species with the highest growth rate outcompetes the rest, leading to a state of competitive exclusion (right).

TIMESCALES OF VARIABILITY Environmental variability occurs on a range of timescales in the ocean. We use the idealized model to examine how the competitive exclusion timescale depends on the period of environmental variation.

Figure 3 The timescale of competitive exclusion for a range of nutrient source timescales, varying from half a day to one year. The timescale of competitive exclusion is the amount of time it takes for one species to account for 90% of the total biomass. At short (days) and long (annual) nutrient source timescales, species coexist for a long time. For long timescales of competitive exclusion, other processes (e.g., transport, climate change, speciation, extinction, mutation) may be significant. At seasonal timescales, competitive exclusion occurs quickly and diversity is low.



## SUMMARY

An ecosystem model<sup>3</sup> shows an equator-to-pole decrease in phytoplankton diversity (Fig. 1)

We hypothesize that this pattern is governed by the timescales of environmental variability in the ocean:

- In a steady environment, arbitrarily many species can coexist if all R\* values are equal (Fig. 2)
- Environmental variability ultimately leads to competitive exclusion and lower diversity (Fig. 2)
- Higher diversity can occur in regions where the exclusion timescale is long (at short or long periods of environmental variability; Fig. 3)
- At these long exclusion timescales, other processes (e.g., transport, climate change, speciation, extinction, mutation) may counteract exclusionary processes
- Lower diversity occurs when the time scale of resource supply is intermediate (seasonal timescales; Fig. 3), such as in the subpolar oceans