

Appendix A from P. Branco et al., “Why Do Phytoplankton Evolve Large Size in Response to Grazing?” (Am. Nat., vol. 195, no. 1, p. E20)

Model with Size-Independent Nutritional Quality of Phytoplankton

Our model assumes that nutritional quality of phytoplankton decreases with cell size. To investigate the implications of this assumption, here we develop an alternative model in which nutritional quality is independent of cell size. Predictions of this alternative model are shown in figure 6A–6C. This alternative model is similar to our model described in the main text except that it uses a different allometric scaling of the cellular nutrient contents of phytoplankton. Specifically, it assumes that the minimum and maximum cellular nutrient content of phytoplankton species i are directly proportional to cell volume:

$$Q_{\min,i} = \gamma_{\min,i} \chi_i^3 \quad \text{and} \quad Q_{\max,i} = \gamma_{\max,i} \chi_i^3, \quad (\text{A1})$$

where $\gamma_{\min,i}$ and $\gamma_{\max,i}$ are proportionality constants.

Inserting equation (A1) into equation (8) shows that the nutritional quality of phytoplankton species i is now bounded between the minimum and maximum values $v_{\min,i}$ and $v_{\max,i}$, respectively:

$$v_{\min,i} = \frac{\gamma_{\min,i}}{\pi/6} \quad \text{and} \quad v_{\max,i} = \frac{\gamma_{\max,i}}{\pi/6}. \quad (\text{A2})$$

Hence, the nutritional quality of phytoplankton is indeed size independent in this model. We chose values of $\gamma_{\min,i}$ and $\gamma_{\max,i}$ such that the nutritional quality was the same as that of phytoplankton cells of $2 \mu\text{m}$ in the size-dependent model of the main text (i.e., $\gamma_{\min,i} = 0.42 \text{ fmol cell}^{-1} \mu\text{m}^{-3}$; $\gamma_{\max,i} = 1.54 \text{ fmol cell}^{-1} \mu\text{m}^{-3}$). All other equations and parameter values of this alternative model were the same as in the model with size-dependent nutritional quality.

Appendix B from P. Branco et al., “Why Do Phytoplankton Evolve Large Size in Response to Grazing?” (Am. Nat., vol. 195, no. 1, p. E20)

Model Predictions If Growth Rate Is a Unimodal Function of Size

Our model assumes that the maximum specific growth rate of phytoplankton is an allometrically decreasing function of cell size (see eq. [5] and fig. 1B). While this model assumption has empirical support (Banse 1976; Chisholm 1992; Savage et al. 2004), other studies suggest that the growth rate of phytoplankton is a unimodal function of cell size (Bec et al. 2008; Chen and Liu 2010; Marañón et al. 2013; Marañón 2015). To assess the robustness of our model predictions, we therefore also analyzed a model where the maximum specific growth rate of phytoplankton is a unimodal function of cell size (Marañón et al. 2013):

$$\mu_{\max,i} = \mu_{\text{opt}} \exp\left(-\frac{(\ln(x_i/x_{\text{opt}}))^2}{2\sigma_\mu^2}\right), \quad (\text{B1})$$

where $x_{\text{opt}} = 5.76 \mu\text{m}$ is the cell size that yields the highest maximum specific growth rate of $\mu_{\text{opt}} = 1.9 \text{ day}^{-1}$ and $\sigma_\mu^2 = 2$ is the width of the lognormal relationship.

All other equations and parameter values of this unimodal model were the same as in the allometric model of the main text (table 1). However, the additive genetic variance of zooplankton size was reduced to $V_z = 0.001$ when nutritional quality was size dependent, to avoid numerical instabilities in the model simulations.

First, we analyzed this unimodal model along a gradient of nutrient enrichment, assuming that zooplankton are nonselective, mildly selective, or highly selective (fig. B1). When zooplankton are nonselective ($S = 0$), the predictions of the unimodal model differ somewhat from those of the allometric model in the main text (compare fig. B1A–B1C with fig. 5A–5C). More specifically, in the unimodal model, nutrient enrichment favors evolution of large-sized phytoplankton and zooplankton (fig. B1A), accompanied by a sharp drop in nutritional quality (fig. B1C). For mildly and highly selective zooplankton, the predictions of the allometric and unimodal model are more similar. For example, both models predict that highly selective grazing favors evolution of larger phytoplankton and zooplankton sizes than mildly selective grazing (compare fig. 5D–5I with fig. B1D–B1I). Hence, in total, large phytoplankton size evolves for an even wider range of zooplankton selectivities in the unimodal model than in the allometric model.

Second, we investigate the joint effects of nutrient enrichment and zooplankton selectivity on the coevolution of phytoplankton and zooplankton size assuming that nutritional quality of phytoplankton is either size independent or size dependent (fig. B2). Similar to the allometric model in the main text, the unimodal model predicts that phytoplankton and zooplankton remain small when nutritional quality is size-independent (compare fig. 6A–6C with fig. B2A–B2C). When nutritional quality is size dependent, both models predict that zooplankton grazing tends to favor large phytoplankton of low nutritional quality (compare fig. 6D–6F with fig. B2D–B2F). However, as noted above, this outcome holds only for selective zooplankton in the allometric model, whereas it holds irrespective of zooplankton selectivity in the unimodal model.

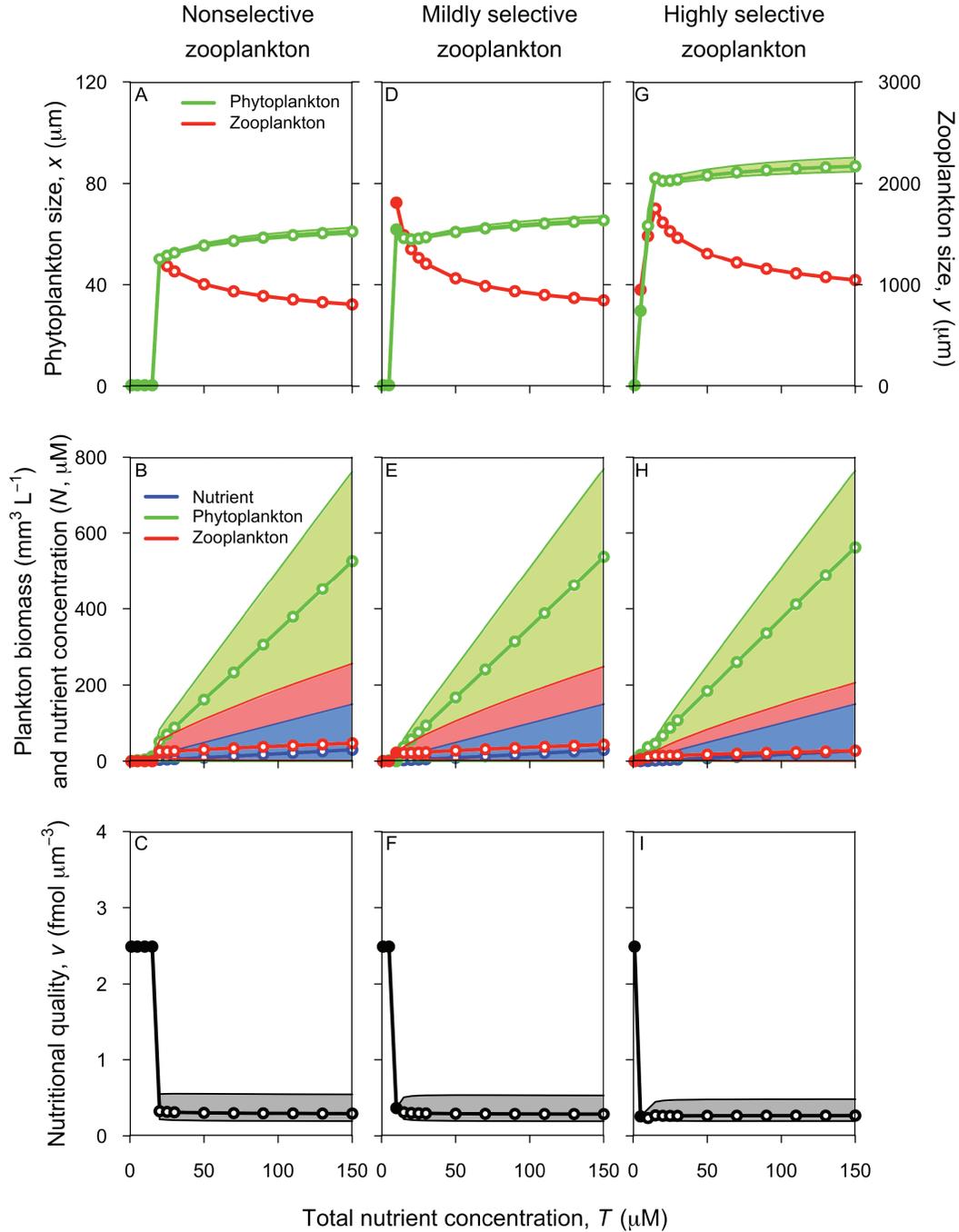


Figure B1: Bifurcation diagrams of eco-evolutionary dynamics along a gradient of nutrient enrichment (T) assuming that the maximum specific growth rate of phytoplankton is a unimodal function of cell size (eq. [B1]). The graphs compare three communities, with non-selective zooplankton (A–C; $S = 0 \mu\text{m}^3 \text{fmol}^{-1}$), mildly selective zooplankton (D–F; $S = 4 \mu\text{m}^3 \text{fmol}^{-1}$), and highly selective zooplankton (G–I; $S = 40 \mu\text{m}^3 \text{fmol}^{-1}$). A, D, G, Individual sizes of phytoplankton and zooplankton. B, E, H, Nutrient concentration, phytoplankton, and zooplankton biomass. C, F, I, Nutritional quality of phytoplankton. Solid symbols denote stable equilibria, open symbols indicate average values, and shaded areas indicate the magnitude of phytoplankton-zooplankton oscillations. Additive genetic variance of zooplankton size is $V_z = 0.001$. Other parameters are as in table 1.

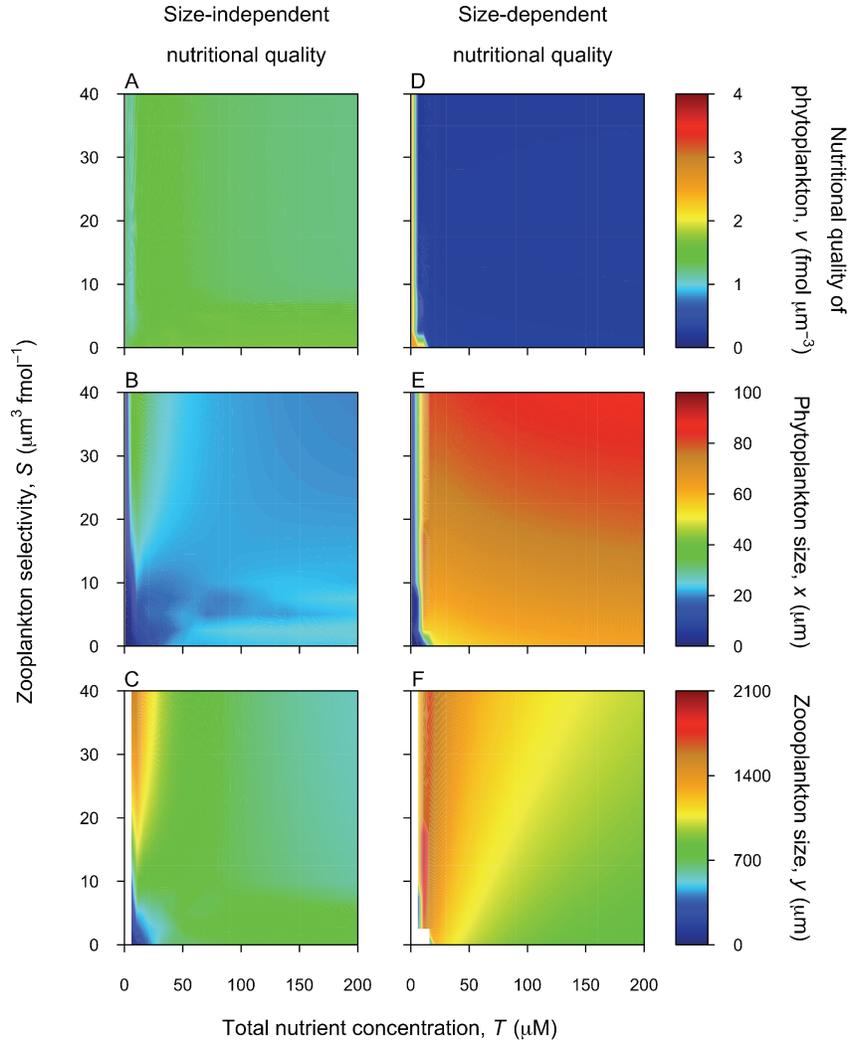


Figure B2: Phytoplankton-zooplankton coevolution along gradients of nutrient enrichment and zooplankton selectivity assuming that the maximum specific growth rate of phytoplankton is a unimodal function of cell size (eq. [B1]). The graphs compare two model scenarios where nutritional quality of phytoplankton is either independent of cell size (*A–C*) or decreases with cell size (*D–F*). *A, D*, Average nutritional quality of phytoplankton. *B, E*, Average cell size of phytoplankton. *C, F*, Average body size of zooplankton. White regions in *C* and *F* indicate zooplankton extinction. Additive genetic variance of zooplankton size is $V_z = 0.001$ in *D–F*. Other parameters are as in table 1.

Appendix C from P. Branco et al., “Why Do Phytoplankton Evolve Large Size in Response to Grazing?” (Am. Nat., vol. 195, no. 1, p. E20)

Invasion Analysis

Thus far, our model assumed that trait evolution proceeds through very small mutational steps (in our case, small changes in cell size). Here, we investigate whether the model allows invasion of a resident community by phytoplankton invader phenotypes with distinctly different cell sizes. Specifically, we assume that phytoplankton invader phenotypes are similar to the resident phenotype except for their cell size (x_{inv}) and are sufficiently rare that they do not affect the population dynamics of the resident community. For the purpose of illustration, consider the resident community shown in figure 4C. The invasion fitness (i.e., the net specific growth rate) of the phytoplankton invader phenotype, $w_{P,\text{inv}}$, can be calculated as

$$w_{P,\text{inv}} = \frac{1}{P_{\text{inv}}} \frac{dP_{\text{inv}}}{dt}, \quad (\text{C1})$$

where P_{inv} is the population abundance of the phytoplankton invader. Substituting equation (4) into equation (C1) yields

$$w_{P,\text{inv}} = \mu_{P,\text{inv}} - d - \frac{g_{\text{inv}}Z}{P_{\text{inv}}}, \quad (\text{C2})$$

where $\mu_{P,\text{inv}}$ is the specific growth rate of a phytoplankton invader phenotype, d is the specific mortality rate, and g_{inv} is the rate at which the invader is grazed by zooplankton. The eco-evolutionary dynamics of the resident community displays periodic fluctuations (fig. 4C). Therefore, we calculated time-averaged invasion fitness over a discrete number of cycles to determine the outcome of invasion. Thus, the fate of a phytoplankton invader depends on the balance between its average specific growth rate ($\mu_{P,\text{inv}}$) and its losses due to natural mortality (d) and grazing ($g_{\text{inv}}Z/P_{\text{inv}}$). Successful invasion occurs if, averaged over time, $\mu_{P,\text{inv}} > d + g_{\text{inv}}Z/P_{\text{inv}}$.

With this technique, we ask if small phytoplankton cells can invade a resident community dominated by large species. The resident community consists of large phytoplankton and zooplankton (i.e., $x \approx 40 \mu\text{m}$ and $y \approx 1,000 \mu\text{m}$; see fig. 4C). The large phytoplankton cells have low nutritional quality and exceed the size preferred by the grazing zooplankton ($x_{\text{pref}} = y/40 = 25 \mu\text{m}$). Therefore, grazing losses in the resident community are low (fig. C1). The average specific growth rate of phytoplankton invaders increases with decreasing cell size (fig. C1). Moreover, small invading phytoplankton ($x_{\text{inv}} \ll x_{\text{pref}}$) are hardly grazed by the large resident zooplankton. As a consequence, small phytoplankton invading the resident community have a high specific growth rate that greatly exceeds their natural mortality and low grazing losses (i.e., $\mu_{P,\text{inv}} > d + g_{\text{inv}}Z/P_{\text{inv}}$). Hence, their invasion fitness is positive (fig. C1). The resident plankton community can therefore be invaded by small phytoplankton of high nutritional quality.

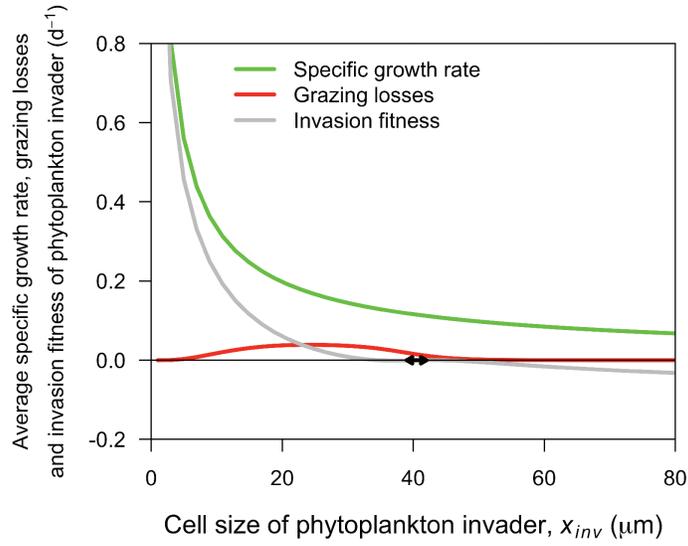


Figure C1: Specific growth rate ($\mu_{P,inv}$), grazing losses ($g_{inv}Z/P_{inv}$), and invasion fitness ($w_{P,inv}$) of phytoplankton invader phenotypes as functions of their cell size. Cell size of the resident phytoplankton population fluctuates between 39 and 42 μm (horizontal double arrow). Small phytoplankton can rapidly invade this resident community. Total nutrient in the ecosystem is $T = 100 \mu\text{M}$, and zooplankton are highly selective ($S = 40 \mu\text{m}^3 \text{fmol}^{-1}$). Other parameters are as in table 1.