



## Stoichiometry is crucial for modelling phytoplankton coexistence

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Owing to global warming, conditions in the pelagic are expected to change significantly. Rising temperatures will trigger shoaling of mixed layer depths, leading to increased light intensity and decreased nutrient supply. Adaptations of the pelagic ecosystems may include shifts in phytoplankton community composition, such as shifting dominance towards species tolerating more light and heat and/or lower nutrient concentrations, as well as changes in the extents of biogeochemical provinces and corresponding distributions of species abundances. Modelling adaptive responses to climate change requires representing phytoplankton biodiversity in global biogeochemical models.

Modelling several species over longer time scales has proven to be difficult, since one species will usually outcompete all others, especially in oligotrophic areas, where the system is almost in equilibrium, resembling a chemostat. The  $R^*$  concept as part of Tilman's resource competition theory (D Tilman, Am. Nat. 1980, Vol 116(3) pp. 362-393) predicts that for any given limiting resource, only the species with the lowest requirement for that resource will survive: In equilibrium, a monoculture of any species will reduce the concentration of its limiting resource to the lowest concentration allowing for its survival ( $R^*$ ), such that growth rate equals losses. In a multi-species assemblage, the species requiring the lowest resource concentration to survive will set the equilibrium resource concentration to its  $R^*$ , which however is too low to allow for any other species to survive. The  $R^*$  concept implies that in equilibrium, there can be at maximum one species for every given limiting resource.

Thus, including several potentially limiting resources and parameterising the phytoplankton species such that each species is limited by a different resource, i.e. each species has the highest requirement for one resource among all species, is a necessary condition for the existence of an equilibrium including each of these species.

A model study is presented in which the stability conditions for the aforementioned equilibrium are evaluated. The conditions for stable coexistence in a chemostat derived by Huisman and Weissing (J Huisman & F Weissing, Ecology 2001, Vol 82(10), pp 2682-2695) imply that the species' stoichiometries need to differ from one another. In this study, it is shown both numerically and analytically that, given each species is limited by a different resource, stable coexistence is still not possible if all species are assigned the same stoichiometry. This collides with the widely applied Redfield stoichiometry, which is routinely applied in phytoplankton models. Thus, to sustain coexistence in plankton models, it is not only necessary to parameterise the resource requirements according to the  $R^*$  concept, but to also vary the stoichiometric coefficients across the species involved.