Trait-based models to capture biodiversity
the phytoplankton test case

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1. Accounting for biodiversity in ecosystem models

Marine ecosystems harbor myriads of species. The combination of individual species defines the system as a whole. However, knowledge on individual species is extremely limited, in particular from a modelers point of view. Also, most marine ecosystem research has no need for species-explicit models.

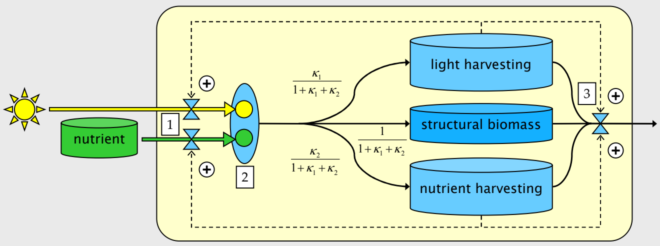
Question: How to model bulk parameters (e.g. total carbon), while accounting for biodiversity, yet leaving out individual species?

Approach: bridging inter-species gaps
- all species share a common make-up: the omnipotent population
- differences between species = differences in parameter values
- parameters that describe inter-species differences: *traits*

2. Two-trait phytoplankton model

Selected phytoplankton traits: *investment in assimilation*...
1. light harvesting: "cell-specific chlorophyll"
2. nutrient harvesting: "surface-to-volume ratio"

... measured in fractions κ_i of structural (non-trait) biomass

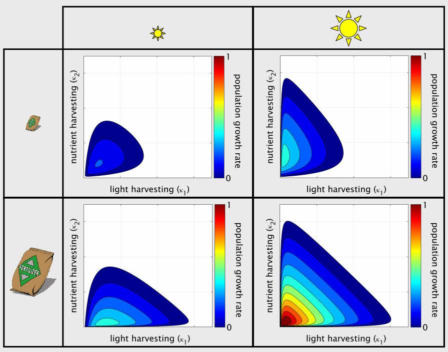


The model is inspired by the work of Kooijman ("Dynamic energy and mass budgets in biological systems", Cambridge University Press, 2000). It accommodates the following processes:

1. **assimilation**: proportional to external substrate and trait biomass
2. **growth**: substrates are combined to form new biomass; capped by structure-specific maximum rate, hyperbolic in substrate arrival
3. **maintenance/death**: biomass turnover proportional to (sum of) all biomasses

Trait trade-off in different environments.

Investment in assimilation brings costs in maintenance and growth. Low light, low nutrient environments favor some investment (top left), whereas high light, high nutrient environments discourage investment (bottom right). Asymmetric limitation favors asymmetric investment.



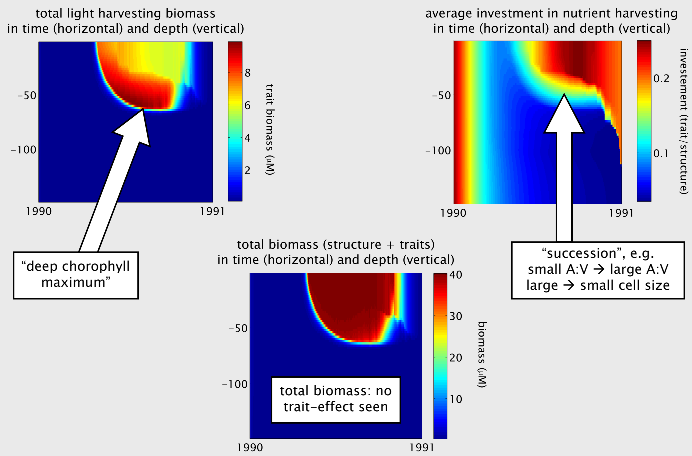
3. From single species to functional group

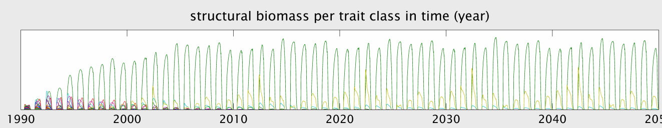
- An infinite number of phytoplankton species is represented by the two-trait population model, plus continuous distributions for trait values
- Natural boundaries for trait distributions
  - trait value too small: low assimilation → extinction
  - trait value too high: high maintenance → extinction
- Discretize trait distributions, allow for change in frequency for every trait class

4. Phytoplankton diversity in a water column

Physics:
- Turbulent water column, ocean top 150m, depth-dependent turbulence/diffusivity: GOTM (http://www.gotm.net), k-ε model
- Real surface forcing: ERA-40 data (http://www.ecmwf.int), lat = 55°, lon = -20°

Biota:
- Start with homogeneous trait distribution, low biomass: "start of spring"
- No explicit predation (but maintenance)
- Competition between trait classes through shared external nutrient pool only





5. Theory: system plasticity and coexistence

How can ecosystem features change?

time scale	source of plasticity
physiological: within generation	physiological adaptation of individual
ecological: few generations	changes in species composition
evolutionary: many generations	evolution of properties of species

This study focuses on the ecological time scale.

- Physiological and evolutionary time scales fit into one theoretical framework (Popul Ecol 46: 13-25, J Math Biol 34: 579-612)
  - movement along fitness gradient, in direction of (local) optimum
- Can ecological time scale be incorporated in the same framework?
- Challenge: collapse trait distributions into single adapting population

Competitive exclusion occurs in homogeneous setting (J Math Biol 50: 133-160). In this study, spatial and temporal heterogeneity permits some coexistence, but realistic biodiversity is short-lived.

6. Conclusions

- Our 4-parameter, trait-based phytoplankton model is able to reproduce key ecosystem features, while accounting for biodiversity
- Caveat: without winter-reset, most biodiversity is lost in time (> 10 years).