

# Stoichiometry is crucial for modelling phytoplankton coexistence

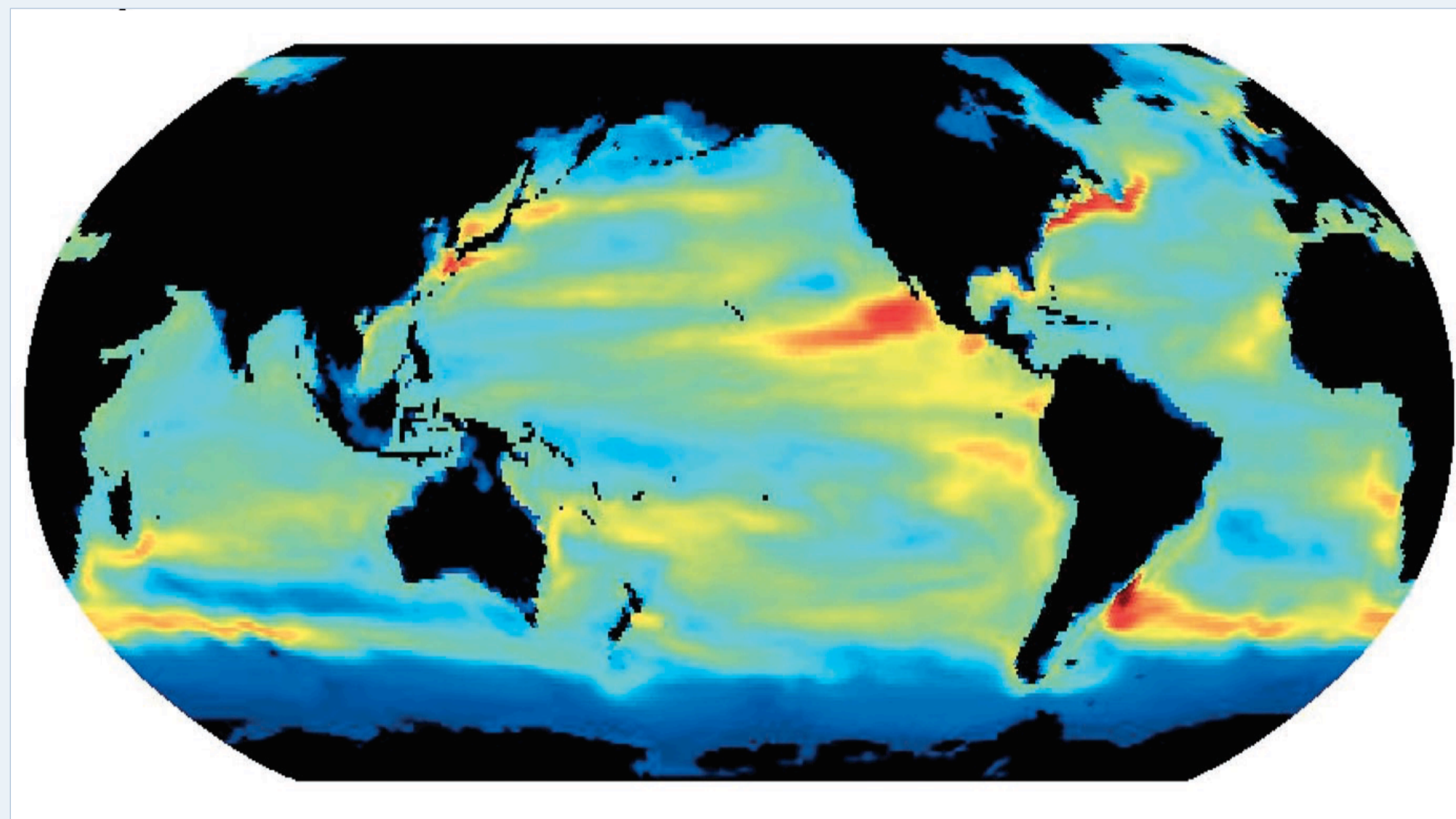
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## Introduction

In marine biogeochemical models, which commonly assume identical elemental composition (stoichiometry), only few phytoplankton species coexist.

Resource competition theory predicts that the maximum possible species number = resource number. Diversity in biogeochemical models is often lower.



Global map of annual average of modelled phytoplankton species no. in the upper 260m, in a model with ~4 resources (Barton et al. 2010).

## Objectives

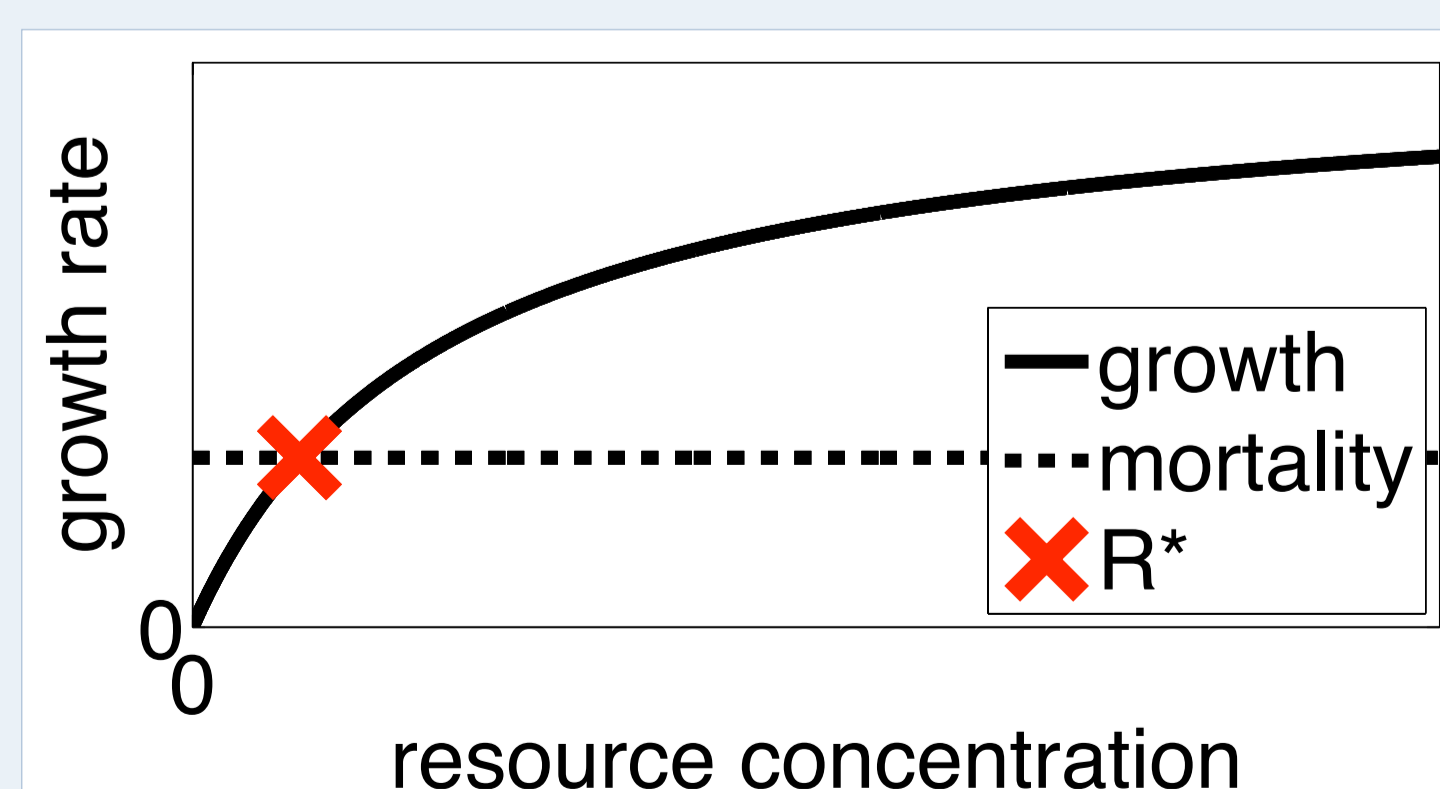
1. Explain low diversity in models with multiple limiting resources
2. Model simple chemostat with stable species number = number of limiting resources.

## Methods

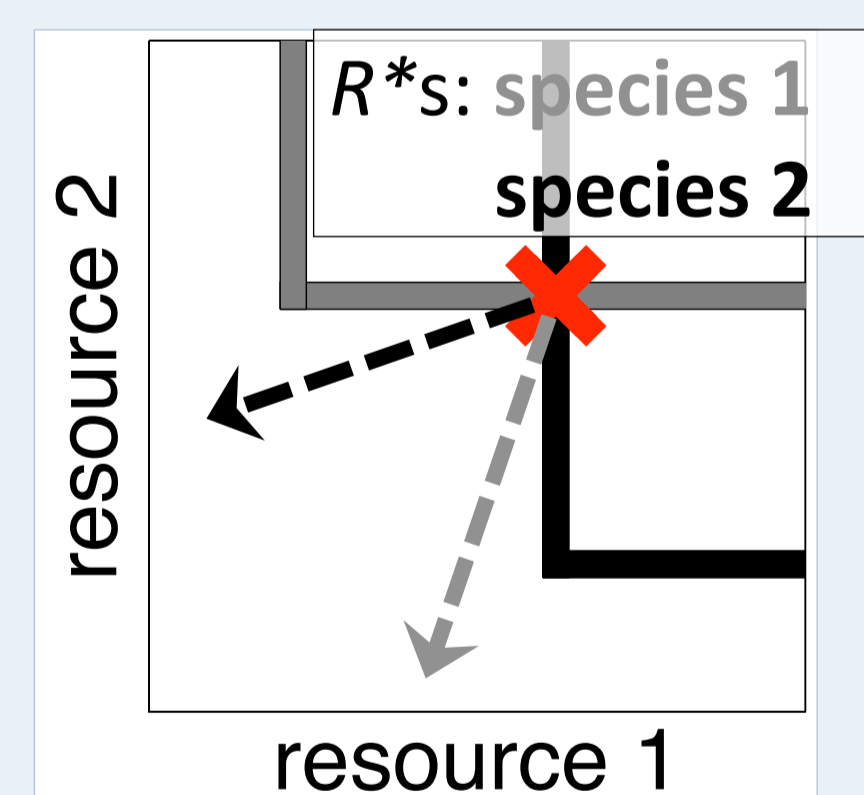
We used a chemostat model of resource competition where (1) growth = nutrient uptake (defined by stoichiometry) and (2) growth is determined by only the most limiting nutrient (Petersen 1975). The model was run for 20 years with 8 initial species on 4 resources.

### Resource competition theory

In equilibrium, the limiting nutrient is depleted to the lowest concentration allowing for survival ( $R^*$ ), where growth = mortality:



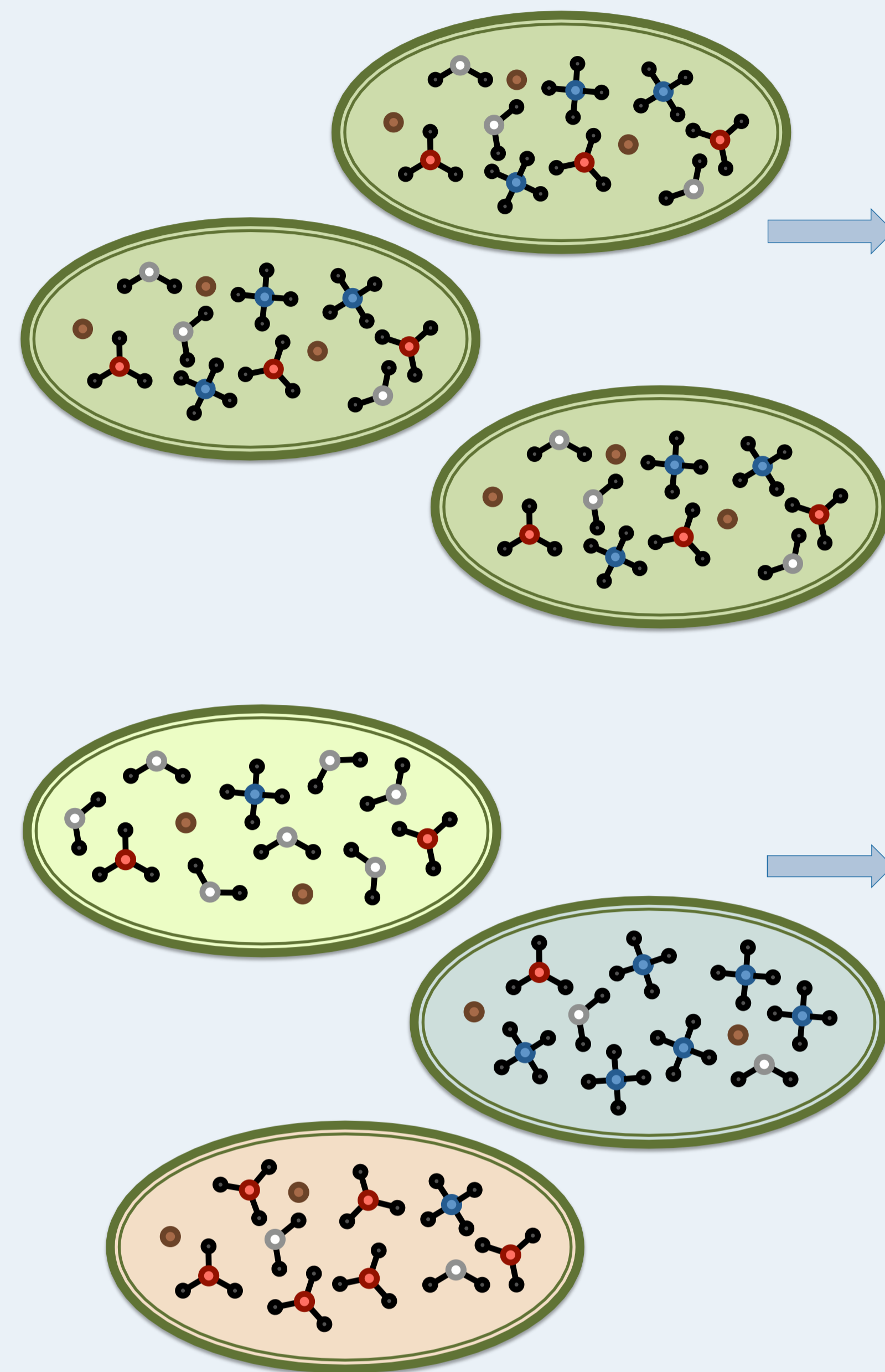
**Coexistence** on two resources requires that each species is limited by a different resource ( $R^*$ s intersect, Tilman 1980).



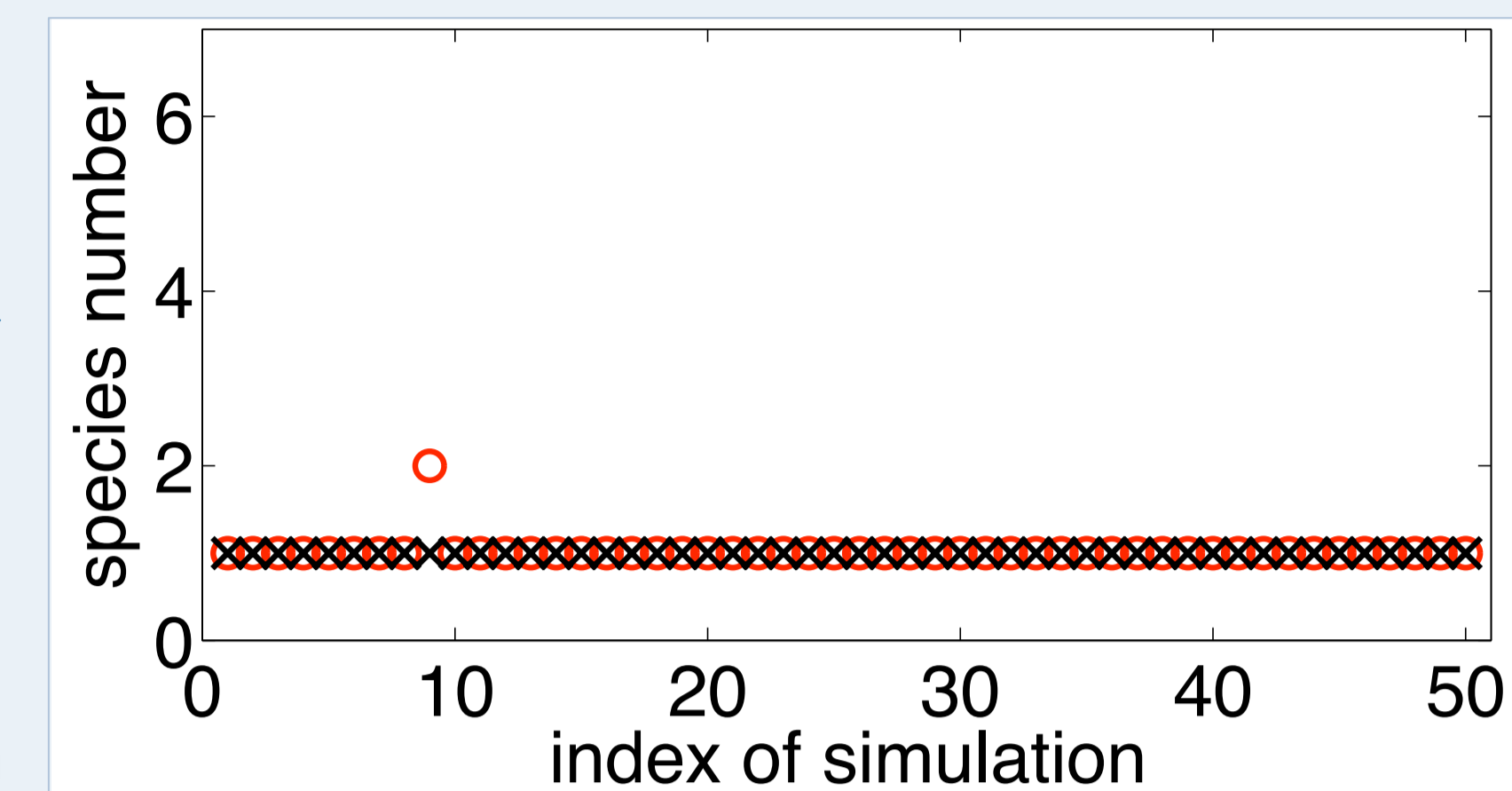
Equilibrium coexistence (x) on two resources is stable if each species consumes more of the resource by which it is limited (see consumption vectors = stoichiometry).

If multiple species are limited by one resource, only the species with the lowest  $R^*$  prevails.

## Results

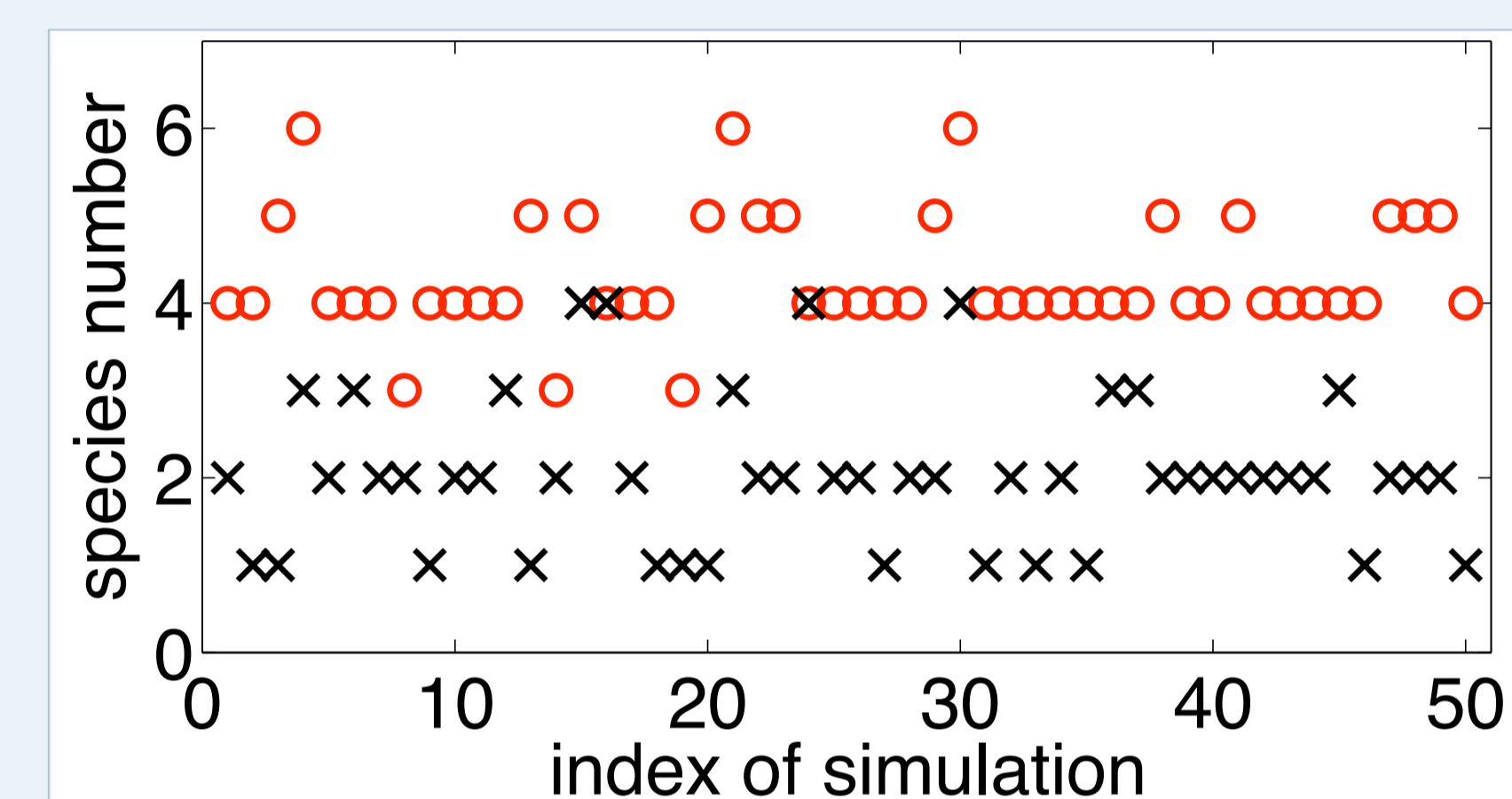


### Identical stoichiometry impedes diversity



Number of surviving species after a 20 year simulation with identical stoichiometry for all species and  $R^*$ s varying randomly (x) or ranked according to the equilibrium condition (o) derived by Petersen (1975): Each species is limited by a different resource.

### Varied stoichiometry allows for diversity



Number of surviving species after a 20 year simulation with stoichiometry assigned such that each species consumes/contains most of its limiting resource (Huisman & Weissing 2001).  $R^*$ s vary randomly (x) or ranked according to the equilibrium condition (o).

Where species number exceeds resource number, competitive exclusion is not yet complete.

## Ecological niche

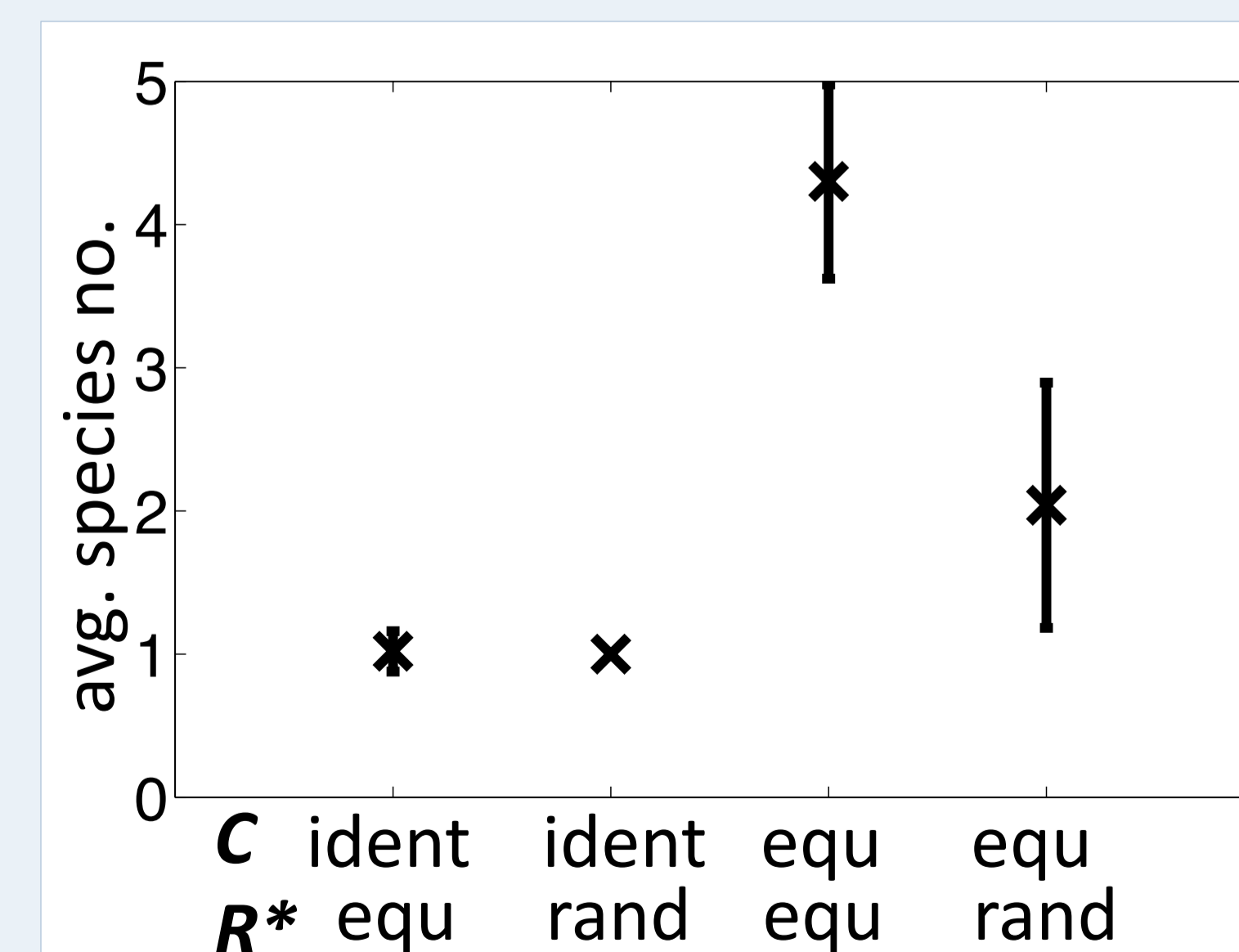
In theoretical ecology, the **requirement niche** is the response of an organism to its environment ( $R^*$ ). The **impact niche** is the impact an organism has on its environment (stoichiometry).

This study shows that both niches need to differ between species to allow for stable coexistence. Ranking the  $R^*$ s such that each species is limited by a different resource is a prerequisite for the **existence of a multi-species equilibrium**.

Assigning the **stoichiometry** such that each species consumes most of its limiting resource ensures the **stability of a given equilibrium**.

## Conclusion

**Identical stoichiometry** ("C"s, 1<sup>st</sup> & 2<sup>nd</sup> from left), as commonly used in marine biogeochemical models, **impedes diversity** irrespective of the way the  $R^*$ s are assigned.



Using **stoichiometry according to equilibrium conditions** (3<sup>rd</sup> & 4<sup>th</sup>) increases the **chance for diversity**, even with randomly assigned  $R^*$ s.

## Outlook

Run global model with varied stoichiometry to test applicability of results in more realistic environment.

## References

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## Acknowledgements

Research was funded through WGL PAKT, project TiPI ([www.pik-potsdam.de/research/research-domains/earth-system-analysis/projects/tipi](http://www.pik-potsdam.de/research/research-domains/earth-system-analysis/projects/tipi)).



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