Modelling the role of selection and complementarity in ecosystem function under climate change

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In our rapidly changing climate, it is crucial to understand how ecosystem function depends on temperature. The response to warming at a species level is relatively well understood, through the metabolic theory of ecology. However, when multiple species are present, interactions between the species are important too. Therefore, to understand community function, we must understand the response of the individual species, and the interactions between them. These interactions may depend on temperature, and can be split into selection and complementarity.

Our understanding of ecosystem function can be improved by using mathematical models to constrain the mechanisms underlying key processes. Using data from laboratory experiments, we model communities of heterotrophs responding to temperature change. To model selection, we use a simple model of a community sharing a resource, with parameters measured empirically. Without complementarity, the model underestimates community function. Complementarity is included through a single parameter, which determines to what extent different taxa share the same resource pool. This parameter is difficult to measure directly, so must be fitted using empirical community function data. Through our model, we show that the strength of complementarity within a community depends on both diversity and temperature. Using one fixed value, we can substantially improve model results across all temperatures and species combinations.

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DIVERSITY, SELECTION AND COMPLEMENTARITY

- **Selection**
  - Higher fitness leads to dominance in a community
  - The sampling effect: higher diversity means that the maximum ‘fitness’ of the species present likely to be higher, leading to overall higher fitness
- **Complementarity**
  - Species ‘working together’ to maximise fitness in an environment
  - Resource partitioning: different species able to access different parts of a resource, maximising use of the resource
  - Resource recycling: a second species is able to make use of the secondary metabolites of the first species

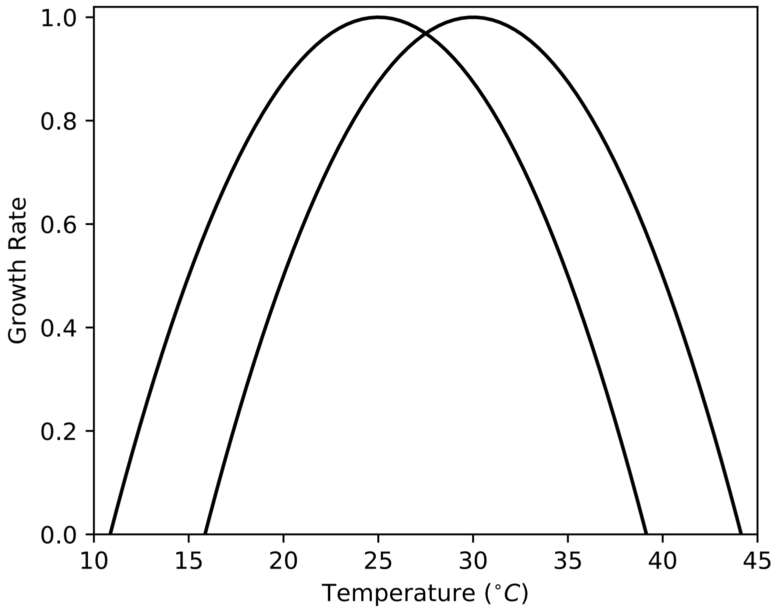
EXPERIMENTAL BASIS

- Our modelling builds on experimental results from *García et al. 2018*
- 24 species of heterotrophic microbes from different thermal environments
- Different cultures, manipulating:
  - Diversity, 1, 2, 4, 8, 16 & 24 species
  - Temperature, 10C - 40C
- Same initial resource. Measured eventual yield.
- Question: Diversity loss is likely to be independent of thermal characteristics. How will this affect functioning?
- We recreate results using a simple model

García, F. C., Bestion, E., Warfield, R., & Yvon-Durocher, G. (2018). Changes in temperature alter the relationship between biodiversity and ecosystem functioning. *Proceedings of the National Academy of Sciences,* 115(43), 10989-10994.

THERMAL TOLERANCE CURVES

- For modelling temperature dependence:
  - Y-axis: measure of fitness, e.g. growth rate, respiration rate, mortality rate
  - X-axis: range of temperatures
- Initially, performance increases with temperature, e.g. due to increasing chemical reaction rates (thermodynamics)
- At high temperatures, performance decreases e.g. due to denaturing of enzymes



RESOURCE LIMITED MODEL

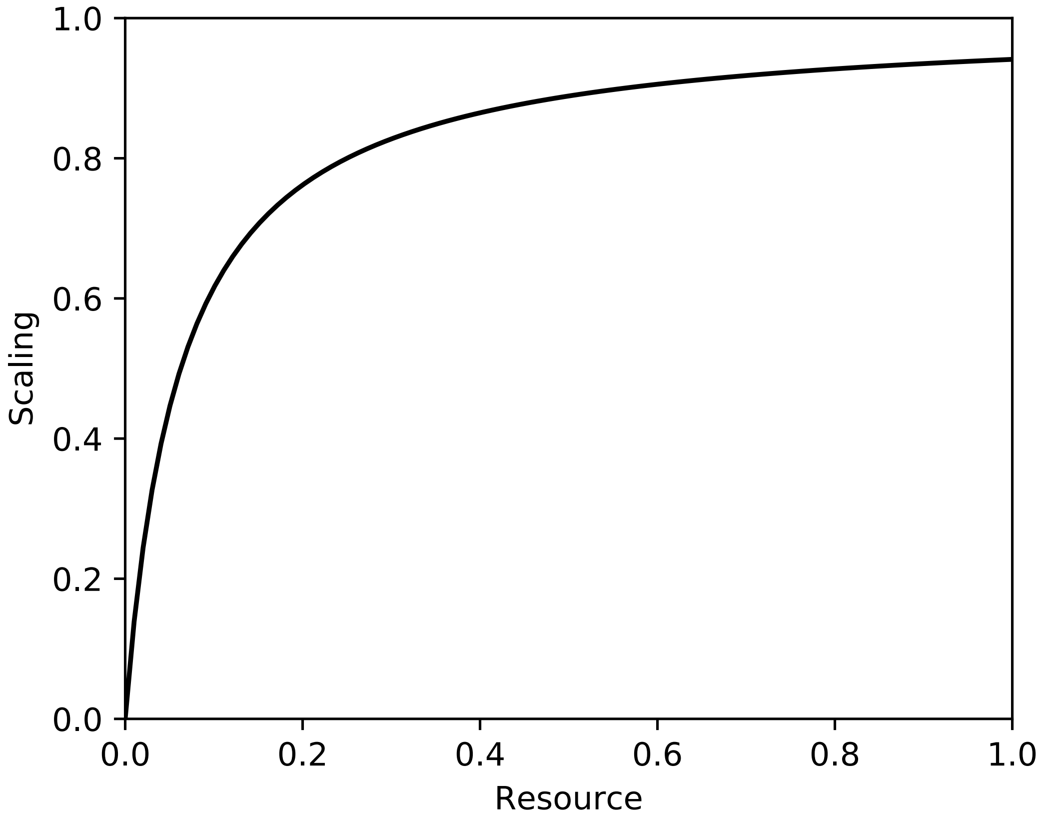
Based on model from Lehman and Tilman, 2000.

Biomass of species

Resource availability (Monod function)

$$\frac{dN_i}{dt} = N_i r_i \frac{R}{R + \frac{R_0}{16}}$$

Growth rate (empirical)



Initial resource and half saturation are approximated.

Lehman, C. L., & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *The American Naturalist*, *156*(5), 534-552.

RESOURCE LIMITED MODEL

Biomass of species

Growth rate

Resource availability

$$\frac{dN_i}{dt} = N_i r_i \frac{R}{R + \frac{R_0}{16}}$$

Initial resource

$$R = R_0$$

Initial biomass

$$N_i = N_0$$

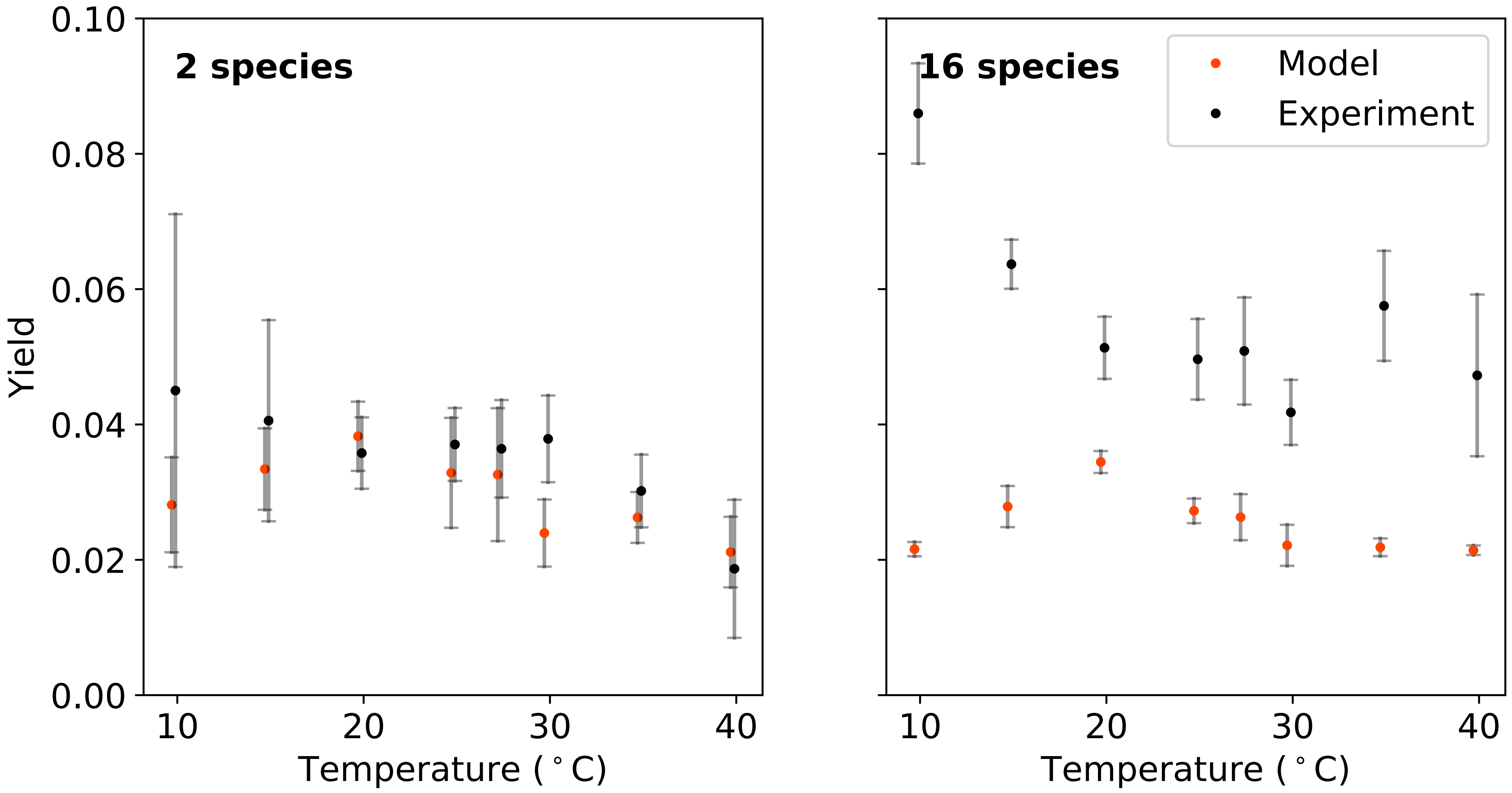
Shared resource

$$\frac{dR}{dt} = -\sum_i N_i (r_i + q_i) \frac{R}{R + \frac{R_0}{16}}$$

Resource use of every species

Resource uptake rate, proxy for respiration rate, calculated using experimental yield and growth rate, assuming all initial resource used.

MODEL RESULTS - SELECTION ONLY



Model under-yielding, especially at higher levels of diversity → Need to include complementarity

INCLUDING COMPLEMENTARITY

Split resource pool between species. Include one additional parameter, describing reduced efficiency on other species' resource pools.

Individual resource limitation

Reduced efficiency on other species' resource pool

$$\frac{dN_i}{dt} = N_i r_i \left[\frac{R_i}{R_i + \frac{R_0}{16}} + \alpha \sum_{i \neq j} \frac{R_j}{R_j + \frac{R_0}{16}} \right]$$

Individual resource pool

$$\frac{dR_i}{dt} = -\left[\underline{N_i(r_i + q_i)} + \alpha \sum_{i \neq j} \underline{N_j(r_j + q_j)} \right] \frac{R_i}{R_i + \frac{R_0}{16}}$$

Own resource usage

Other species' resource usage

Complementarity parameter

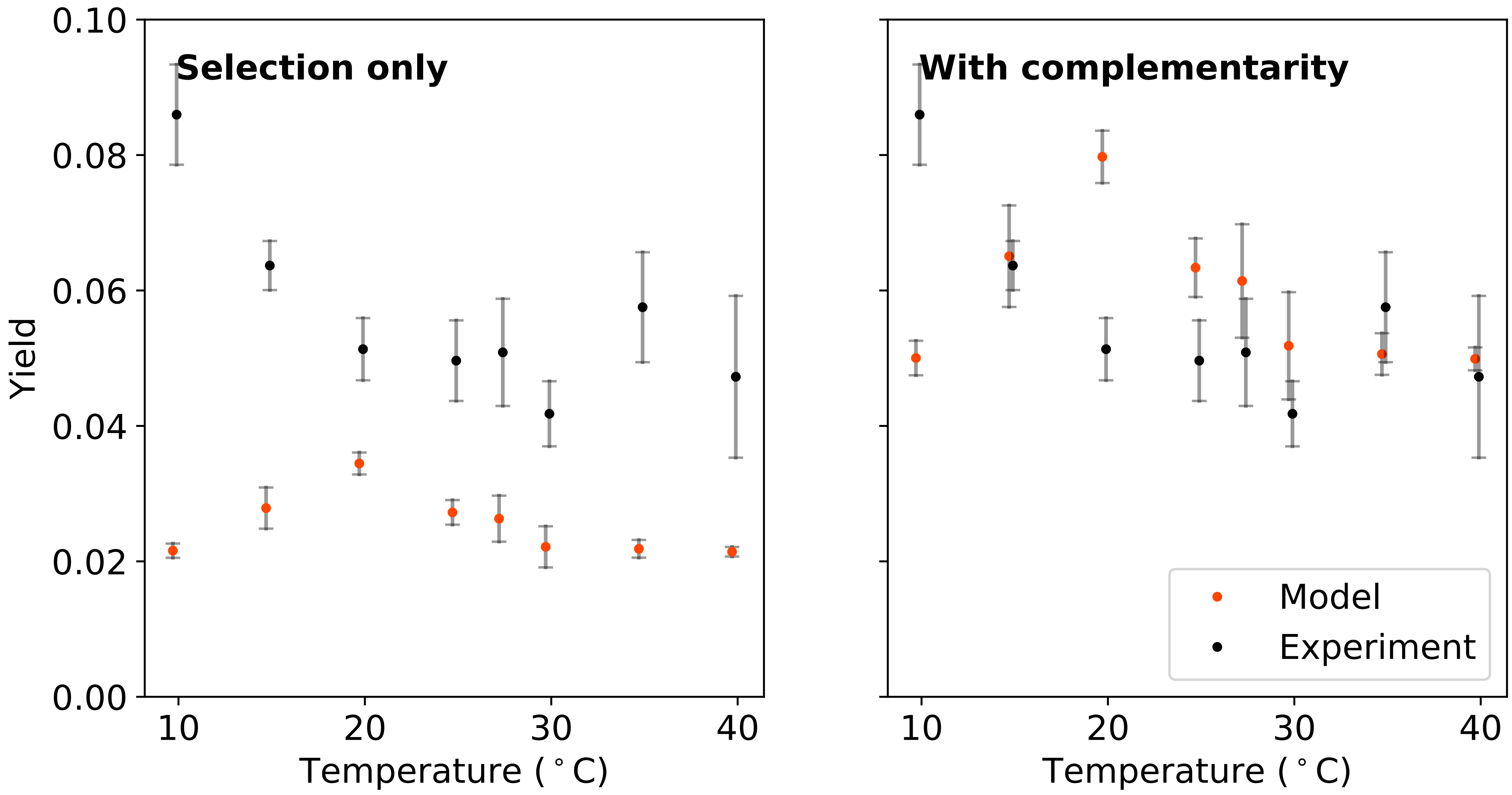
COMPLEMENTARITY PARAMETER

- Bounded, $0 \leq \alpha \leq 1$
- Complete resource partitioning - $\alpha = 0$
- Complete resource sharing - $\alpha = 1$, which is equivalent to the original, selection only model.
- Total initial resource scales with α, due to resource uptake rate including unused resource and secondary metabolites:

  $$R_{tot} = (S + \alpha(1 - S))R_0$$

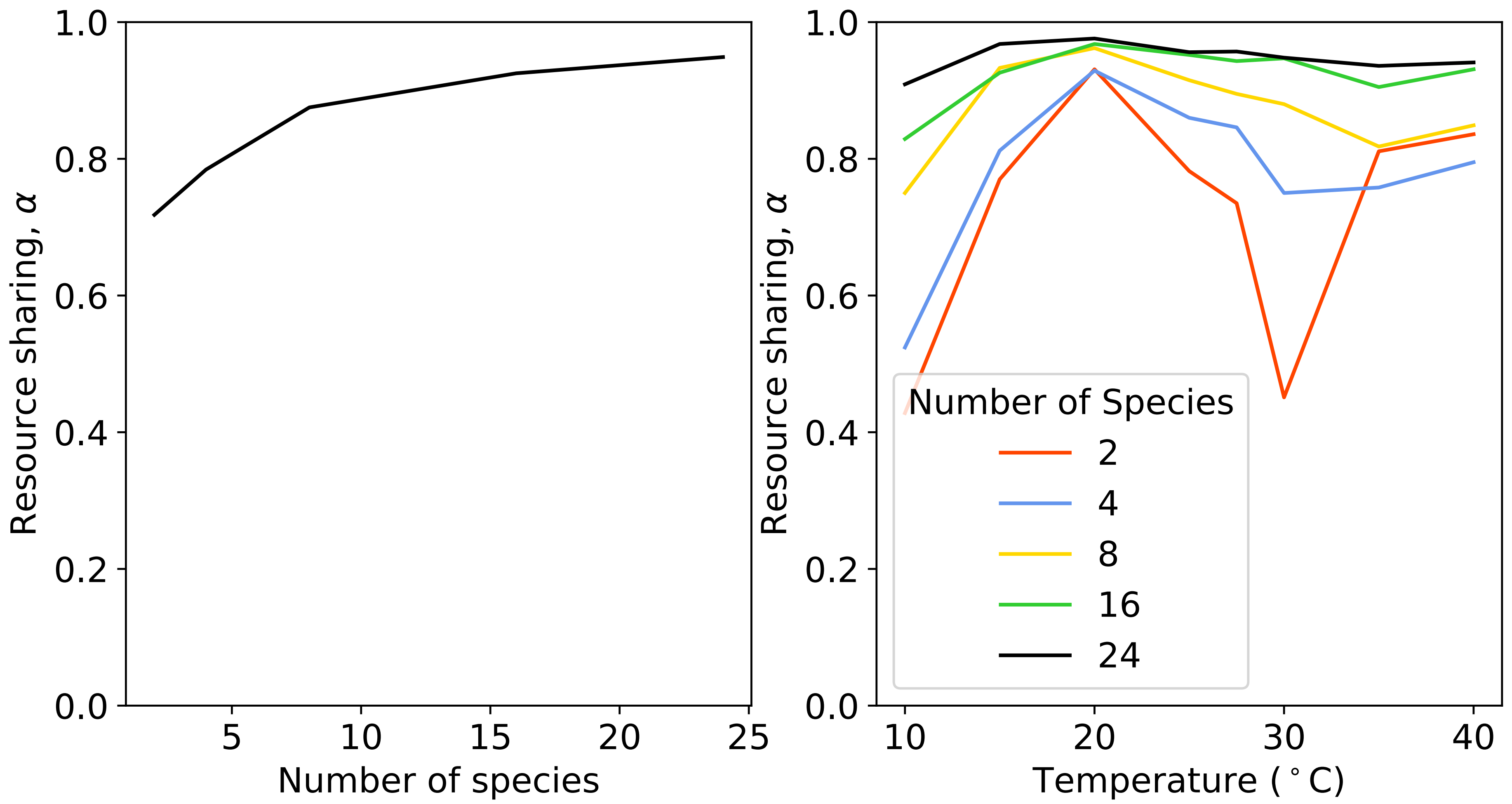
  Where S is the total number of species.
- If respiration rate is used instead resource uptake, initial resource would not scale with α.

MODEL RESULTS - WITH COMPLEMENTARITY



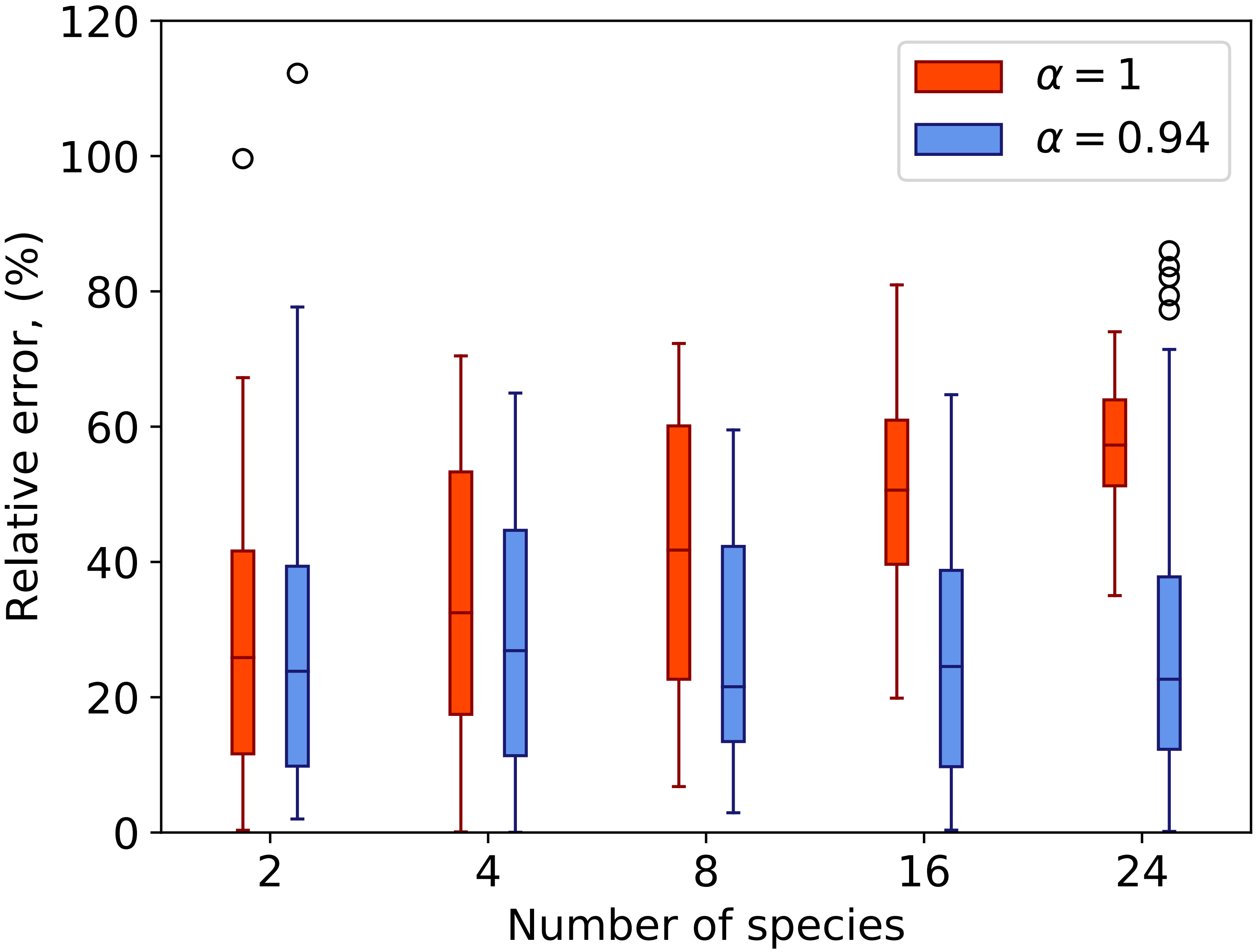
- Complementarity fitted to empirical data
- Model no longer consistently under-yielding

COMPLEMENTARITY: DIVERSITY AND TEMPERATURE



- Total resource use increases with diversity. However, adding more species at higher levels of diversity has a smaller effect on the amount of resource accessed.
- Complementarity is strongest at temperature extremes.

MODEL FIT



We can substantially improve model results by using one value of the complementarity parameter, across all combinations of species and temperatures.

CONCLUSIONS

- Mechanistically model selection and complementarity
- Complementarity
  - Increases with diversity
  - Stronger at temperature extremes
- Future work:
  - Can easily get a long term equilibrium, with emergent levels of diversity
  - Explore different warming scenarios

THANK YOU FOR LISTENING (READING)!