# Trade-offs modify ecosystem structure along trophic gradients

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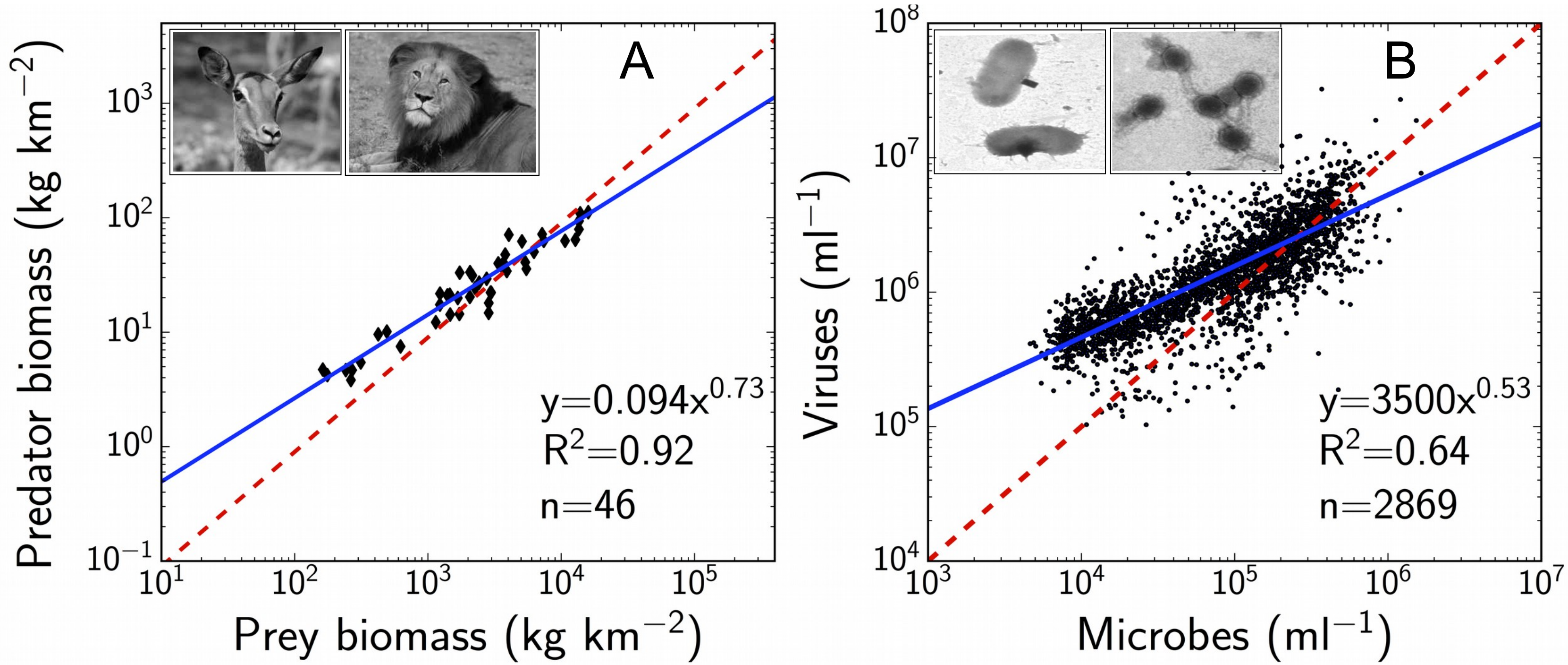
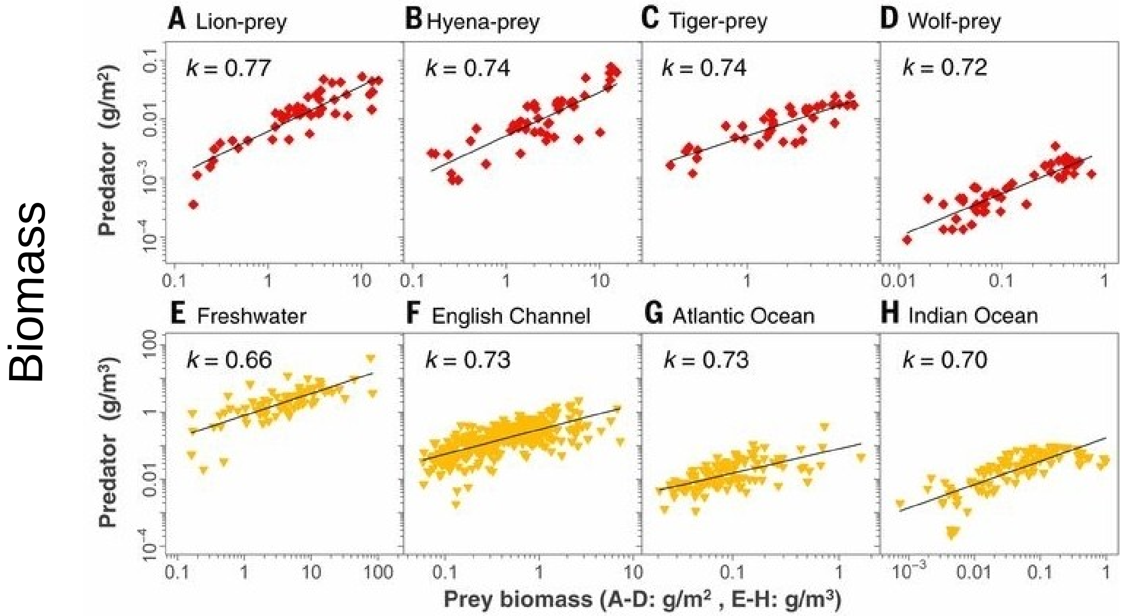
Can a simple ecological mechanism explain "universal" large-scale patterns in aquatic and terrestrial ecosystems?

# Global meta-data sets(*) show sublinear consumer/producer biomass scaling




(*) e.g. Hatton et al 2015, Parikka et al 2016, Knowles et al 2016, Wigington et al 2016, Cael et al 2018

# What could cause sublinear biomass scaling?




Hatton et al 2015

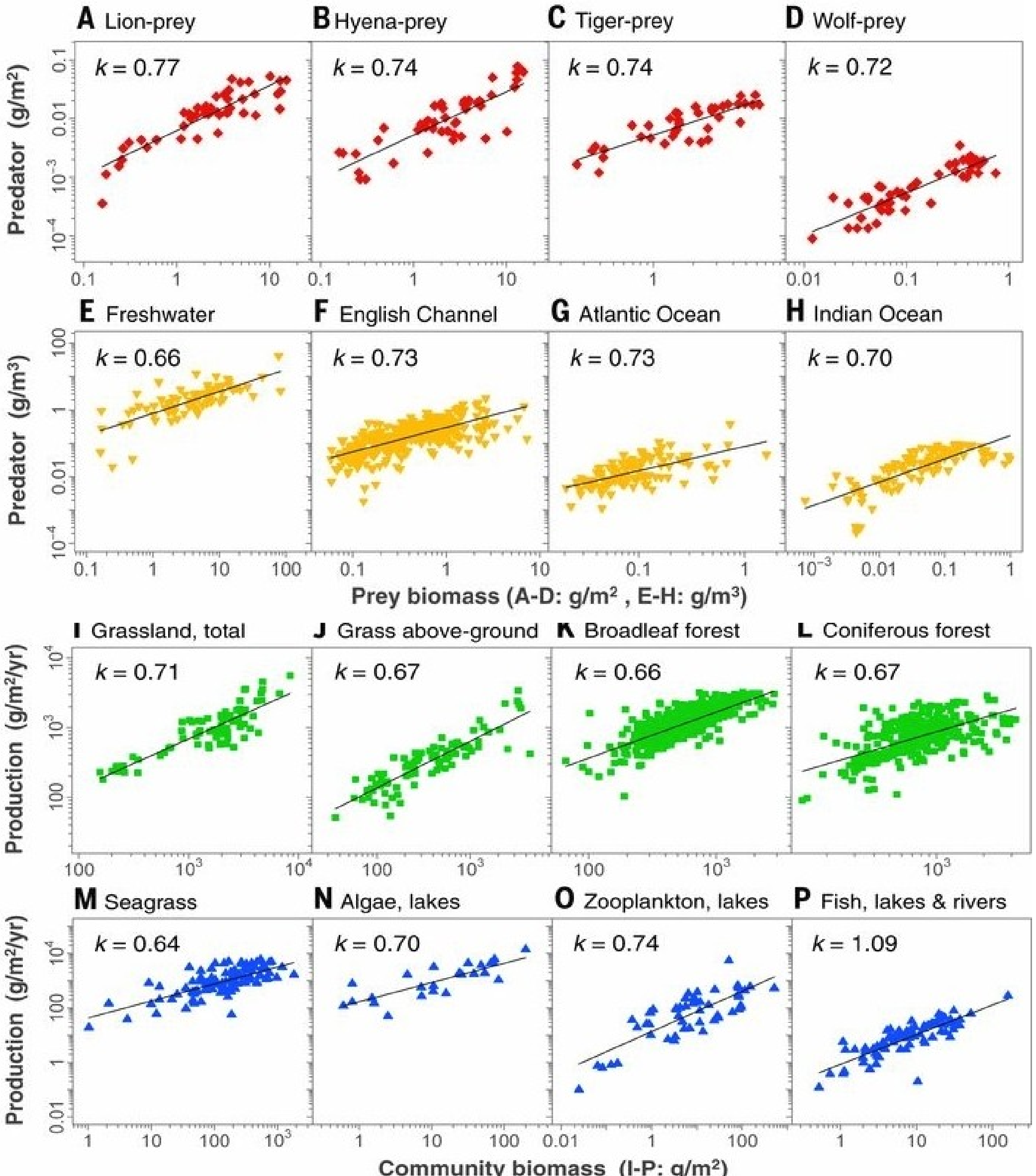
# What could cause sublinear biomass scaling?

Reduced production per ‘biomass’ as systems total biomass increases.

→ Less food for consumers as systems total biomass increases.

Biomass

Production



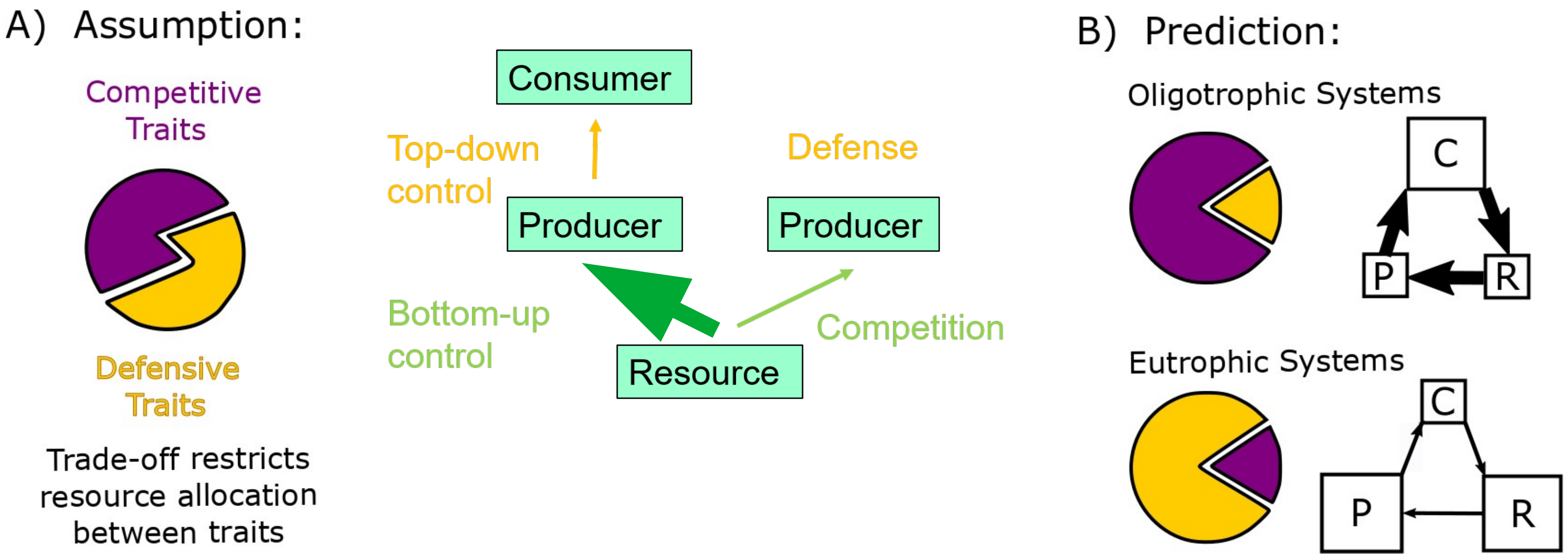

Hatton et al 2015

# What could reduce “production per unit biomass” as total biomass increases?

- Increased body size (less efficient production)??
- Increased omnivory (less efficient production)??
- External removal of top-consumers??

→ Looking for generic mechanism that applies to any kind of ecosystem!

# We suggest trade-off between competition and defense




Talmy et al, in prep

# Model framework

## Resource (R) - Producer (P) – Consumer (C) model

$$\frac{dR}{dt} = S_R - \sum_{i=1}^{n} \mu_i R P_i$$

$$\frac{dP_i}{dt} = \mu_i R P_i - \varphi_i P_i C - m_p P_i$$

$$\frac{dC}{dt} = \sum_{i=1}^{n} \varepsilon_i \varphi_i P_i C - m_c C$$

$\mu$ resource affinity

$\varphi$ interaction strength

$\varepsilon$ transfer efficiency

General “N - populations” model:

$$\frac{dN_j}{dt} = \underbrace{\varepsilon_j f_{j-1}\left(N_{j-1}, N_j\right)}_{production} - \underbrace{f_j\left(N_j, N_{j+1}\right)}_{losses}$$

Two steady-states, depending on model parameter allocation:

1. Producer increases with nutrient supply ($S_R$)
2. Consumer increases with $S_R$

# Incorporated trade-off between competition and defense:

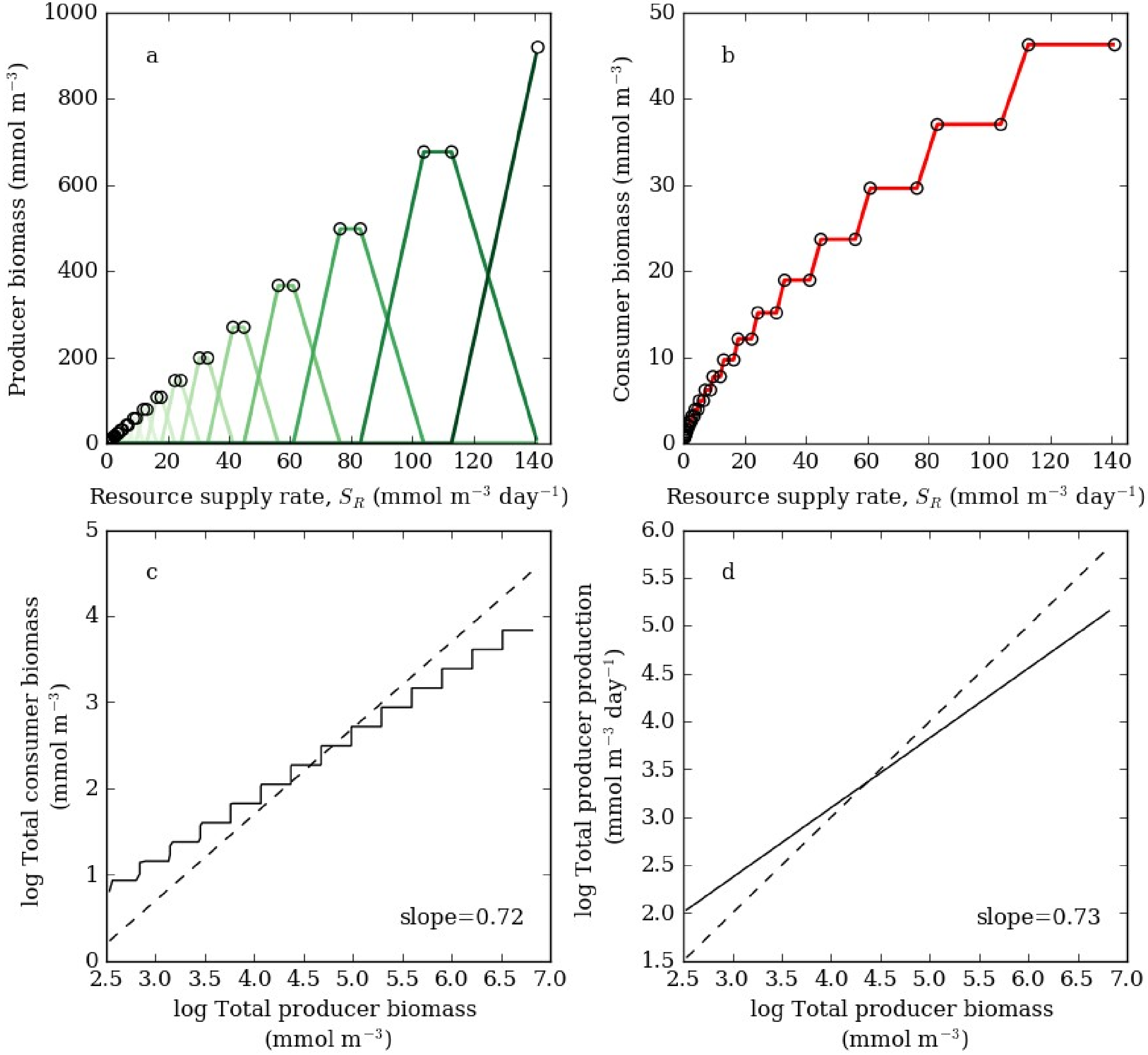
Resource affinity : $\mu_i = \mu_1 \rho^i$ P-C interaction strength : $\varepsilon_i = \varepsilon_1 \rho^i$ Transfer efficiency : $\varphi_i = \varphi_1 \nu^i$ (ρ, ν < 1)

"Producers with reduced resource affinity (cost of resistance) have reduced interaction strenght with consumers (benefit of resistance). This also reduces transfer efficiency."

$$\frac{dN_j}{dt} = \underbrace{\varepsilon_j f_{j-1}(N_{j-1}, N_j)}_{production} - \underbrace{f_j(N_j, N_{j+1})}_{losses}$$

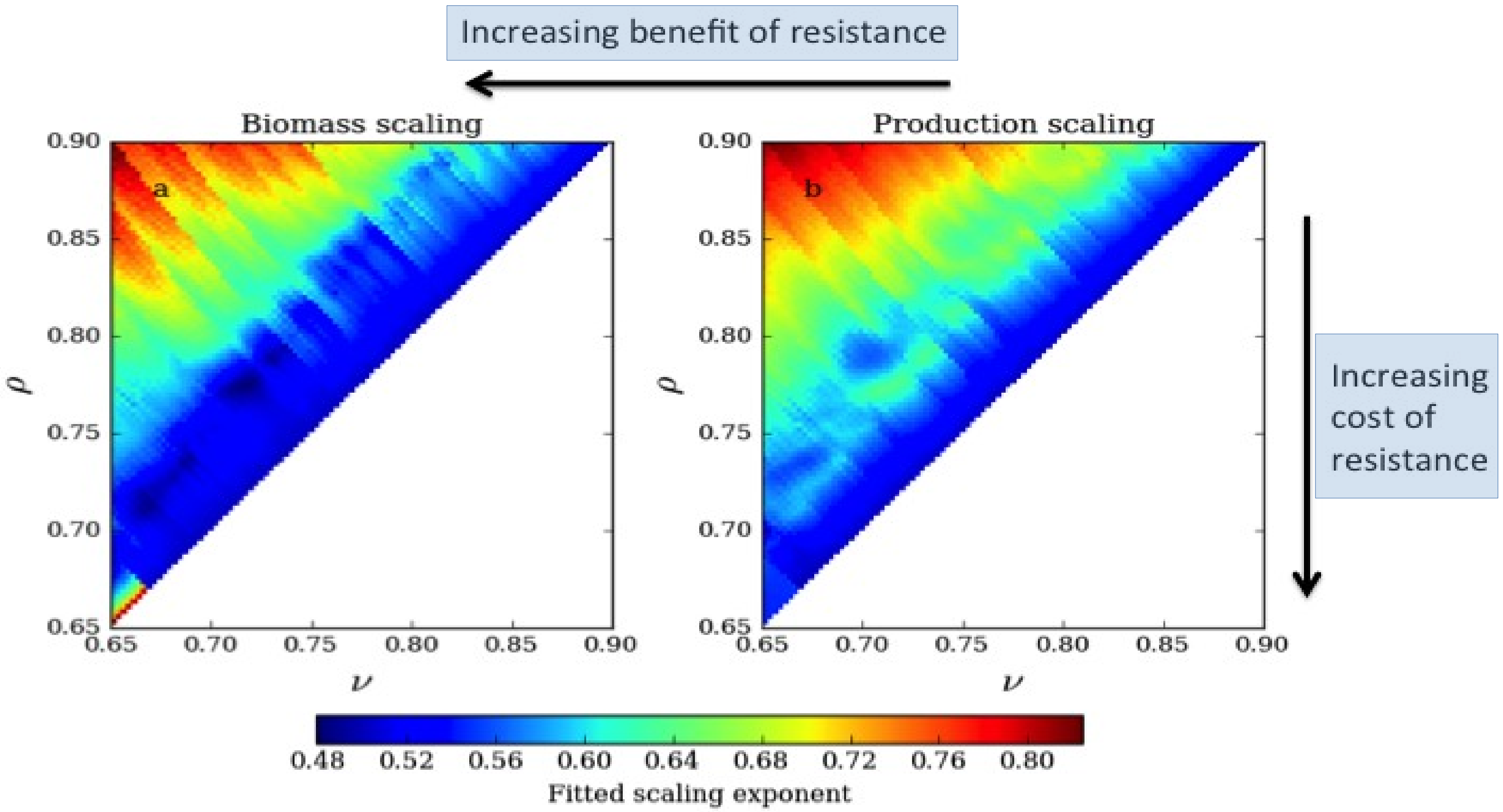
$$\left( \frac{dR}{dt} = S_R - \sum_{i=1}^{n} \mu_i R P_i , \quad \frac{dP_i}{dt} = \mu_i R P_i - \varphi_i P_i C - m_p P_i , \quad \frac{dC}{dt} = \sum_{i=1}^{n} \varepsilon_i \varphi_i P_i C - m_c C \right)$$

→ Gives succession of more defensive producers(*) as $S_R$ increases



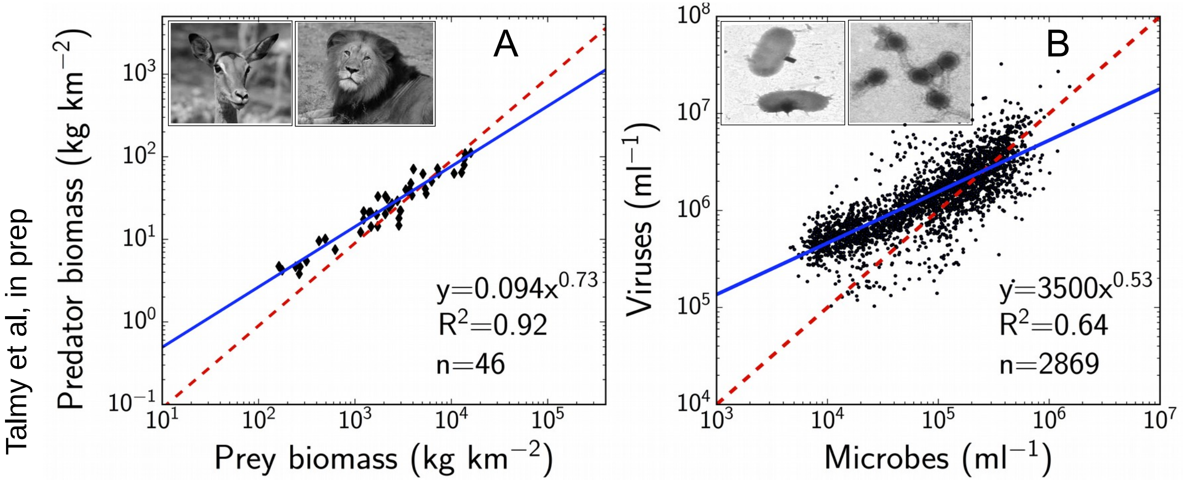

(*) darker shading of green

# Scaling exponent depends on trade-off strenght



# Trade-off between competition and defense may explain sublinear productivity and biomass scaling across trophic gradients

Sublinear productivity and biomass scaling laws

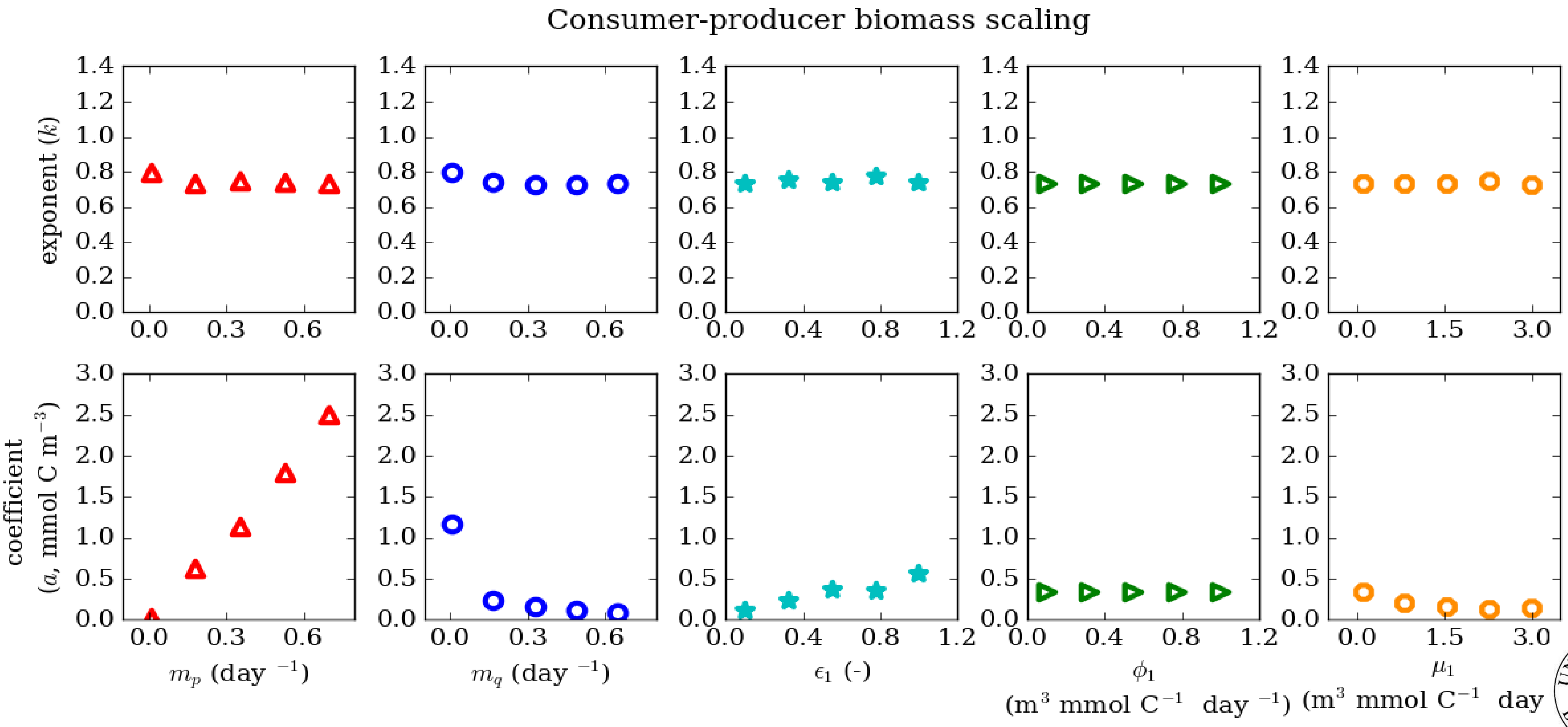



“from big game ... ... to microbes”

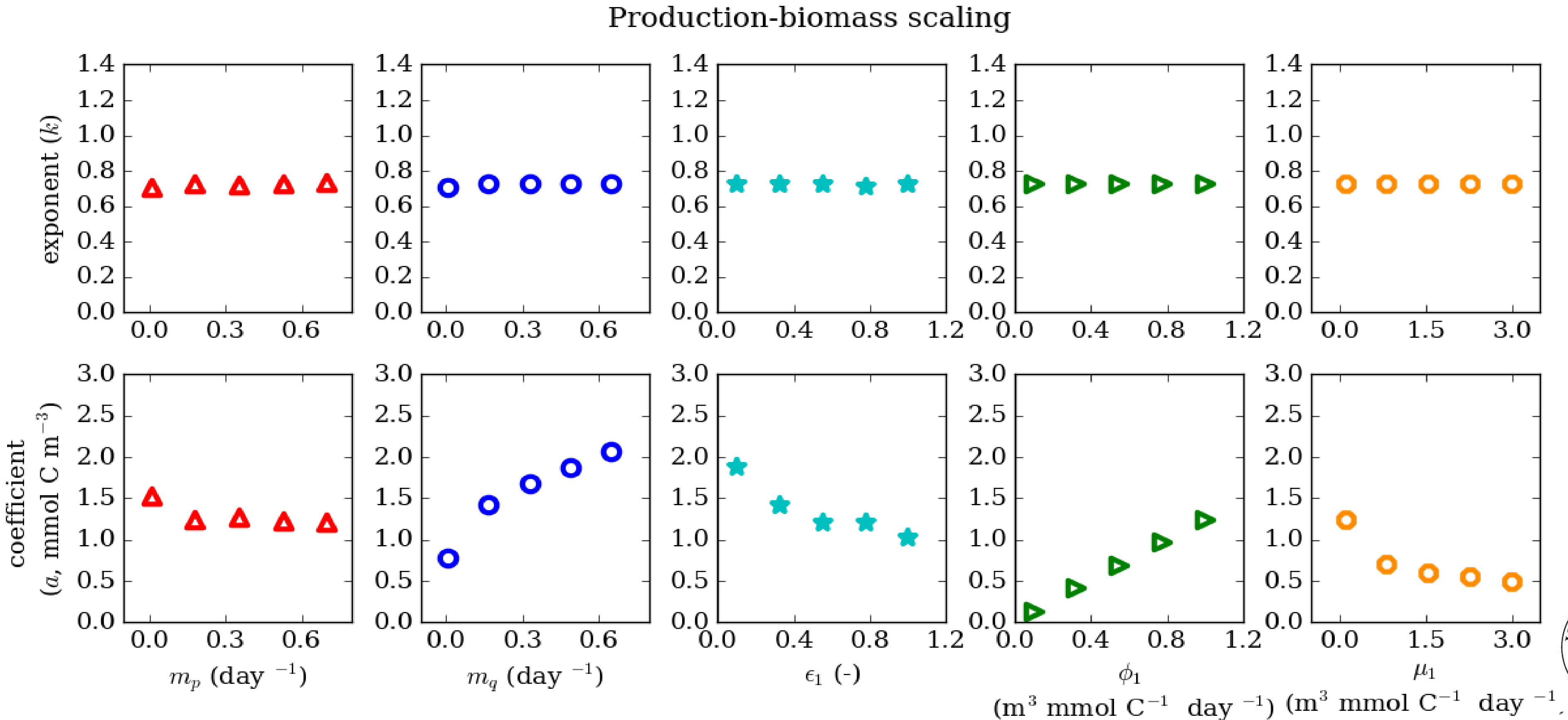
Other general mechanisms that could explain these “universal” scaling laws??

| Description | Considered in our theory? | External or internal |
|---|---|---|
| Transfer efficiency | Considered, | Internal |
| Turnover rates | Considered, , , | Internal |
| Habitat structure | Not considered | Internal or external |
| Omnivory | Not considered | Internal |
| Historical subsidization at any trophic level | Not considered* | External |
| Changes in organism size | Not considered+ | Internal |
| Allochthonous subsidization at any trophic level | Not considered* | External |
| Movement of organisms across system boundaries | Not considered | External |
| Intraguild predation or parasitism | Not considered | Internal |
| Presence of more costly metabolic physiology in the consumer | Considered, | Internal |
| Reduced edibility of prey | Considered, | Internal |
| External extraction at any trophic level, e.g. by humans | Not considered | External |
| Interference competition | Considered; resource competition | Internal |

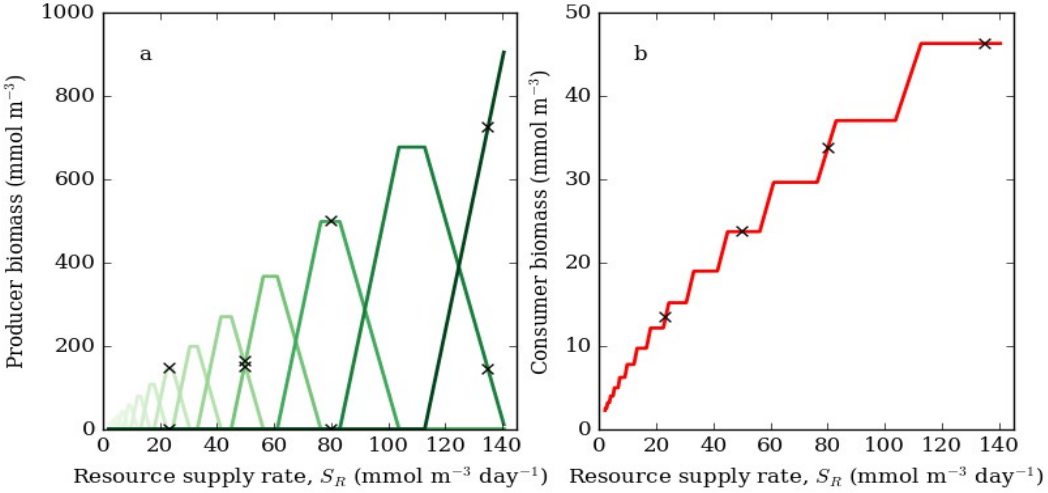
# Sensitivity analysis

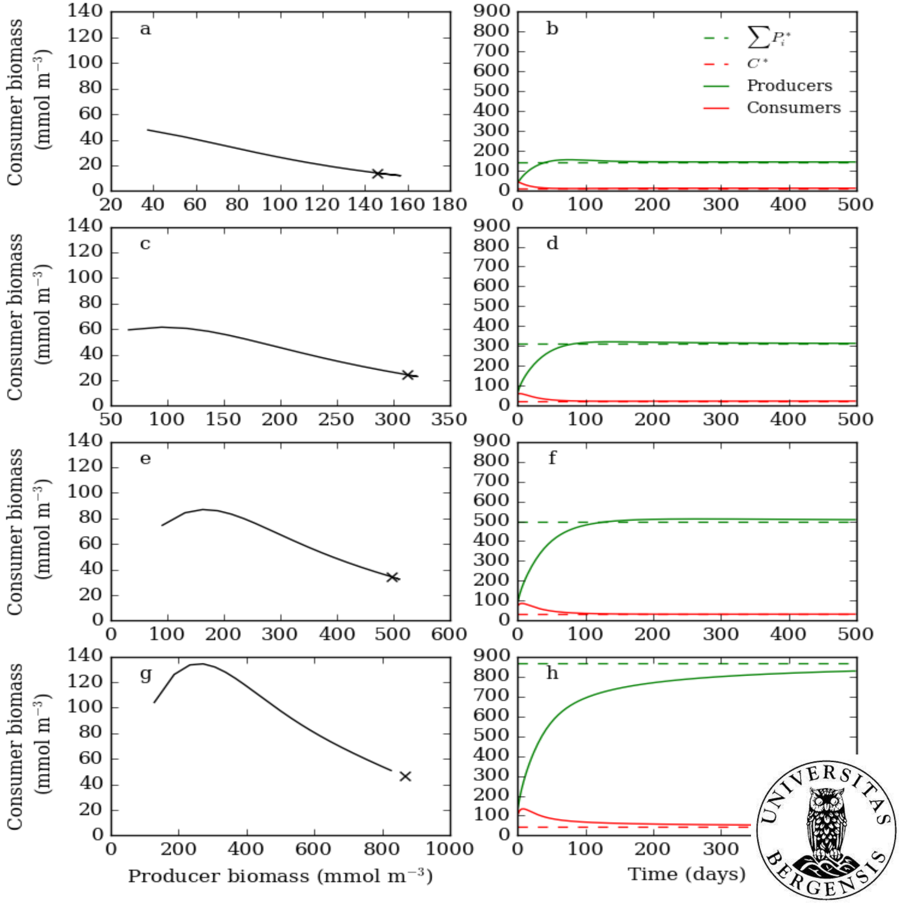


# Sensitivity analysis



# Dynamic solutions (found numerically) fall towards analytic steady state



# Scaling exponent depends on trade-off function (!)

Linear trade-off

$$\mu_i = \mu_1 - i * \delta_\mu$$

$$\varphi_i = \varphi_1 - i * \delta_\varphi$$

$$\epsilon_i = \epsilon_1 - i * \delta_\epsilon$$

Trade-offs as before but with high cost and low benefit

$$\mu_i = \mu_1 \rho^i$$

$$\varepsilon_i = \varepsilon_1 \rho^i$$

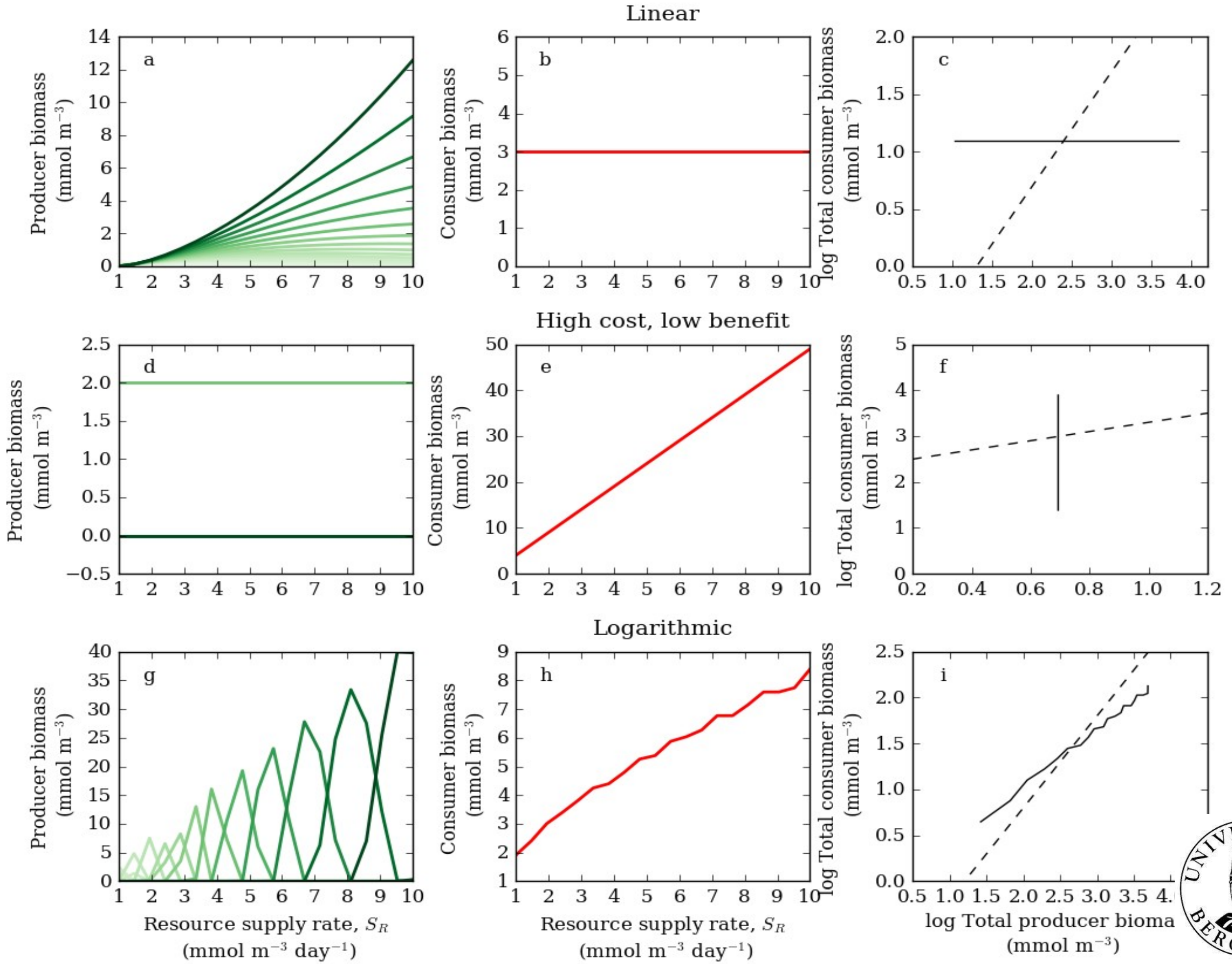
$$\varphi_i = \varphi_1 \nu^i$$

Logarithmic trade-off

$$\varphi_i = 10^{\log_{10}(\varphi_1 - i * \delta_\varphi)}$$

$$\mu_i = 10^{\log_{10}(\mu_1 - i * \delta_\mu)}$$

$$\epsilon_i = 10^{\log_{10}(\epsilon_1 - i * \delta_\epsilon)}$$



# Model framework

## Producer-Consumer population model

$$\frac{dR}{dt} = S_R - \sum_{i=1}^{n} \mu_i R P_i$$

$$\frac{dP_i}{dt} = \mu_i R P_i - \varphi_i P_i C - m_p P_i$$

$$\frac{dC}{dt} = \sum_{i=1}^{n} \varepsilon_i \varphi_i P_i C - m_c C$$

## General model

$$\frac{dN_j}{dt} = \underbrace{\varepsilon_j f_{j-1}\left(N_{j-1}, N_j\right)}_{production} - \underbrace{f_j\left(N_j, N_{j+1}\right)}_{losses}$$

Two steady-states, depending on how resource uptake affinity, consumption affinity and transfer efficiency are connected:

1. Producer increase with increasing nutrient supply:

$$C^{¿} = \frac{m_p\left(\mu_i - \mu_j\right)}{\left(\mu_j \varphi_i - \mu_i \varphi_j\right)} \qquad \sum_{\square}^{\square} \mu_l P_l^{¿} = \frac{S_R}{R^{¿}} \qquad R^{¿} = \frac{m_p\left(\varphi_i - \varphi_j\right)}{\left(\mu_j \varphi_i - \mu_i \varphi_j\right)}$$

2. Consumer increase with increasing nutrient supply:

$$C^{¿} = \frac{\varepsilon_k}{m_c} S_R - \frac{m_p}{\varphi_k} \qquad P_k^{¿} = \frac{m_c}{\varepsilon_k \varphi_k} \qquad R^{¿} = \frac{\varepsilon_k \varphi_k}{m_c \mu_k} S_R$$

| Symbol | Definition | Value (units) |
|---|---|---|
| $R$ | Ambient resource concentration | Variable (mmol C m$^{-3}$) |
| $P_i$ | Producer biomass | Variable (mmol C m$^{-3}$) |
| $C$ | Consumer biomass | Variable (mmol C m$^{-3}$) |
| $S_R$ | Resource supply rate | Variable (mmol C m$^{-3}$ day$^{-1}$) |
| $\mu_i$ | Resource uptake affinity of producer $i$ | Equation 15 (m$^3$ mmol C$^{-1}$ day$^{-1}$) |
| $\varphi_i$ | Interaction strength between $C$ and producer $P_i$ | Equation 16 (m$^3$ mmol C$^{-1}$ day$^{-1}$) |
| $\varepsilon_i$ | Transfer efficiency of producer $P_i$ to consumer $C$ | Equation 17 (n.d.) |
| $\mu_1$ | Resource uptake affinity for producer $P_1$ | 1.0 (m$^3$ mmol C$^{-1}$ day$^{-1}$) |
| $\varphi_1$ | Interaction strength between $C$ and $P_1$ | 0.1 (m$^3$ mmol C$^{-1}$ day$^{-1}$) |
| $\varepsilon_1$ | Transfer efficiency of producer $P_1$ to consumer $C$ | 0.3 (n.d.) |
| $m_p$ | Producer mortality | 0.1 (day$^{-1}$) |
| $m_c$ | Consumer mortality | 0.1 (day$^{-1}$) |
| $\rho$ | Resource uptake and transfer cost constraint | 0.92 (n.d.) |

# Model behaviour

We wish to solve Equations 8-10 in the main text for all , , and . The following analysis shows that there are two sets of non-zero equilibrium solutions. In the first set of solutions, predator biomass is independent of supply rate, and increases in supply rate cause biomass accumulation only in the producers. In the second set, the producer biomass is independent of supply rate , and enriching the system through enhanced supply rate drives increases only in the ambient resource concentration and the consumer biomass.

We show that whether the system exists in either state is determined by the allocation of key traits,producer affinity ,consumer affinity  and transfer efficiency. The allocation of traits according to a trade-off between resource competition, and defense against consumers, can lead to transitions between system states in response to increases in  in a manner that explains widely observed biomass and production scaling relationships.