University of Amsterdam
Faculty of Science

Institute for Biodiversity and Ecosystem Dynamics

Ontogenetic development: the ecologically unique and unavoidable life history process

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A short biography: André de Roos

http://staff.fnwi.uva.nl/a.m.deroos

- Ecologist with a strong interest in understanding how ecological systems ***function*** (***dynamics***) and (some) mathematical skills

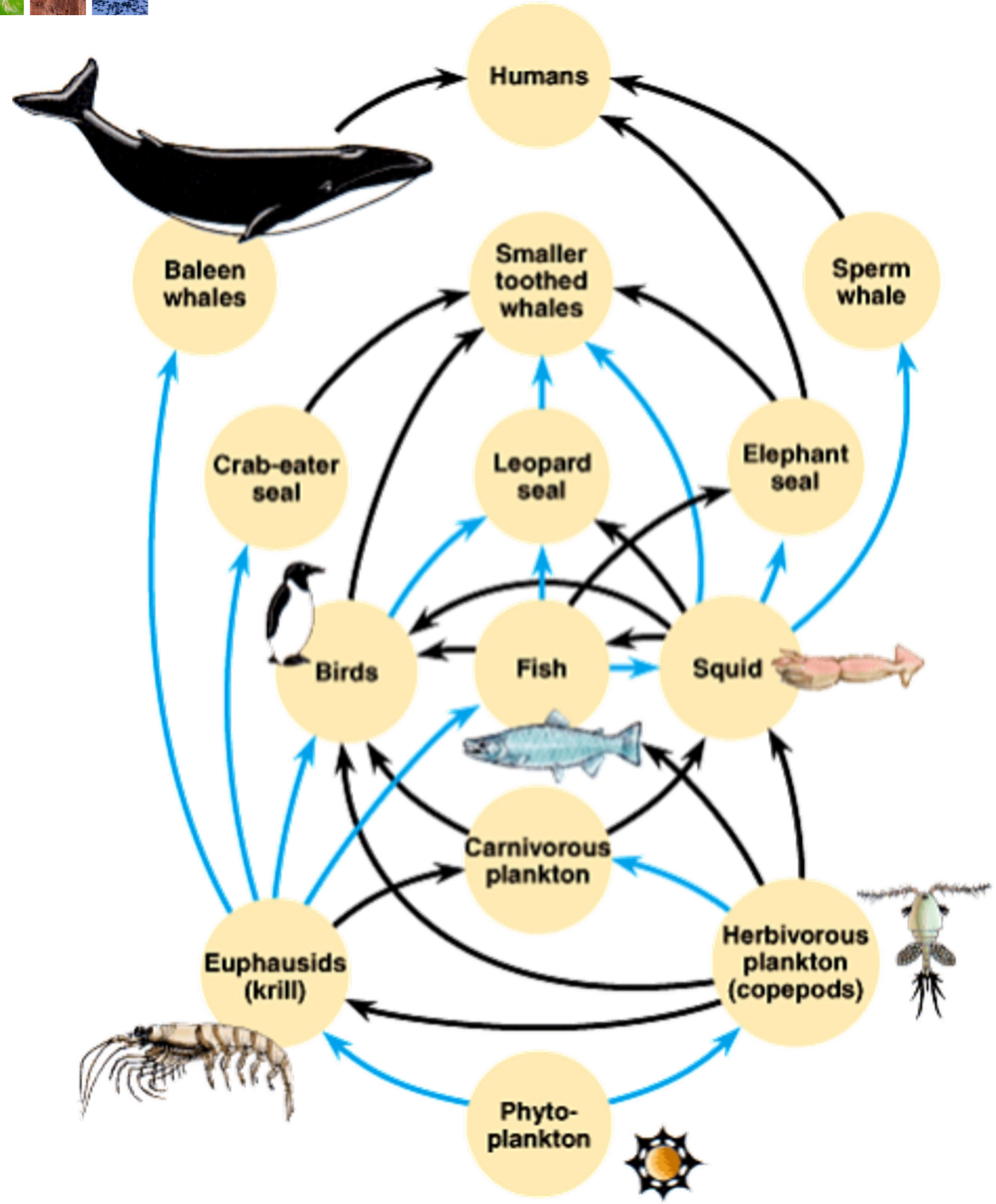
- PhD in Theoretical Biology at Leiden University (1989)
  Supervisors: ***Hans Metz*** and ***Odo Diekmann***
  Topic: Numerical methods of ***physiologically structured population models (PSPMs)***

- Nowadays: using state-of-the-art (numerical) toolbox (dynamics, bifurcation analysis, adaptive dynamics) for studying dynamics of structured population models (PSPMs) to ***answer ecological and evolutionary questions***

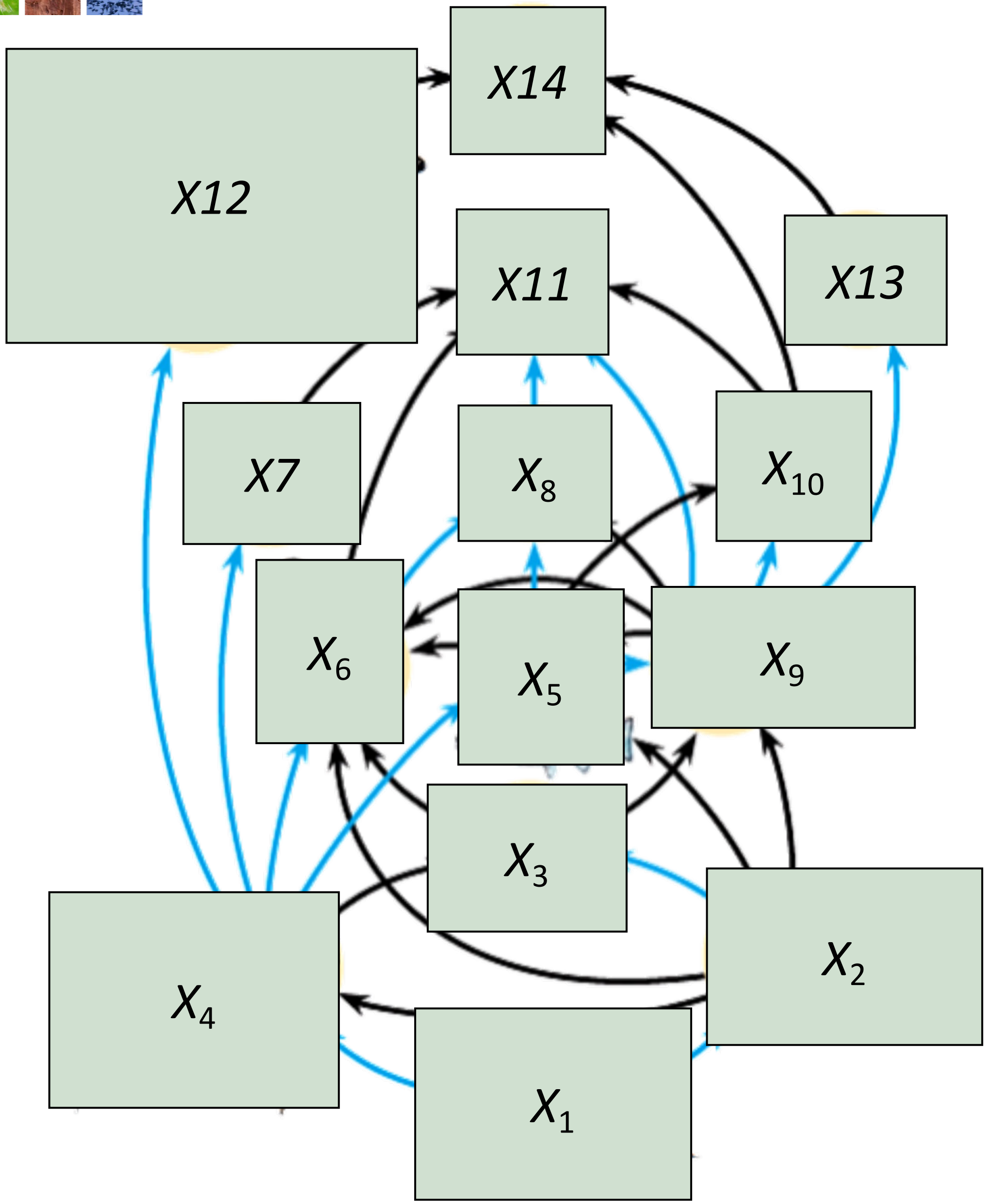
- In case of PSPMs ***biology has driven the mathematical progress***

$\Rightarrow$ **Do not blindly apply existing methods from mathematics or physics, think carefully about your biological system first**

Standard approach to modeling ecological dynamics



Standard approach to modeling ecological dynamics




Alfred Lotka


Vito Volterra

- Individuals within a population are identical
- Only accounting for reproduction and mortality
- Focus on the network topology (structure) of the species interactions

$$\frac{dx_i}{dt} = g_i(x_1,\ldots,x_N), \quad i = 1,\ldots,N$$

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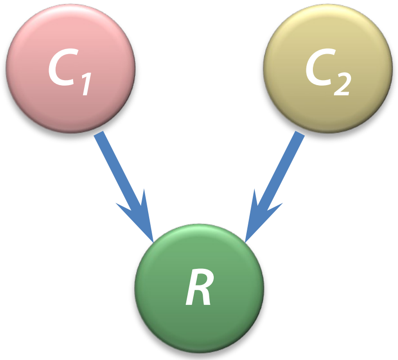
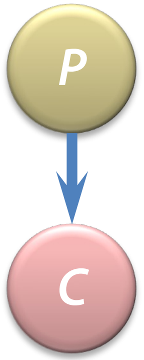
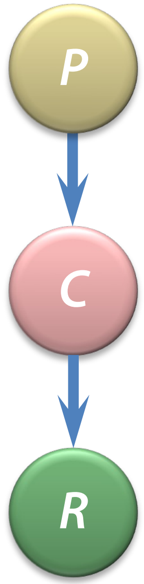
Basis of current ecological community theory



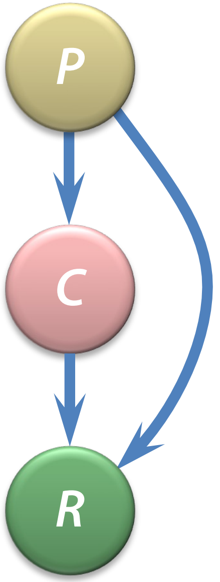
Competition



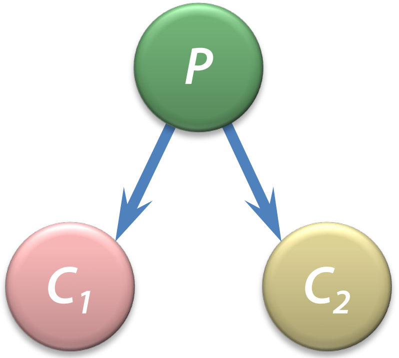
Predation



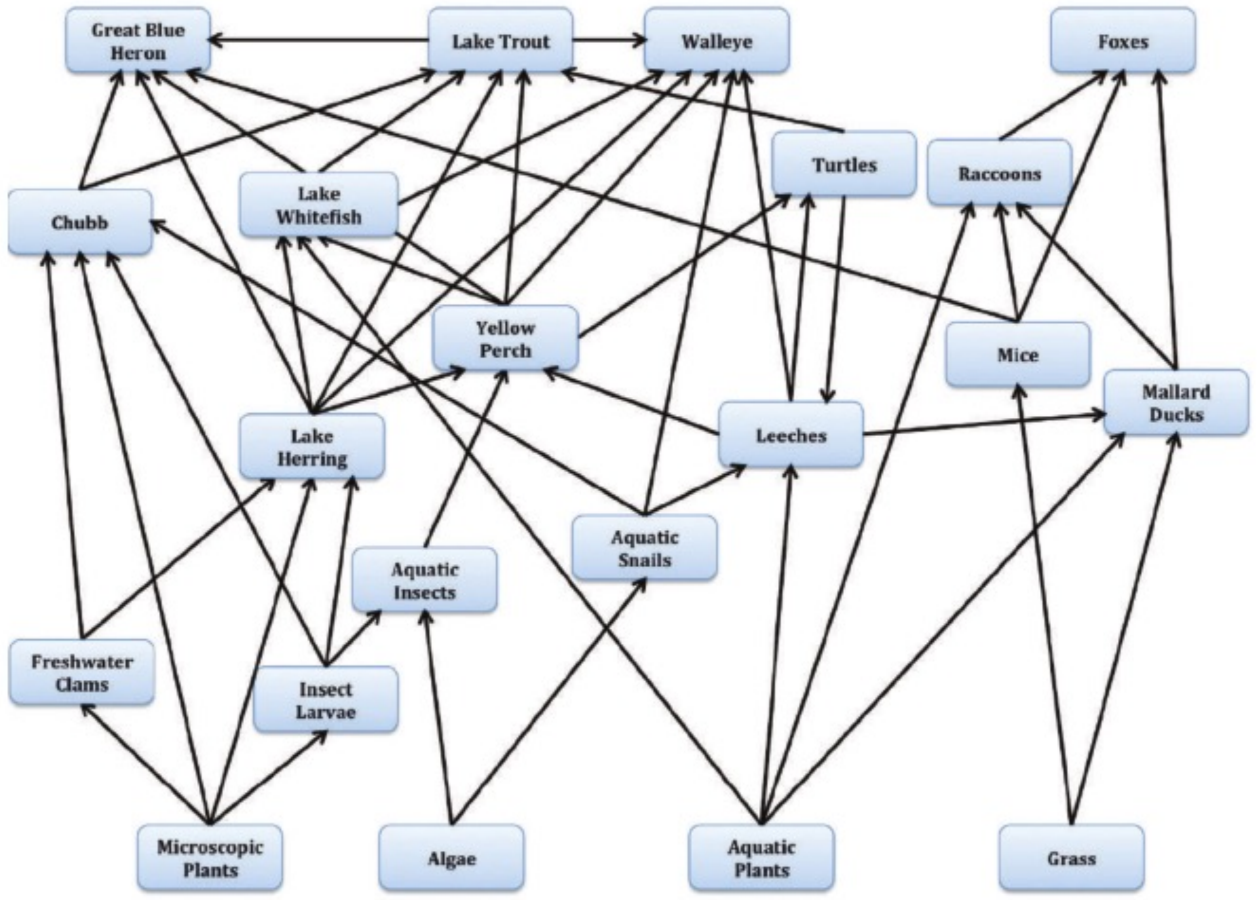
Food chain



Omnivory



Apparent competition



- ***Population-level*** interactions based on reproduction and mortality

Dynamics of interacting populations

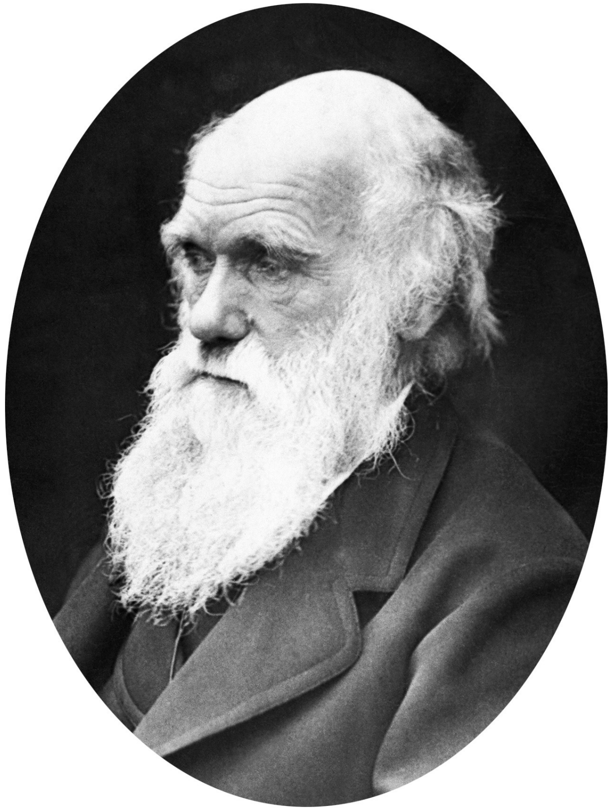
*"Population dynamics: the variations in time and space in the sizes and densities of populations (the **numbers of individuals** per unit area)"*

M.Begon, C.R.Townsend, J.L.Harper (2005)
Ecology: From Individuals to Populations, Wiley-Blackwell

Populations considered as ***collections of elementary particles***, increasing and decreasing in abundance through ***reproduction and mortality***, respectively

Is there a problem?

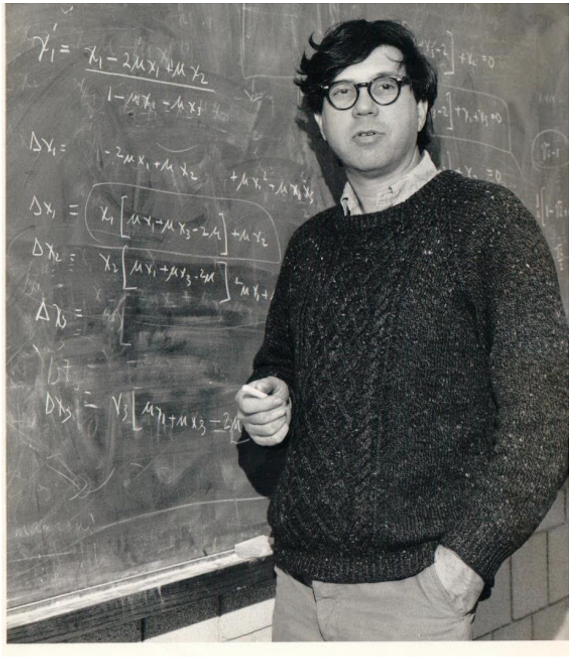
The neglected issue



Charles Darwin

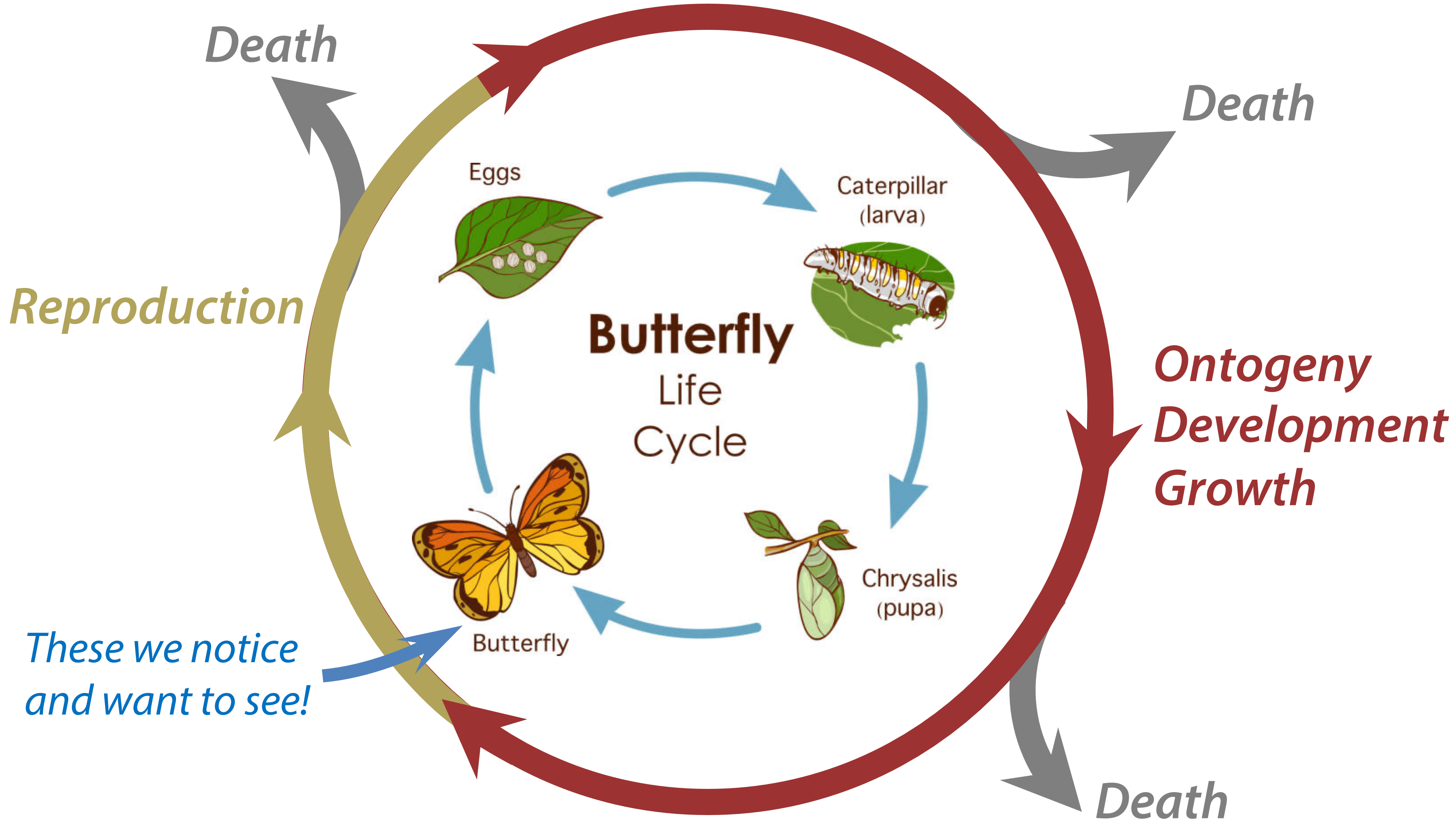
….the essential nature of the Darwinian revolution was neither the introduction of evolutionism as a world view (since historically that is not the case) nor the emphasis on natural selection as the main motive force in evolution (since empirically that may not be the case), but rather the replacement of a metaphysical view of variation among organisms by a materialistic view.

- **Every individual is unique**
- **Variation among individuals**



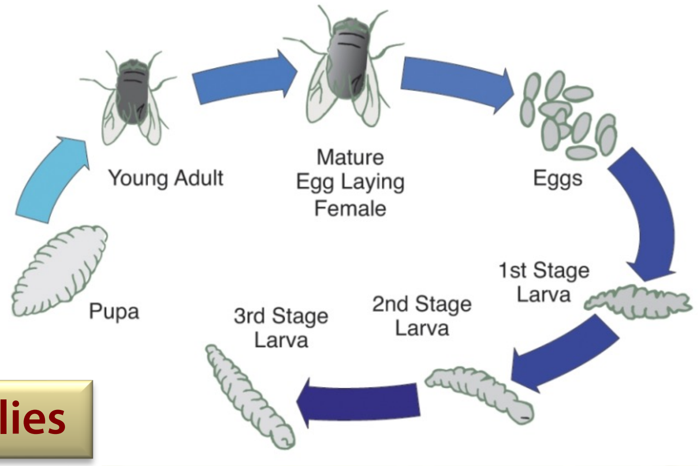
Richard Lewontin
(revolutionary geneticist, evolutionary biologist, long-time member of the SFI Science Board)

The main source of variation among individuals

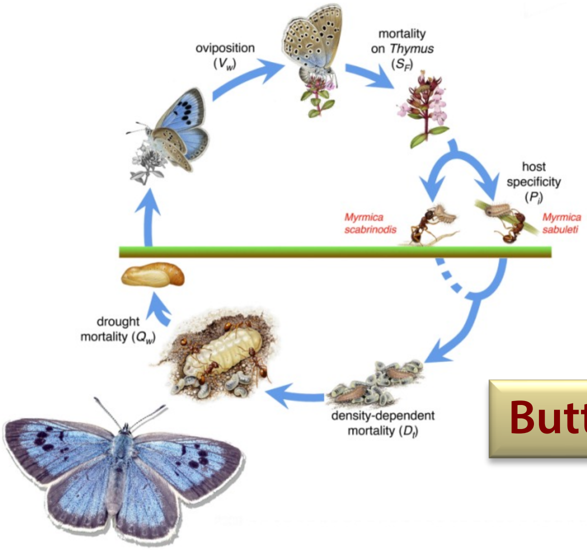


All individuals develop and die, but only the lucky few reproduce!

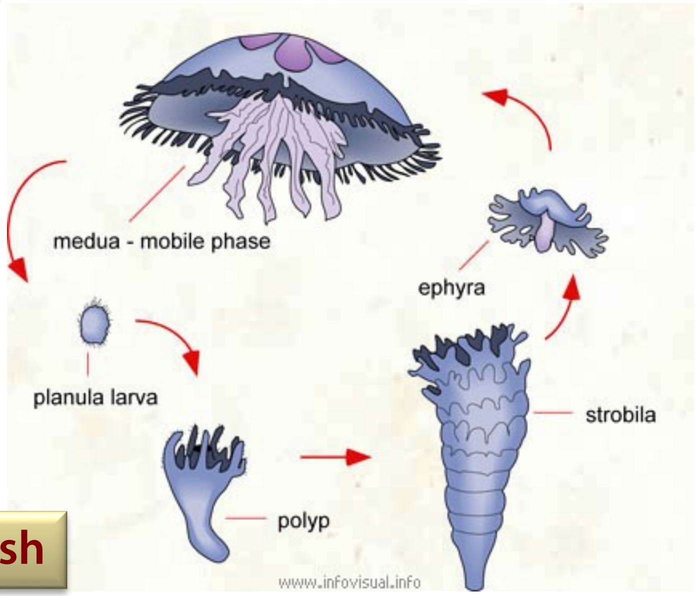
The main source of variation among individuals



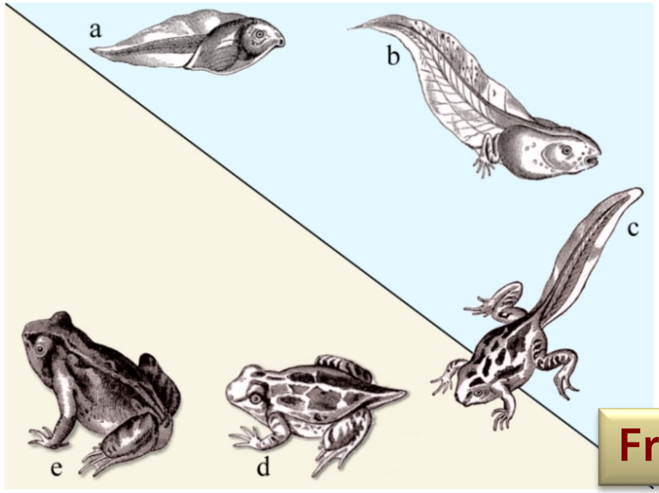
Flies



Butterflies



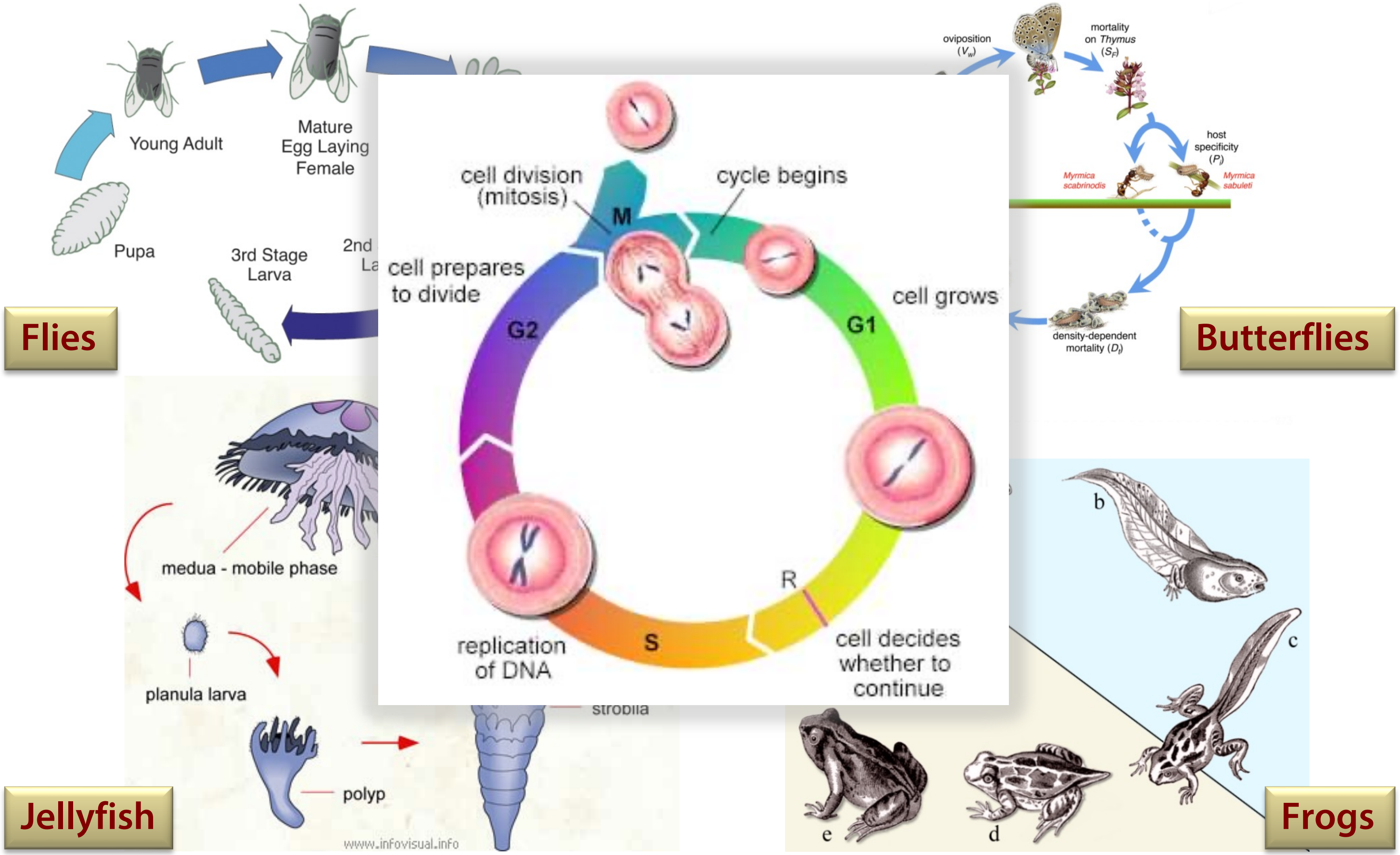
Jellyfish



Frogs

Development: unique and ubiquitous!

The main source of variation among individuals



Development: unique and ubiquitous!

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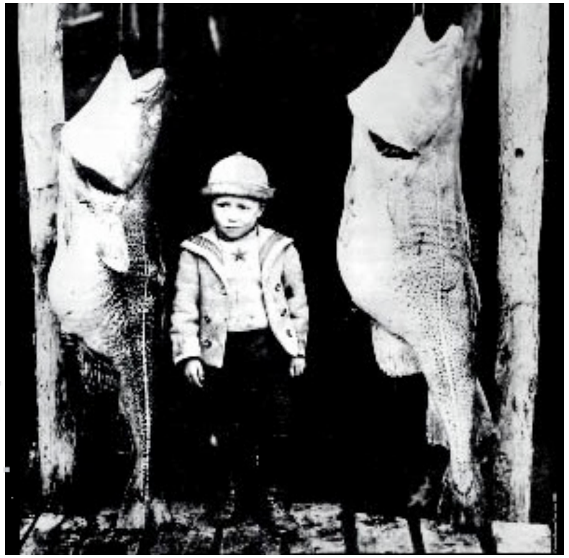
"... the life cycle is the central unit in biology. The notion of the organism is used in this sense, rather than that of an individual at a moment in time, such as the adult at maturity. Evolution then becomes the alteration of life cycles through time..."

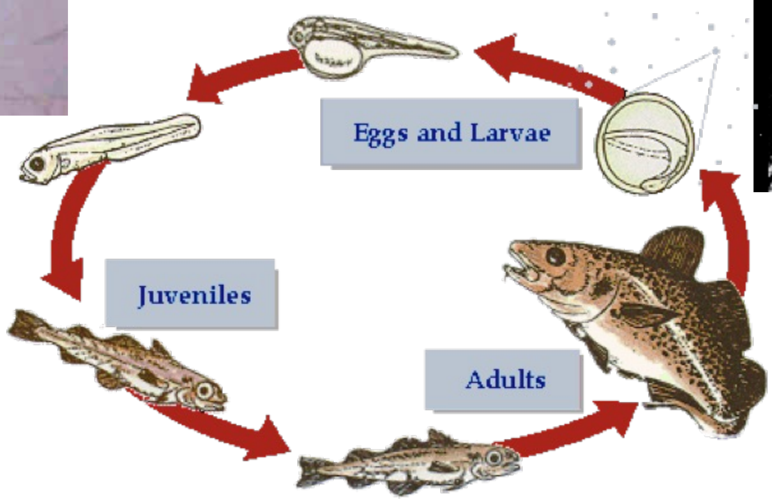
J. T. Bonner (1965)
Size and Cycle: An Essay on the Structure of Biology

- **Question**: Does accounting for ontogeny (individual development through life history) make a fundamental difference to our understanding of ecological dynamics?
- **Answer**: Yes! Accounting for ontogeny messes up our intuition about responses of ecological communities to perturbations and changes

Development's most elementary feature: Growth in body size (a doubling at least)

x 10^9





Intra-specific variation in body size!

Development's most elementary feature: Growth in body size (a doubling at least)

Unlike aging, development is highly plastic!

Development's most elementary feature: Growth in body size (a doubling at least)

Unlike aging, development is highly plastic!

Foto by Emma van der Woude

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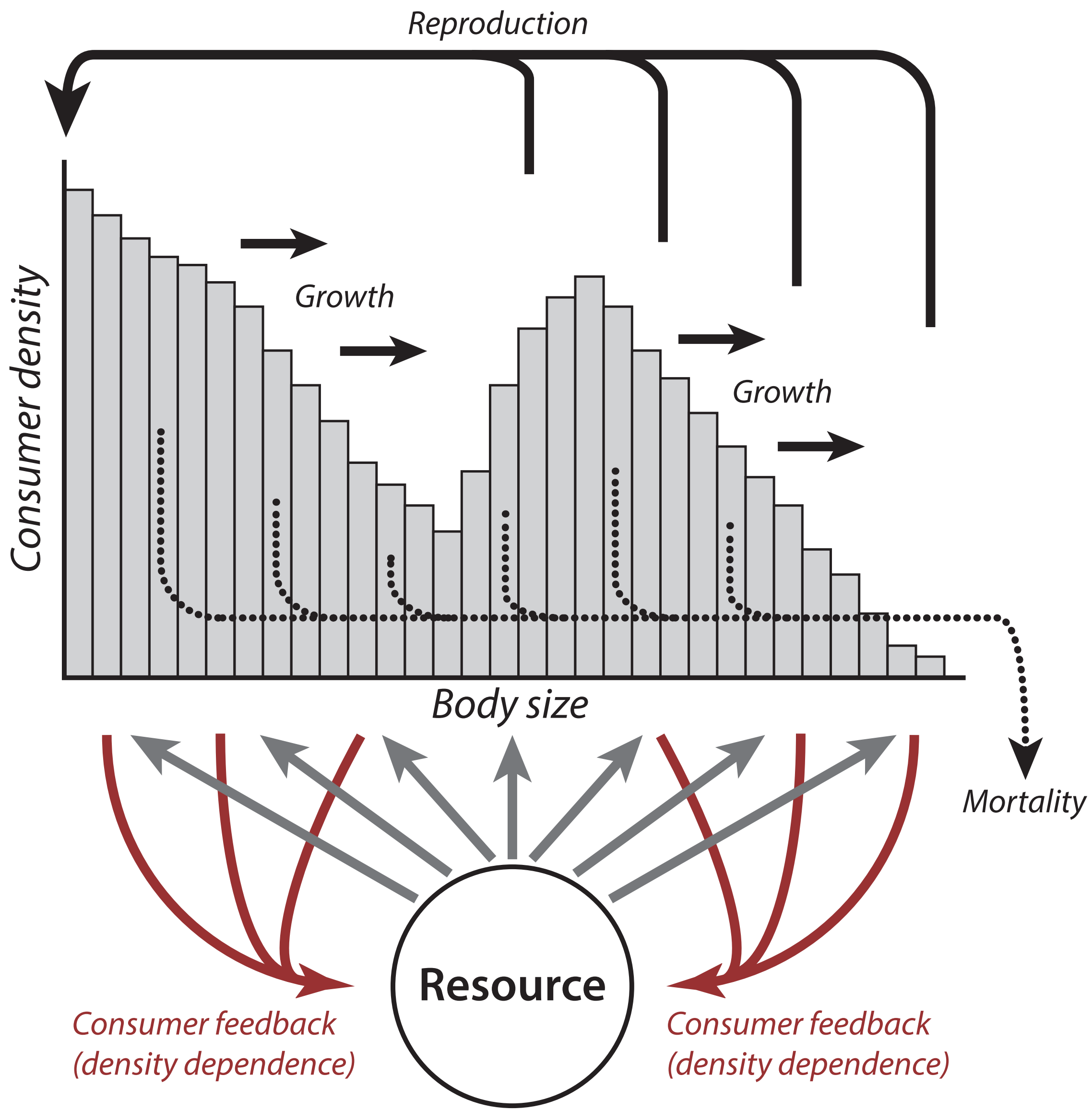
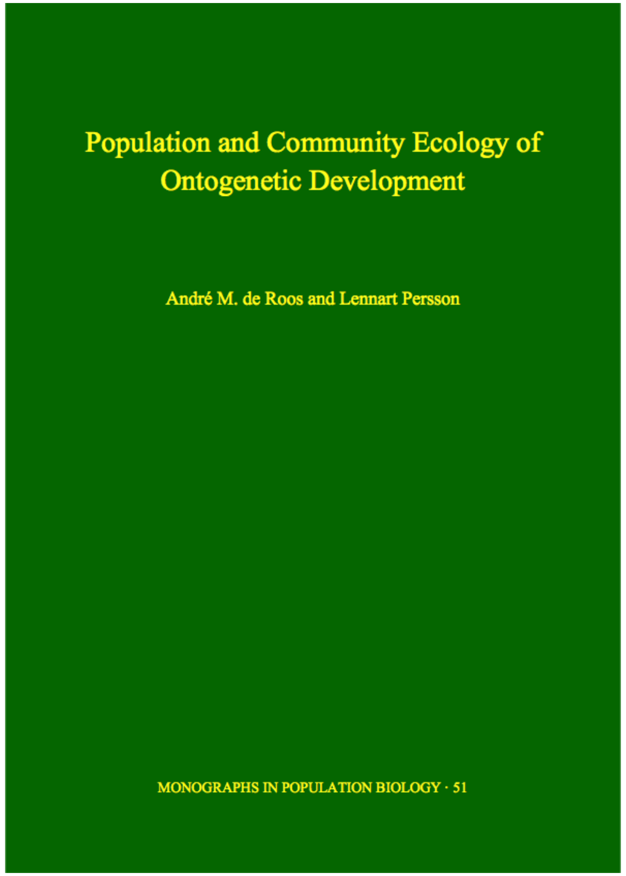
Size-structured population models





Population and Community Ecology of Ontogenetic Development
André M. de Roos & Lennart Persson
Princeton Monographs 51

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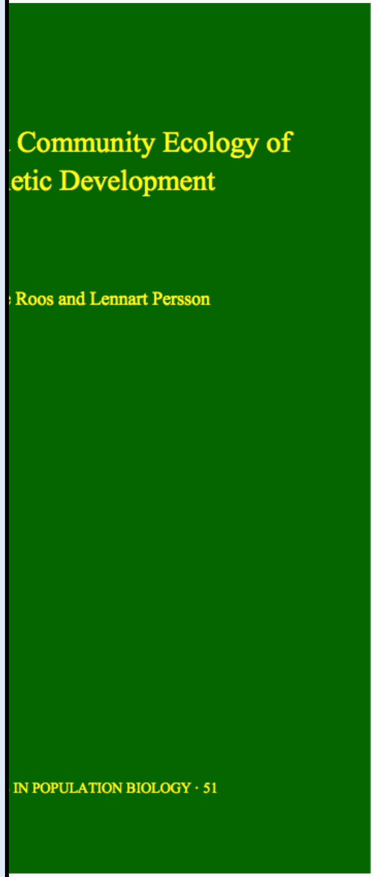
Size-structured population models

$$
\begin{cases}
\dfrac{dR}{dt} = p(R) - \displaystyle\int_{s_b}^{s_m} \gamma(s,R)\, c(t,s)\, ds \\[2ex]
\dfrac{\partial c(t,s)}{\partial t} + \dfrac{\partial g(s,R)\, c(t,s)}{\partial s} = -\mu(s,R)\, c(t,s) \\[2ex]
g(s_b,R)\, c(t,s_b) = \displaystyle\int_{s_b}^{s_m} \beta(s,R)\, c(t,s)\, ds
\end{cases}
$$

- Growth rate in body size: $g(s,R)$
- Reproduction rate: $\beta(s,R)$
- Resource intake rate: $\gamma(s,R)$
- Mortality rate: $\mu(s,R)$



Community Ecology of
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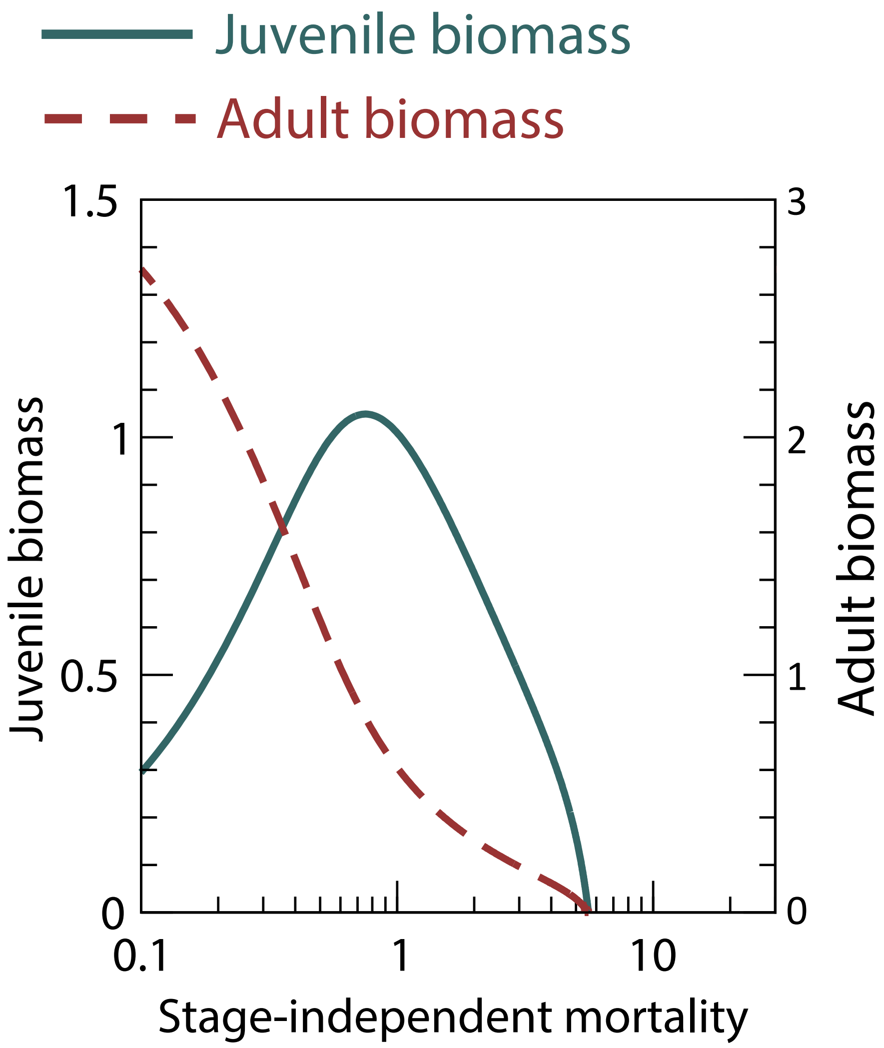
Equilibrium changes with increasing mortality



Reproduction more limited by food than growth and development

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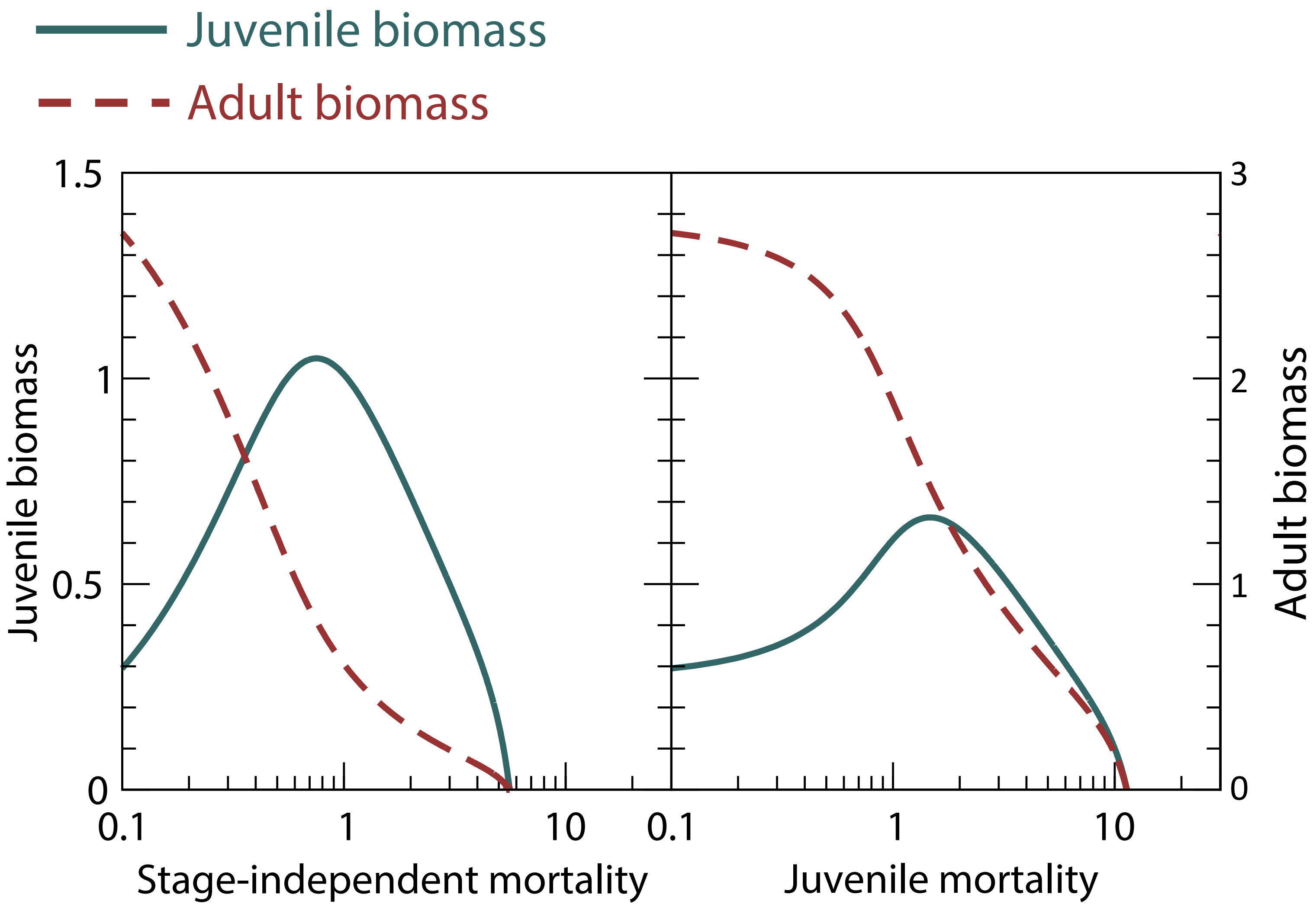
Equilibrium changes with increasing mortality



Reproduction more limited by food than growth and development

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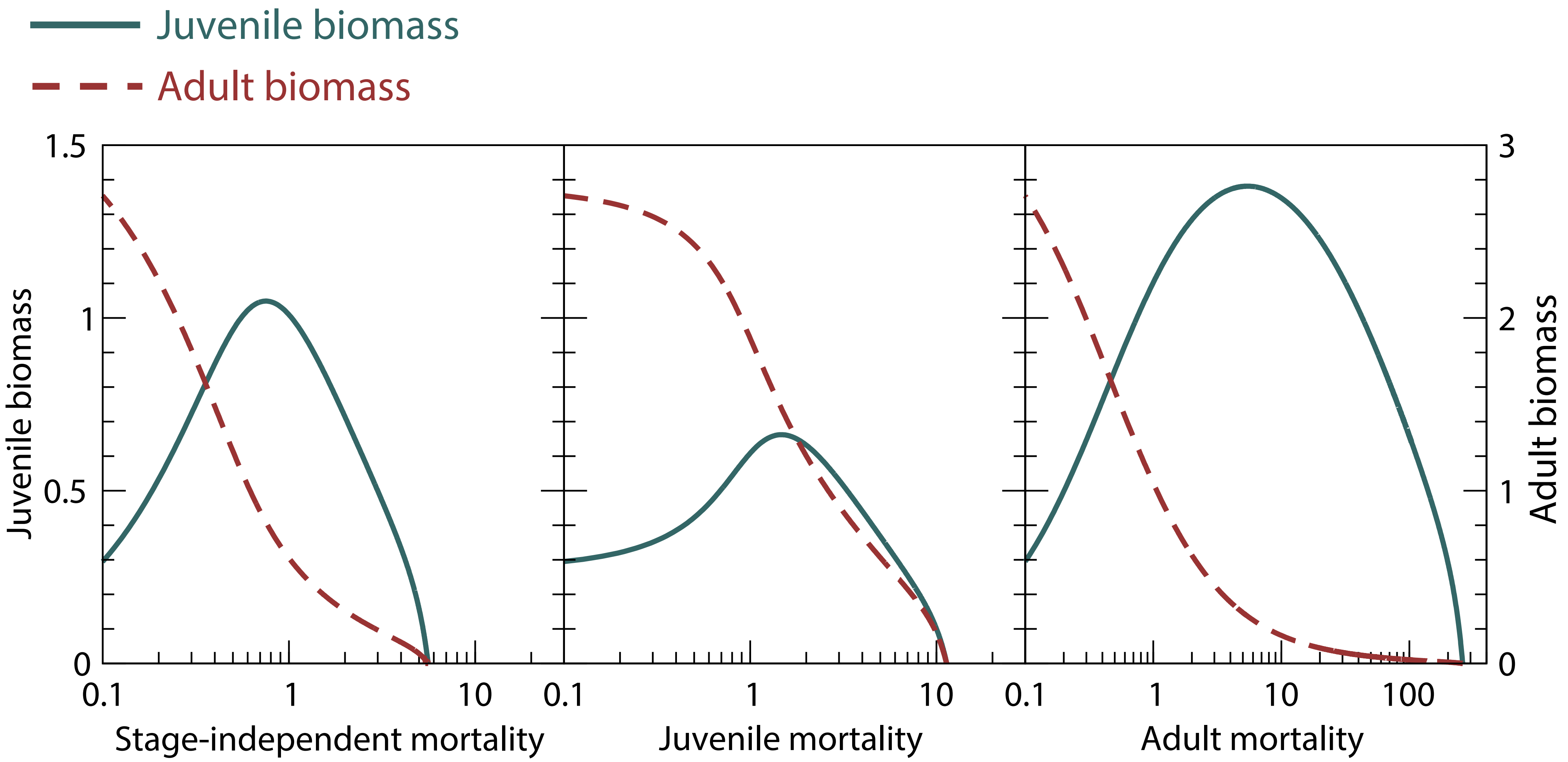
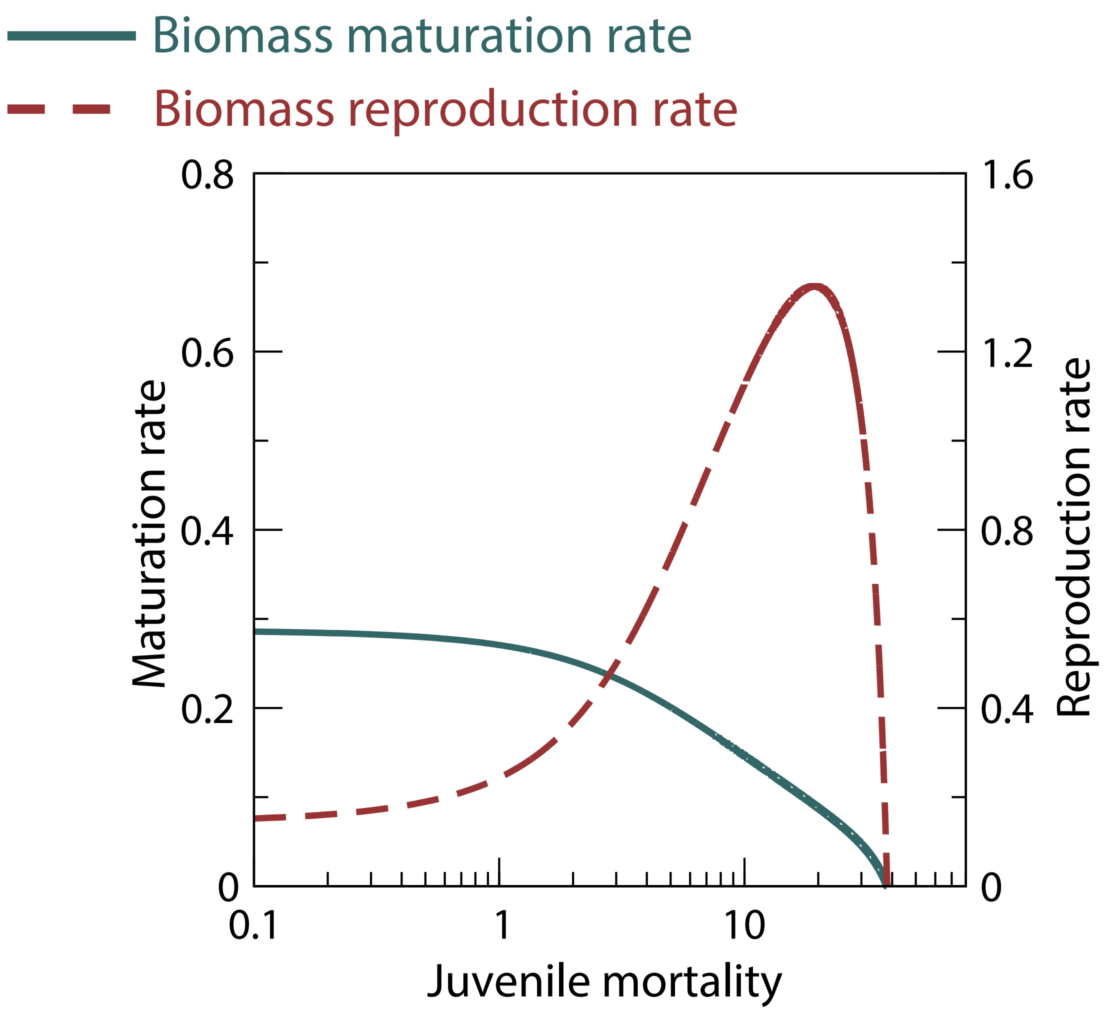
Equilibrium changes with increasing mortality



Reproduction more limited by food than growth and development

Asymmetric changes in reproduction and maturation with increasing mortality



When adults compete more:

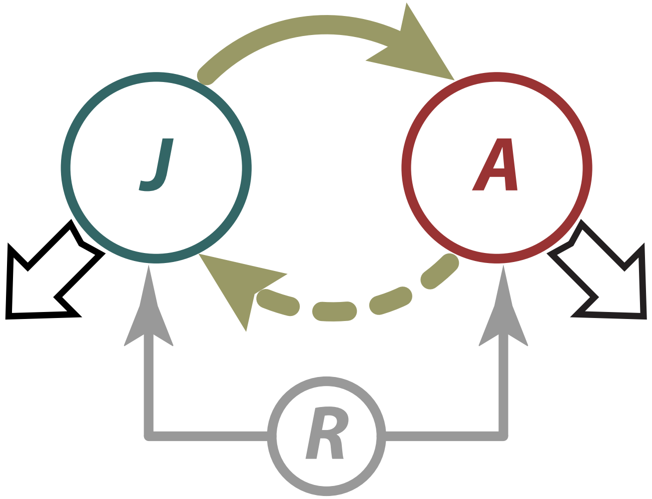
- Low adult fecundity, high juvenile survival
- Adults dominate
- ***Adults use most of their intake for maintenance*** (no production)
- Mortality releases adult competition, increases reproduction and juvenile biomass

Disproportionally large increase in population birth rate

Ontogenetic symmetry breaking

Development and reproduction limited by food to the same extent

Ontogenetic symmetry



Reduces to classic, unstructured model in terms of total population biomass

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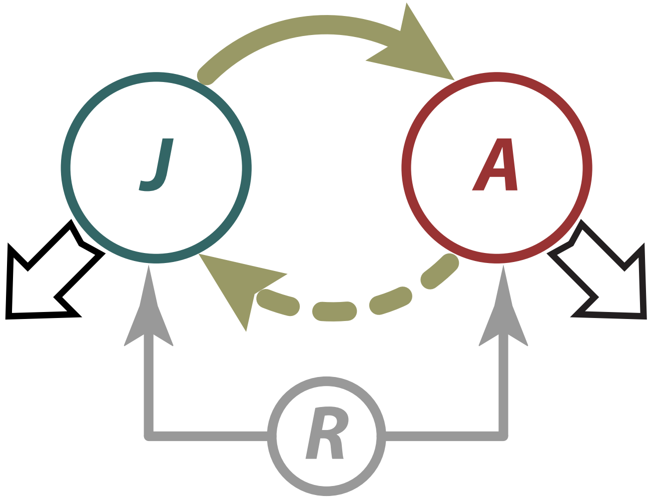
Ontogenetic symmetry breaking

Development and reproduction limited by food to the same extent

Ontogenetic symmetry

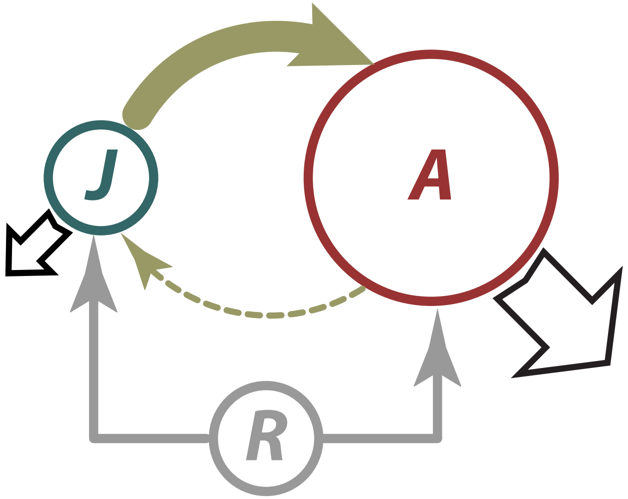


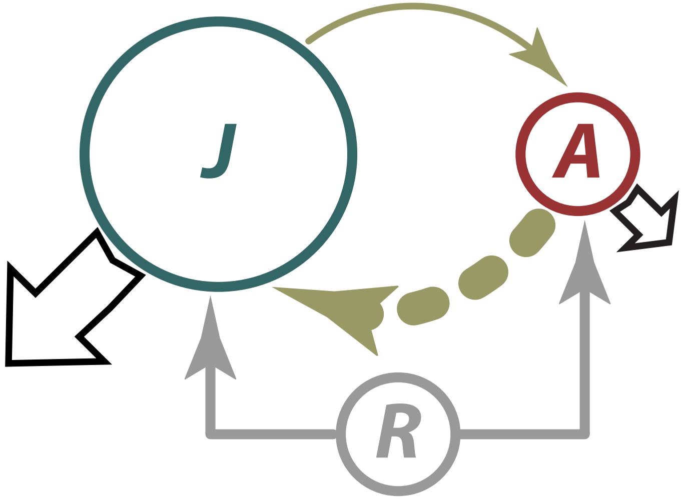
Reduces to classic, unstructured model in terms of total population biomass

Reproduction more limited by food

Development more limited by food

Ontogenetic asymmetry

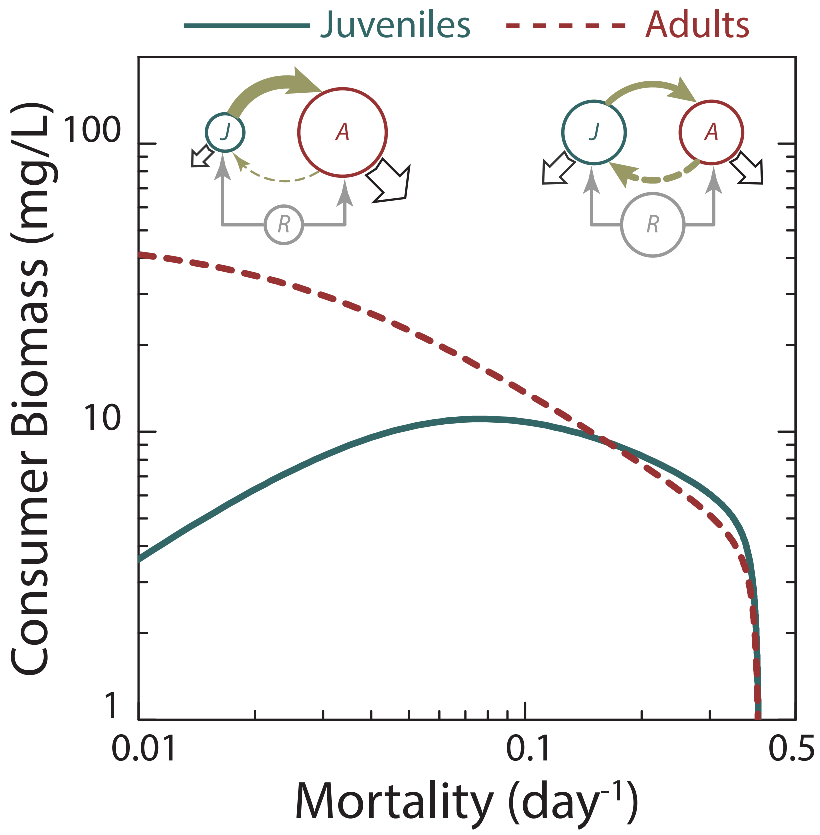




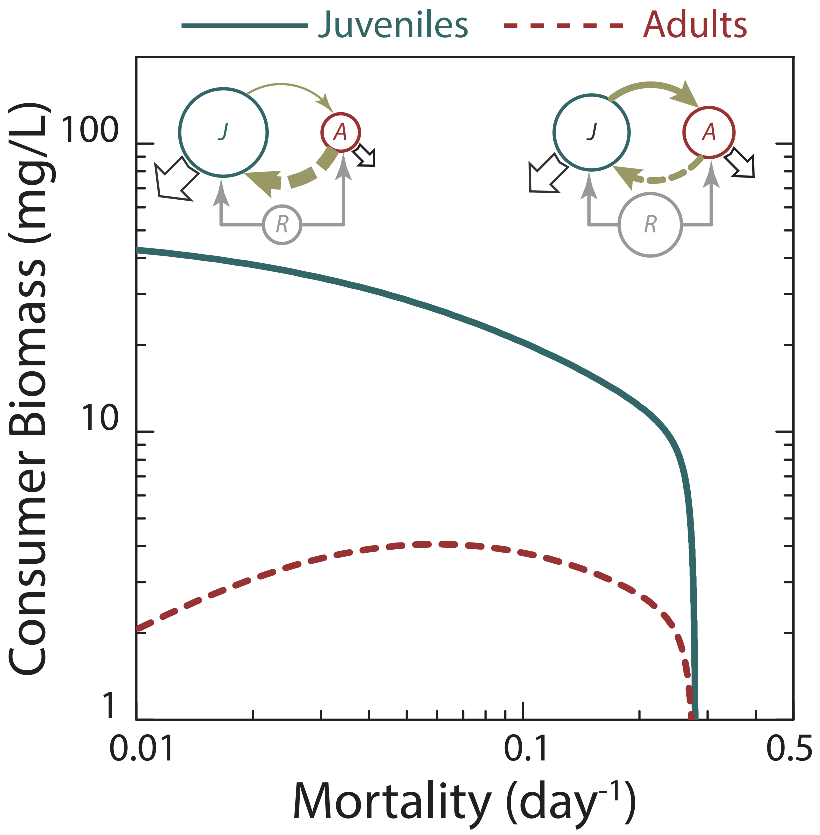
Ontogenetic asymmetry

Reproduction more limited by food

Development more limited by food



Mortality increases juvenile biomass

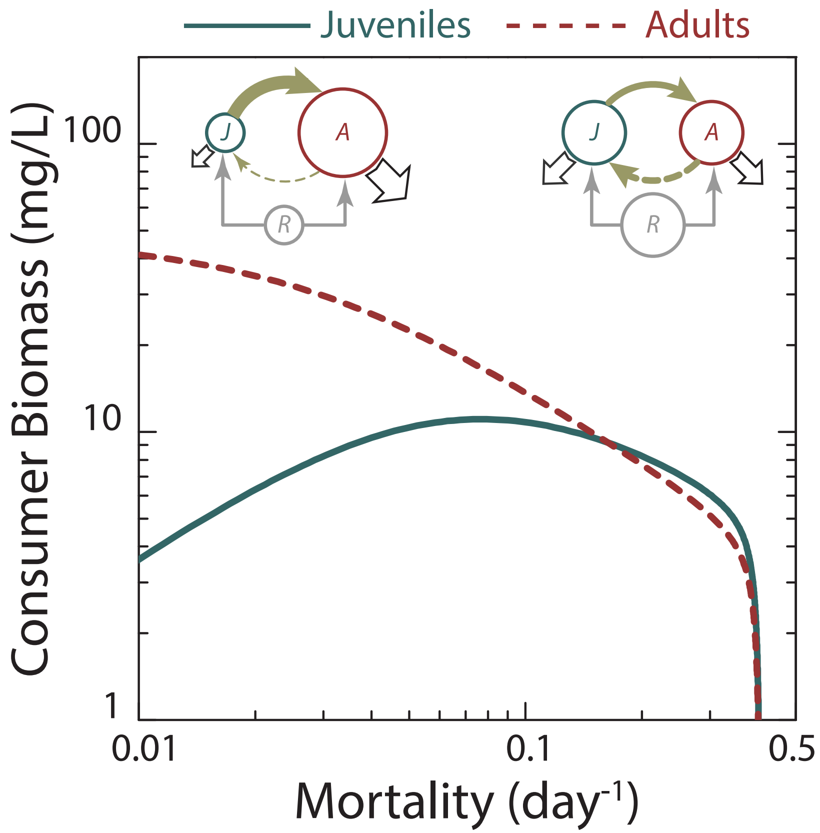


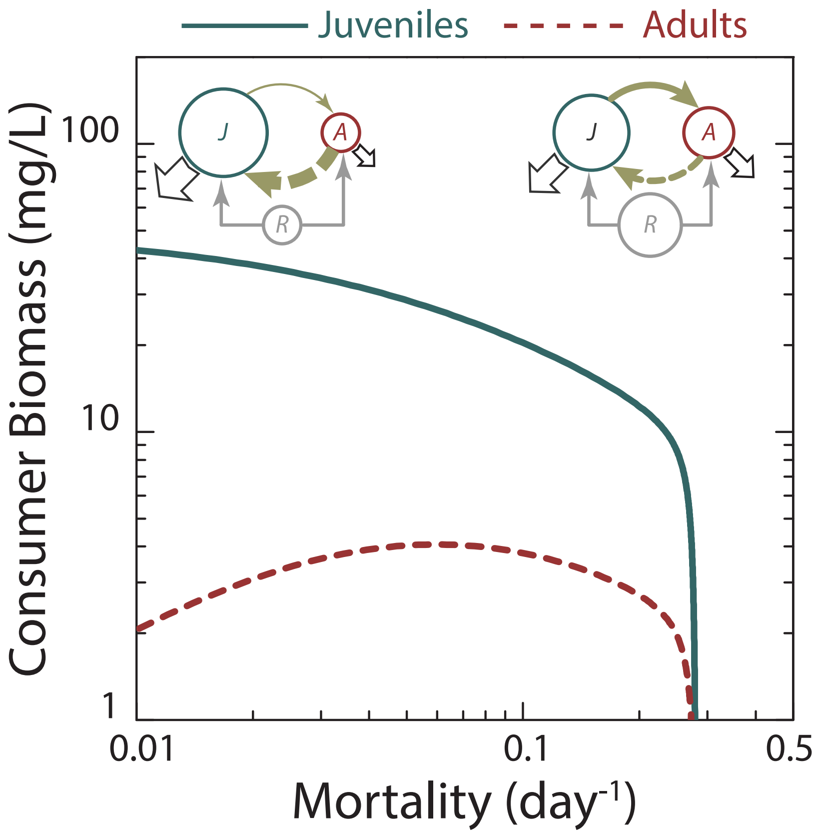
Mortality increases adult biomass

Ontogenetic asymmetry

Reproduction more limited by food

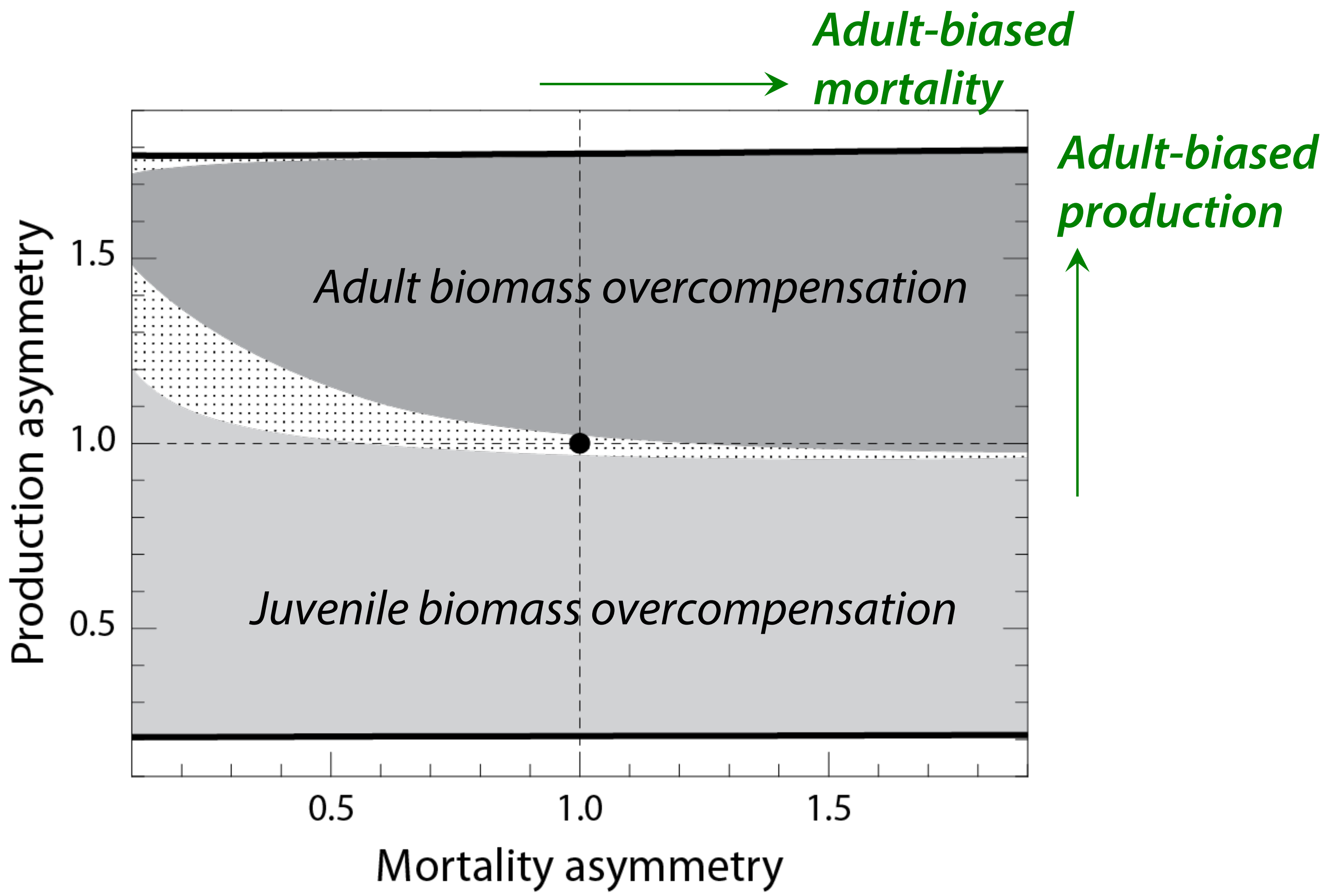
Development more limited by food





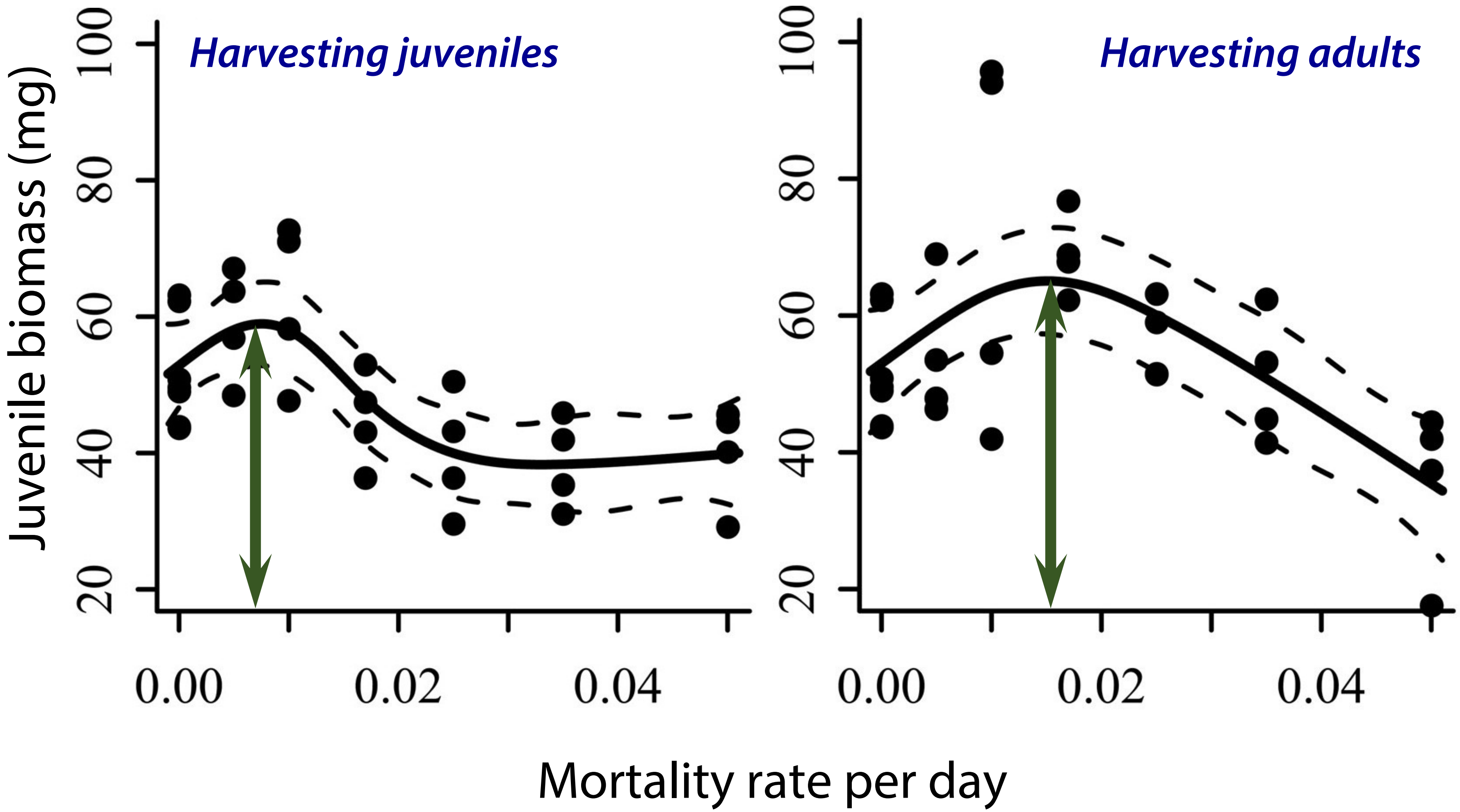
Mortality increases densities of all non-bottleneck life history stages

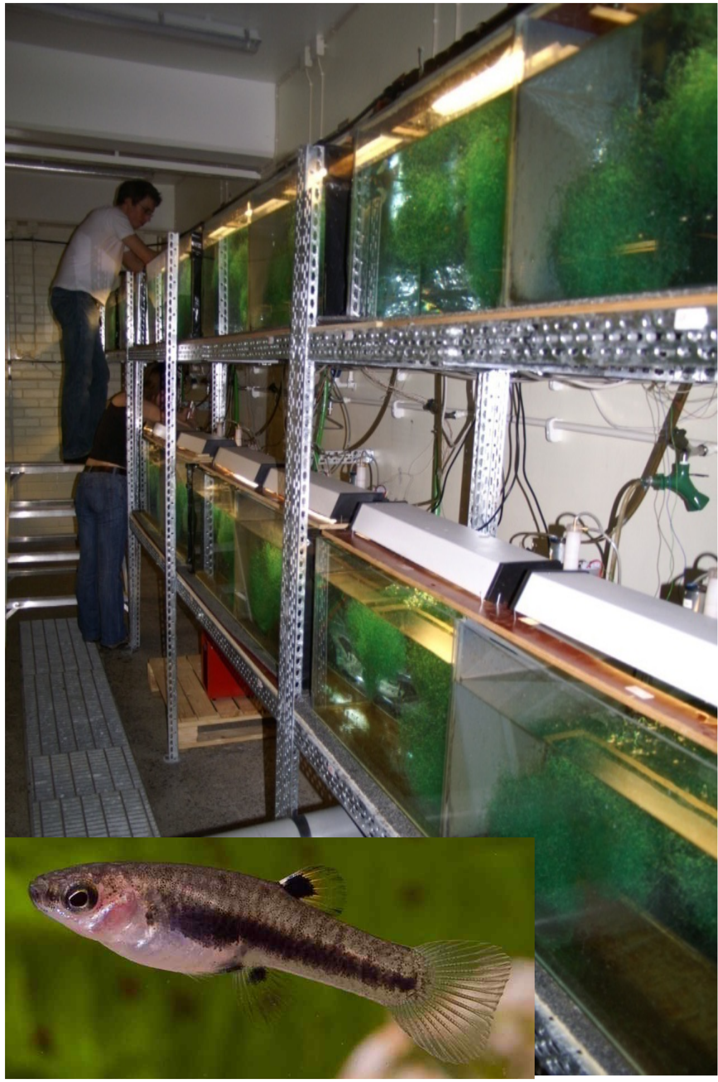
Overcompensation is (almost) everywhere



- Predictions for (unstructured) cases with ontogenetic symmetry hold under limited conditions
- Overcompensation mostly influenced by production asymmetry, little influence of mortality asymmetry

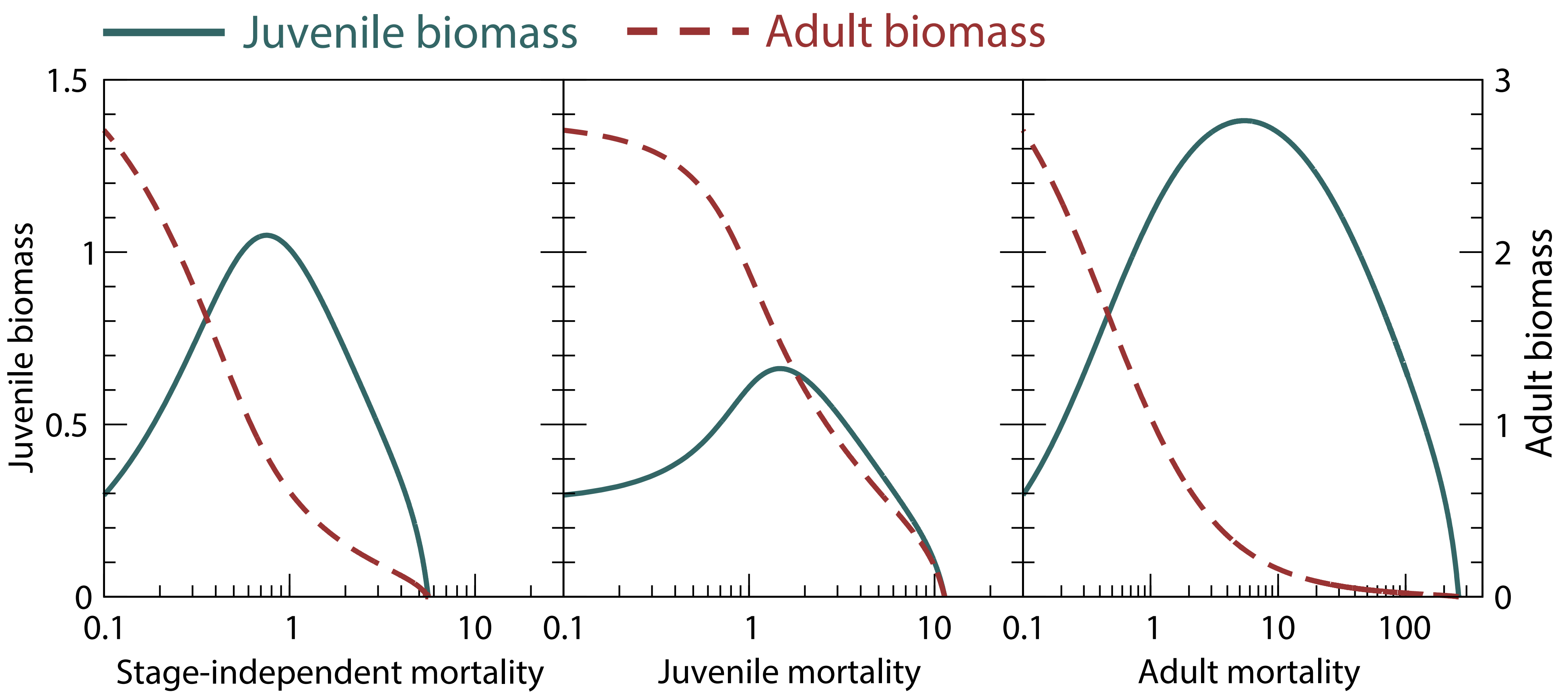
Testing predictions





Schröder, Persson & De Roos (2009) *PNAS* 106:2671

Biomass overcompensation with increasing mortality



What life history characteristics cause these changes in population structure with changing abundance?

An abstract, theoretical analysis

$$\begin{cases} \dfrac{dR}{dt} = p(R) - f_J(R)C_J - f_A(R)C_A \\ \dfrac{dC_J}{dt} = g_A(R)C_A - g_J(R)C_J - \mu_J C_J \\ \dfrac{dC_A}{dt} = g_J(R)C_J - \mu_A C_A \end{cases}$$

Resource

Juvenile consumers

Adult consumers

$$f'_J(R),\ f'_A(R),\ g'_J(R),\ g'_A(R) > 0 \quad \text{and} \quad \boxed{p'(R) \leq 0}$$

Analysis:

- Changes in equilibrium densities with increasing mortality (*applying the implicit function theorem to the equilibrium conditions*)
- Equilibrium stability (*applying the Routh–Hurwitz stability criterion to the Jacobian matrix*)

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An abstract, theoretical analysis

$$\begin{cases} \dfrac{dR}{dt} = p(R) - f_J(R)C_J - f_A(R)C_A \\ \dfrac{dC_J}{dt} = g_A(R)C_A - g_J(R)C_J - \mu_J C_J \\ \dfrac{dC_A}{dt} = g_J(R)C_J - \mu_A C_A \end{cases}$$

Resource

Juvenile consumers

Adult consumers

$$f'_J(R),\ f'_A(R),\ g'_J(R),\ g'_A(R) > 0 \quad \text{and} \quad p'(R) \leq 0$$

Equilibrium densities ***can increase*** with ***increasing*** mortality, when:

$$\left(\frac{f_J(\bar{R})}{g_J(\bar{R})}\right)' < 0 \quad \text{or} \quad \left(\frac{f_A(\bar{R})}{g_A(\bar{R})}\right)' < 0$$

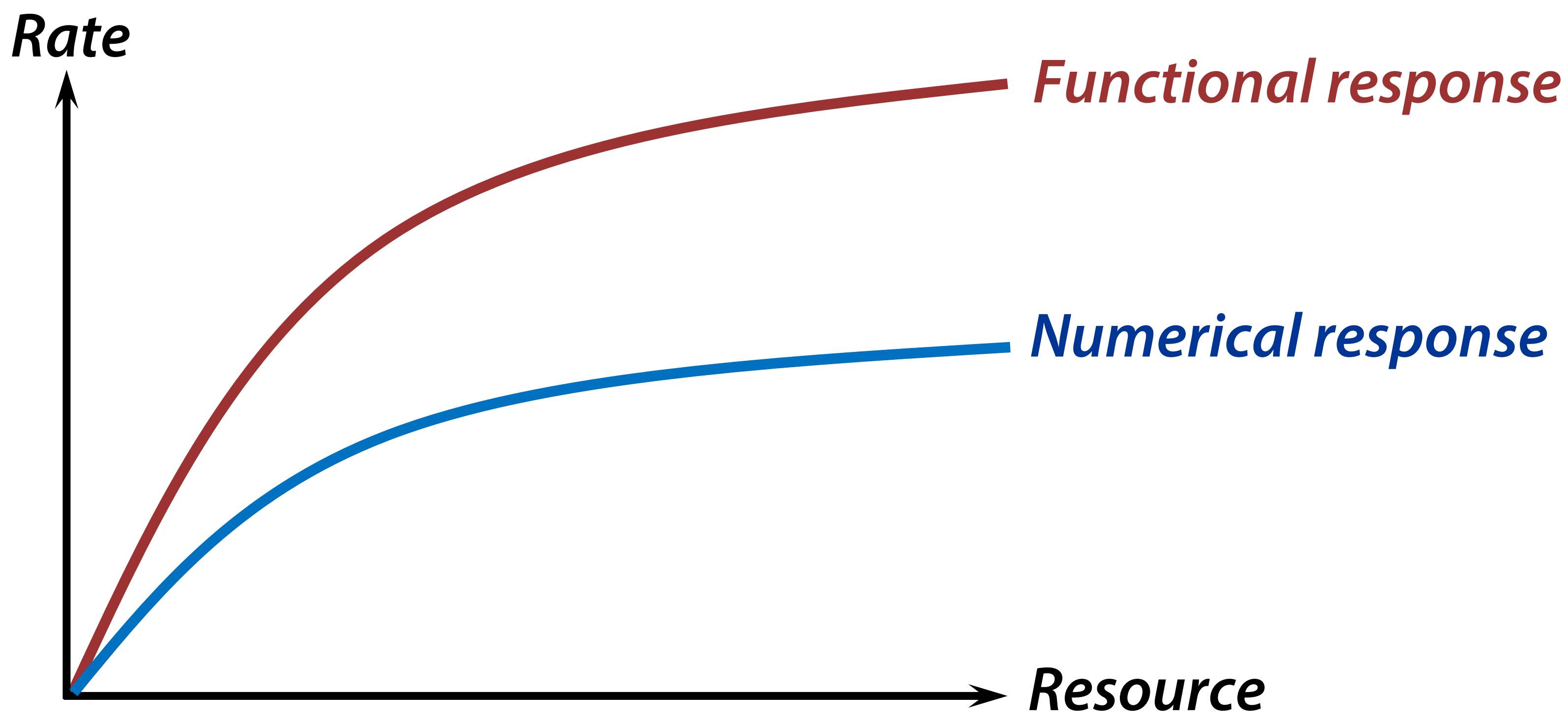
Maturation increases faster than ingestion when resource increases

Fecundity increases faster than ingestion when resource increases

Classic theory: numerical and functional response

$$g_J(R) = \sigma_J f_J(R)$$

$$g_A(R) = \sigma_A f_A(R)$$



Constant efficiency
(constant ratio between ingestion and fecundity or maturation)

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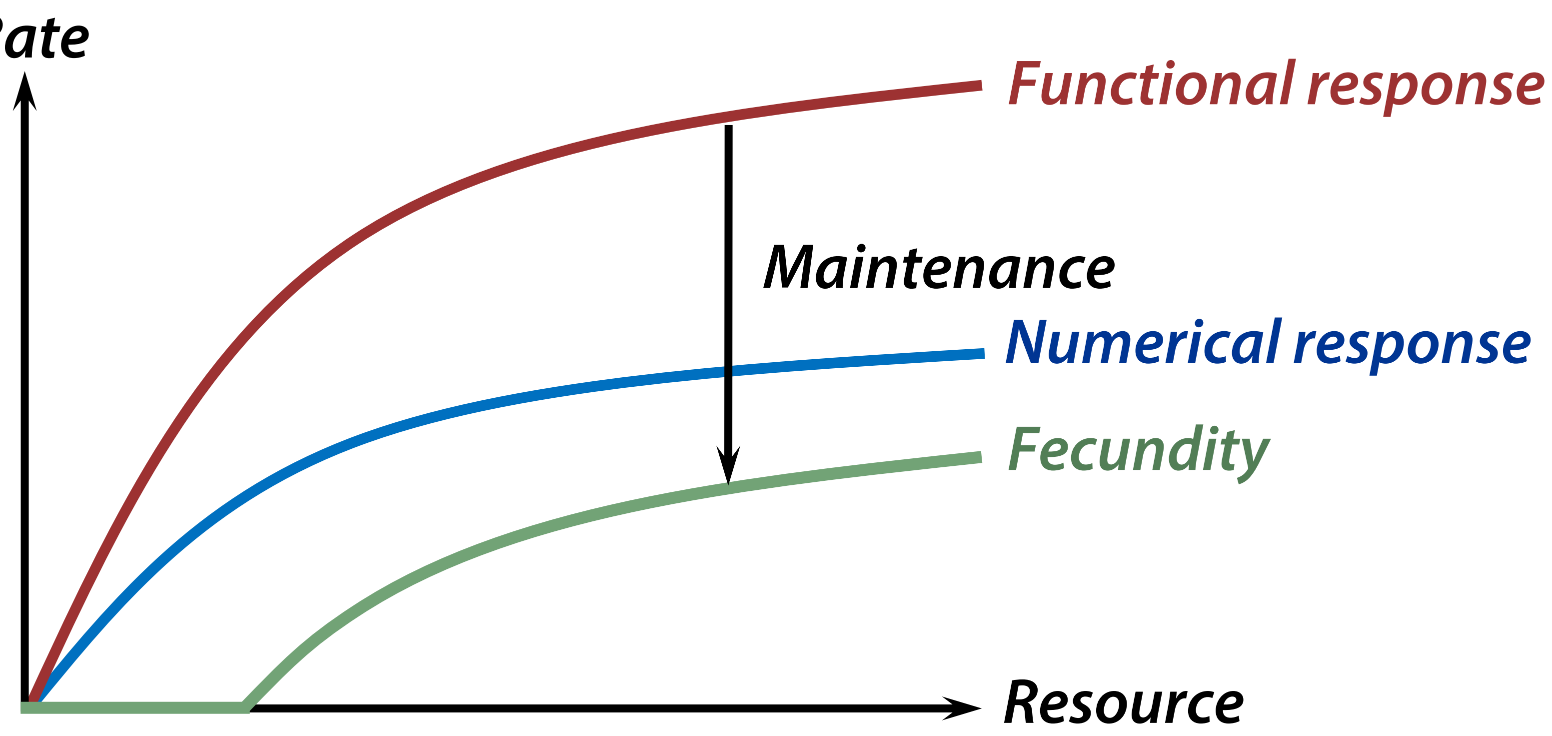
The effect of maintenance costs on production

$$g_J(R) = \left(\sigma_J f_J(R) - T_J\right)^+$$

$$g_A(R) = \left(\sigma_A f_A(R) - T_A\right)^+$$



Changing efficiency
(variable ratio between ingestion and fecundity or maturation)

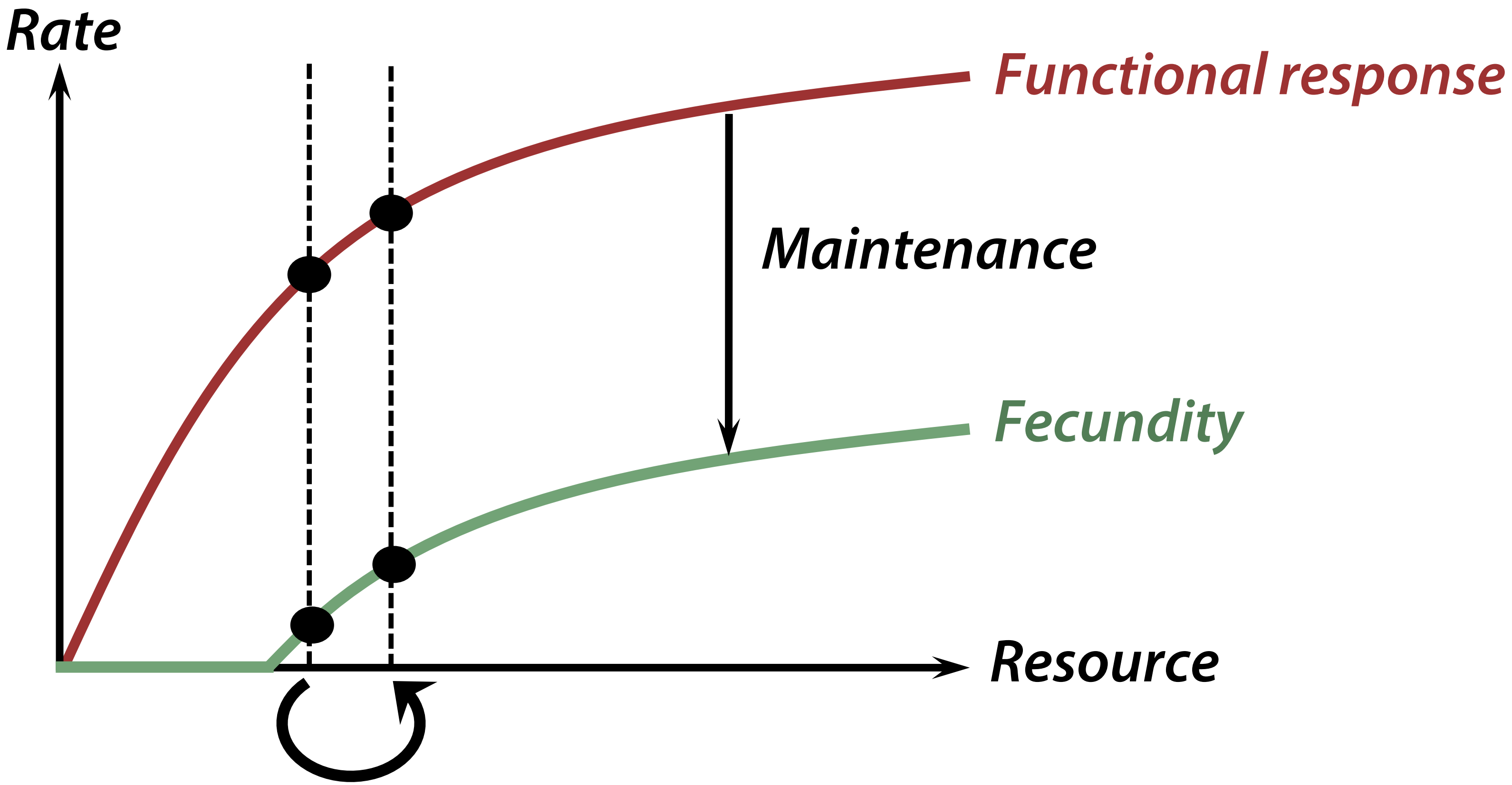
The effect of maintenance costs on production

$$g_J(R) = \Big(\sigma_J f_J(R) - T_J\Big)^+$$

$$g_A(R) = \Big(\sigma_A f_A(R) - T_A\Big)^+$$

20% decrease in density increases ingestion by roughly 20%, but *doubles* adult fecundity

⇒ *60% increase in total reproduction*



$$\left(\frac{f_A(\bar{R})}{g_A(\bar{R})}\right)' < 0$$

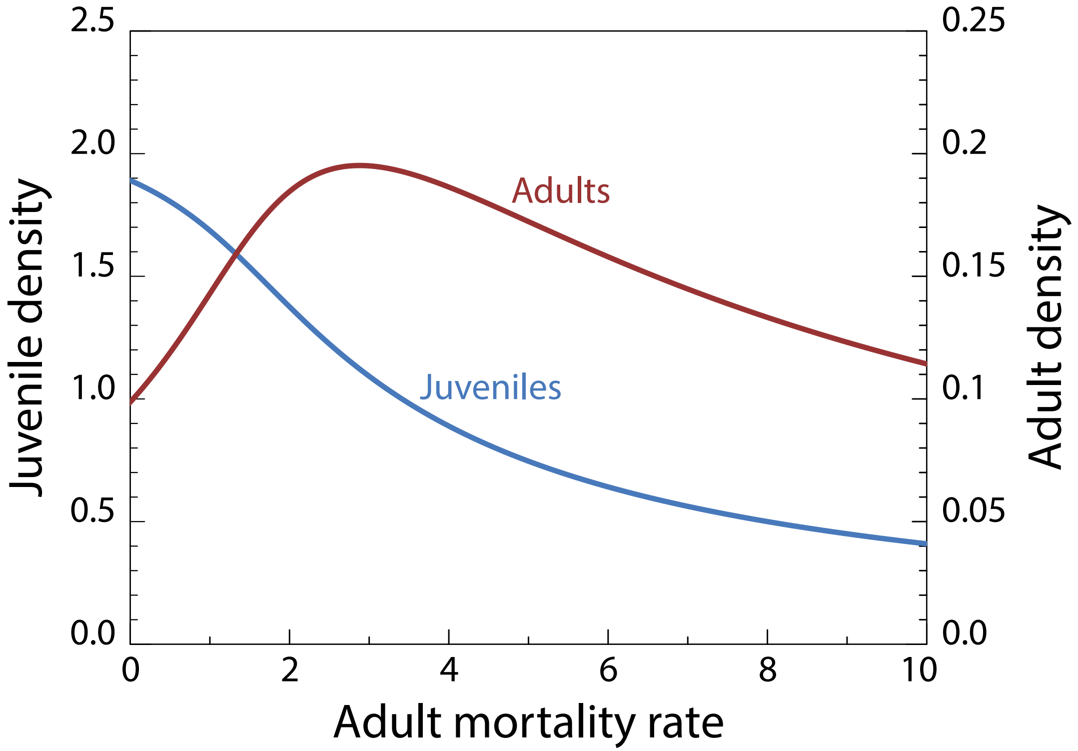
Because of maintenance costs efficiency with which resource is used for population growth increases with mortality

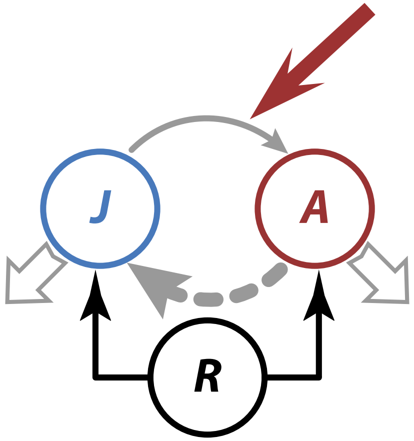
Maintenance and stage structure together

$$\begin{cases} \dfrac{dR}{dt} = P - (\alpha_J C_J + \alpha_A C_A)\, R \\ \dfrac{dC_J}{dt} = \boxed{(\beta R - T)^+} C_A - \boxed{(\gamma R - T)^+} C_J - \mu C_J \\ \dfrac{dC_A}{dt} = \boxed{(\gamma R - T)^+} C_J - \mu C_A \end{cases}$$

Maintenance and stage structure together

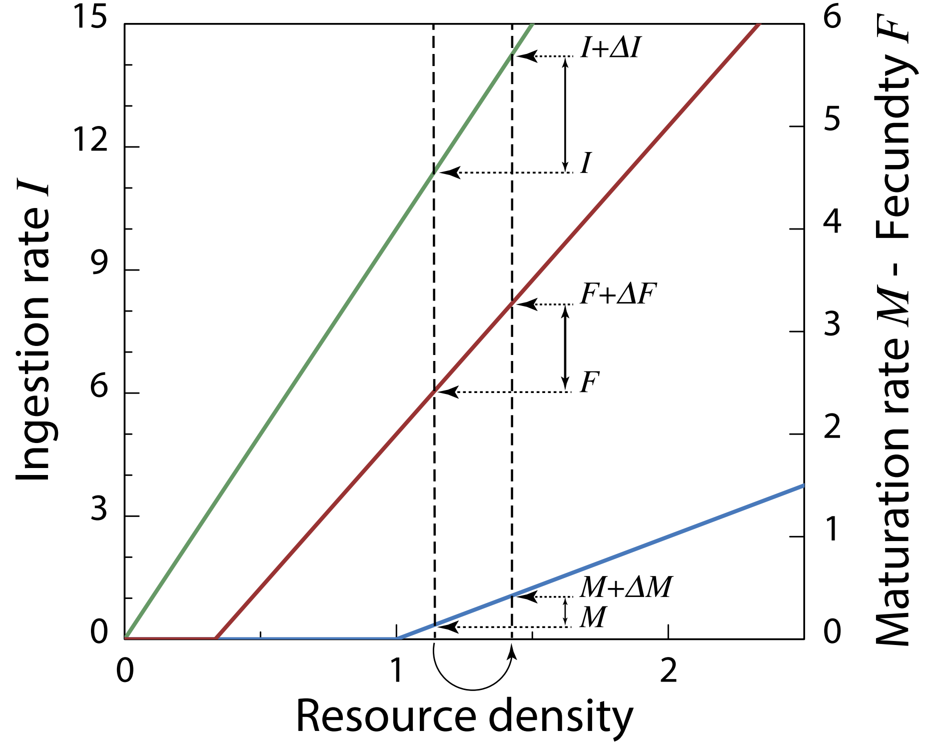
$$P = 20,\ \alpha_J = \alpha_A = 10,\ \gamma = T = 1,\ \beta = 3,\ \mu = 0.1$$

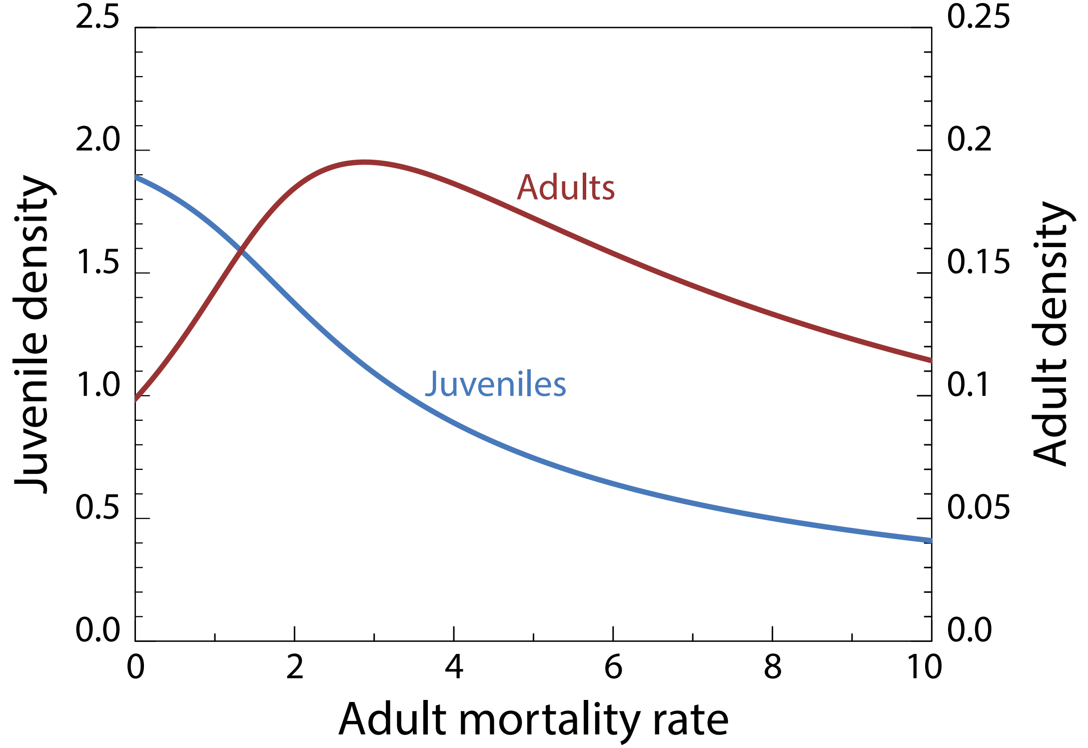


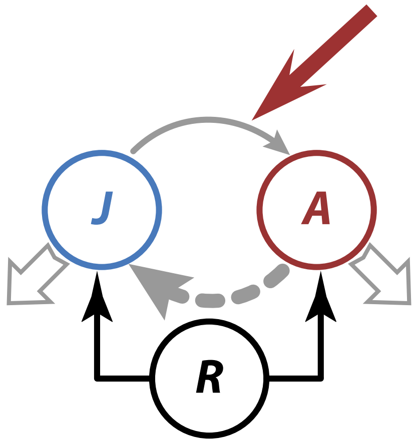


Maintenance and stage structure together

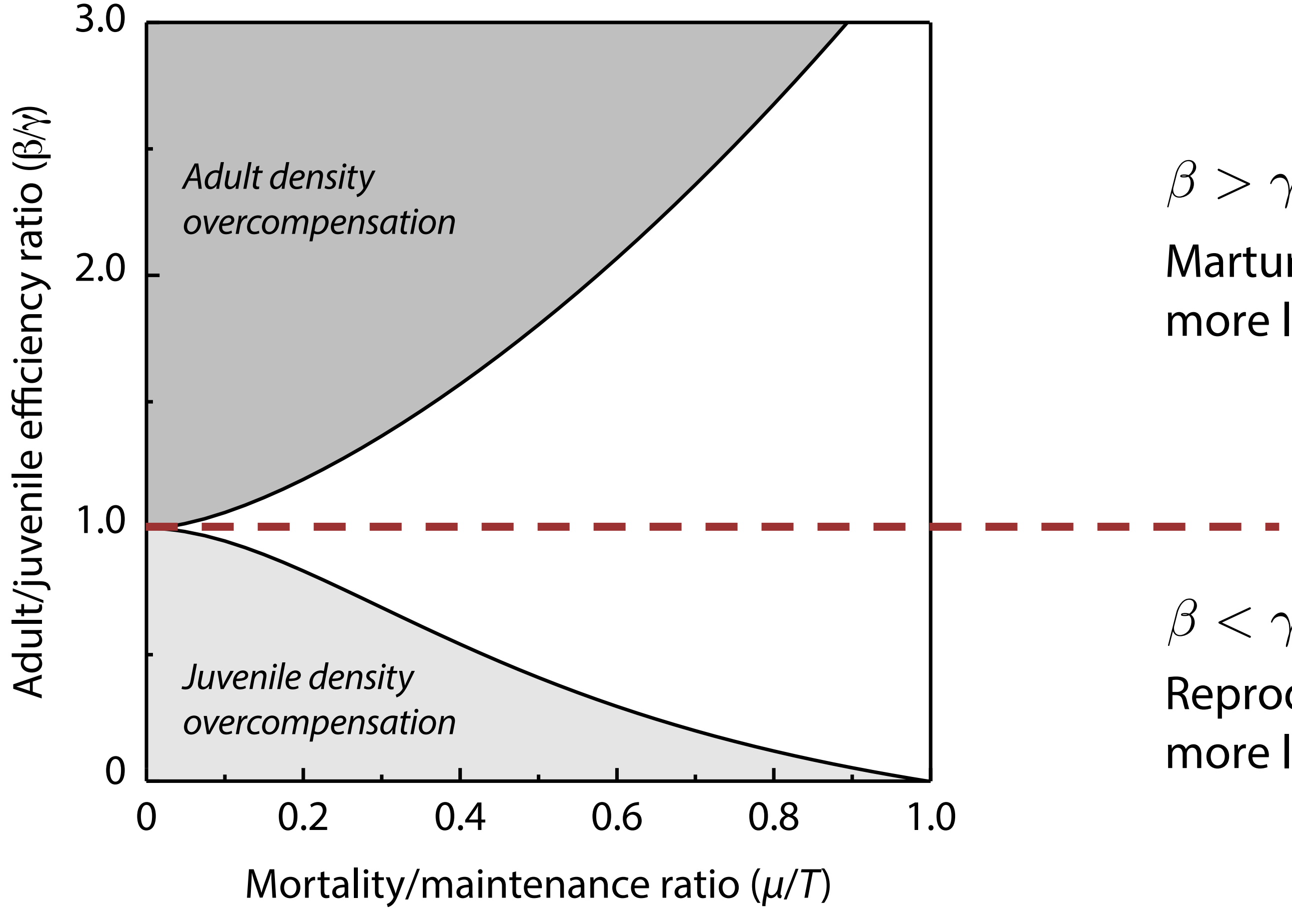
$$P = 20, \ \alpha_J = \alpha_A = 10, \ \gamma = T = 1, \ \beta = 3, \ \mu = 0.1$$







Maintenance and stage structure together



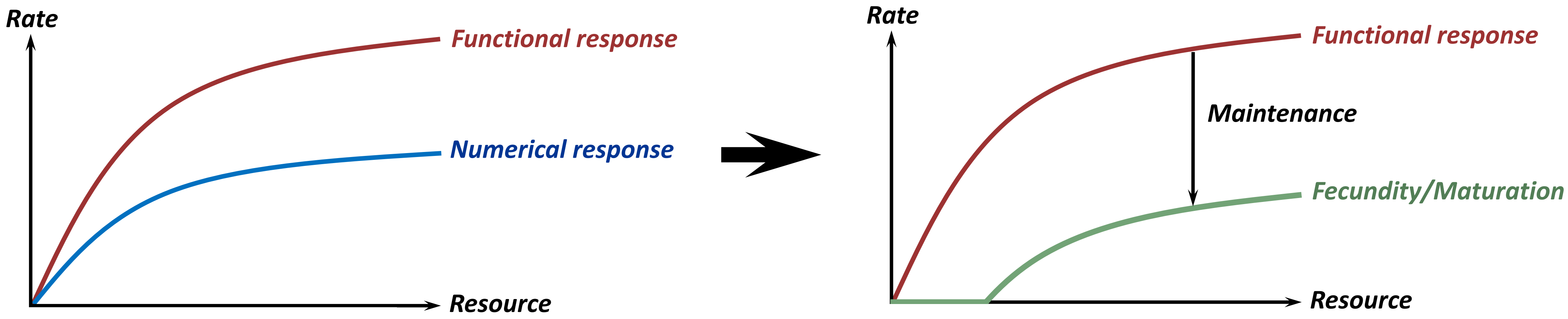
$\beta > \gamma$

Marturation
more limited by food

$\beta < \gamma$

Reproduction
more limited by food

- Results are independent of the resource growth function $p(R)$ (as long as $p'(R) \leq 0$), the foraging parameters α_J and α_A, and the functional response $f(R)$
- Similar results can be obtained with differences in maintenance requirements of juveniles and adults



Implications beyond consumers and resources

Increasing mortality decreases maintenance losses and increases effective resource use for population growth in case of juvenile-adult asymmetry

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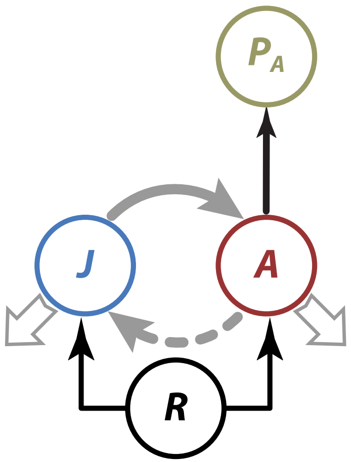
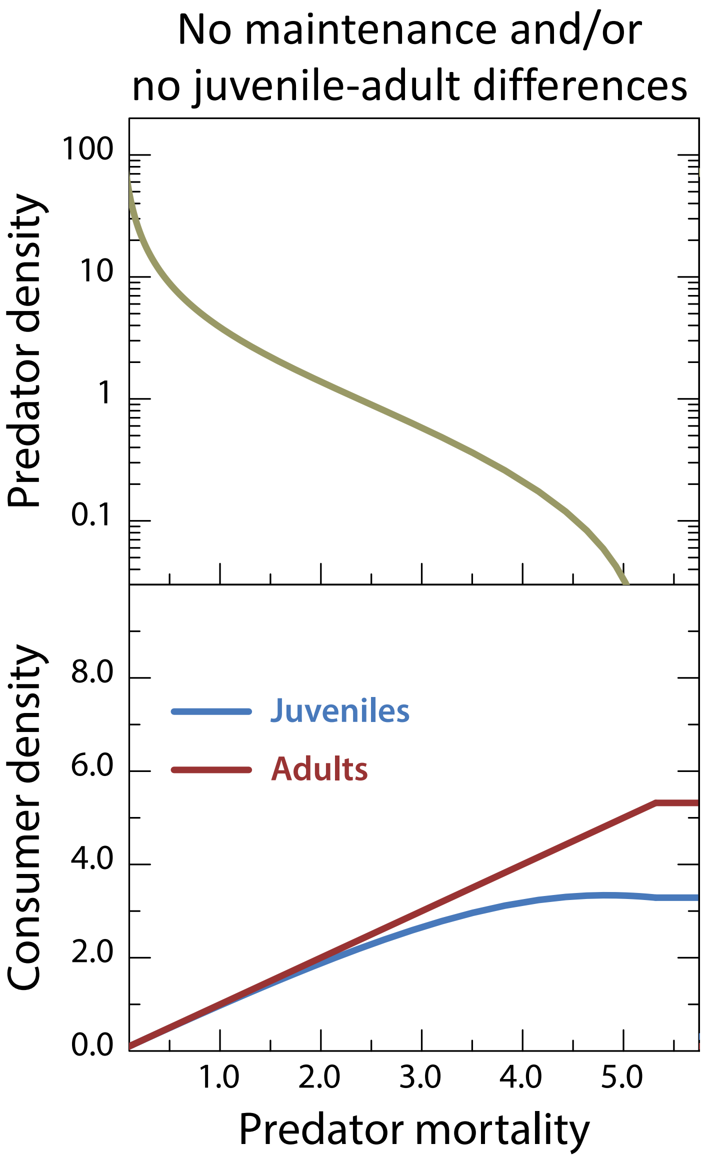
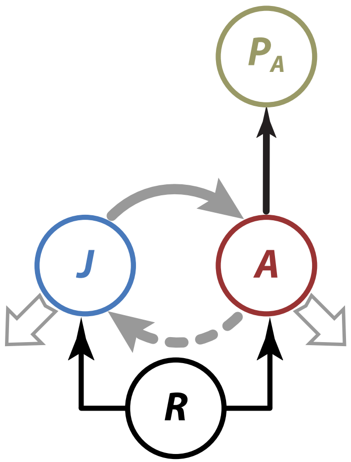
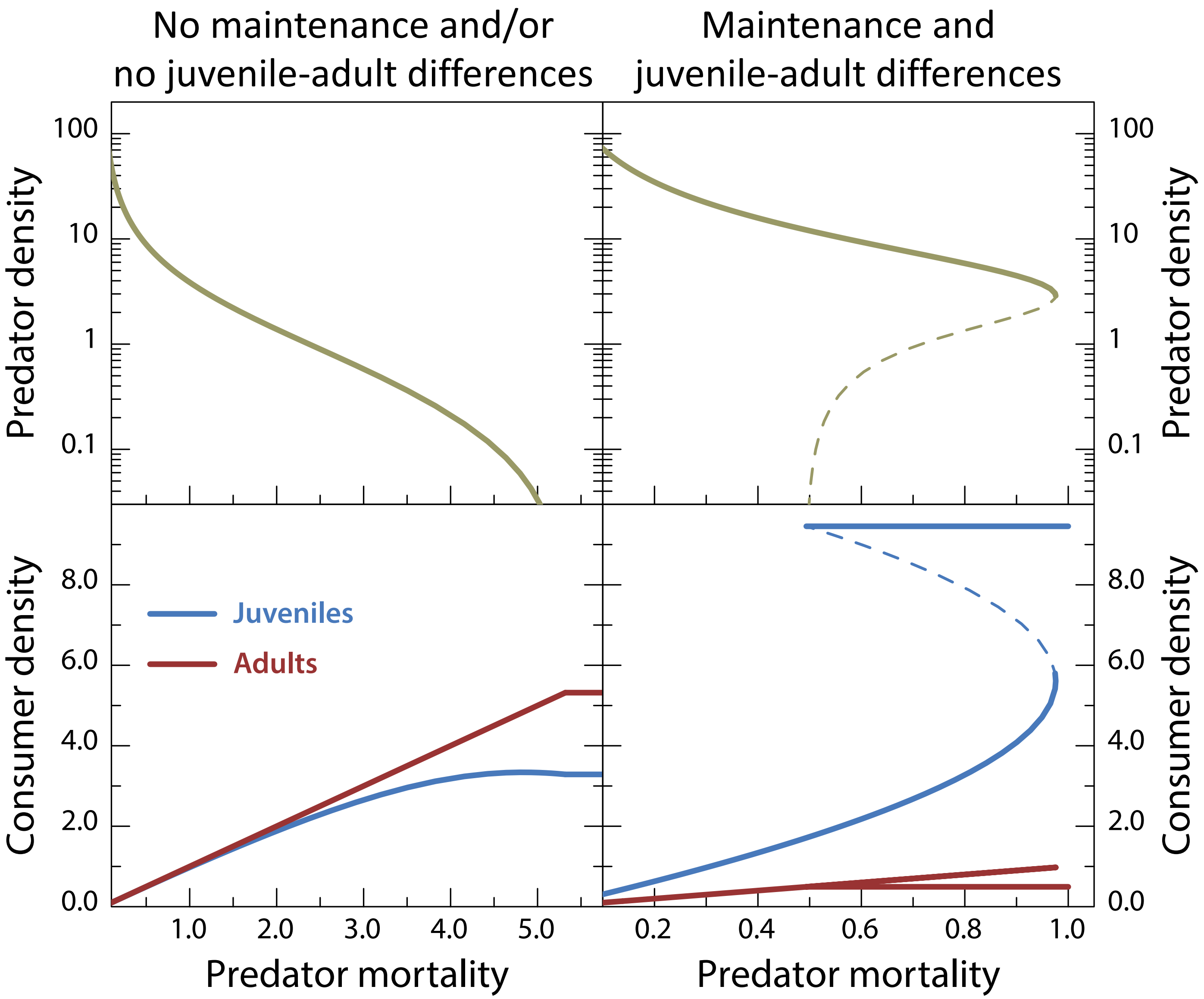
Linear food chains



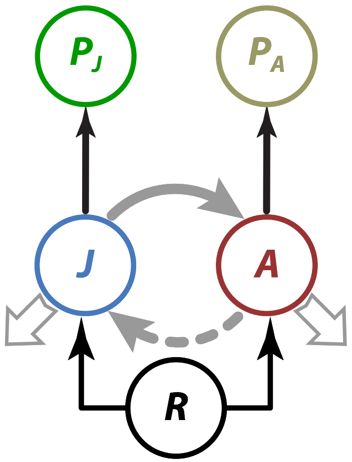


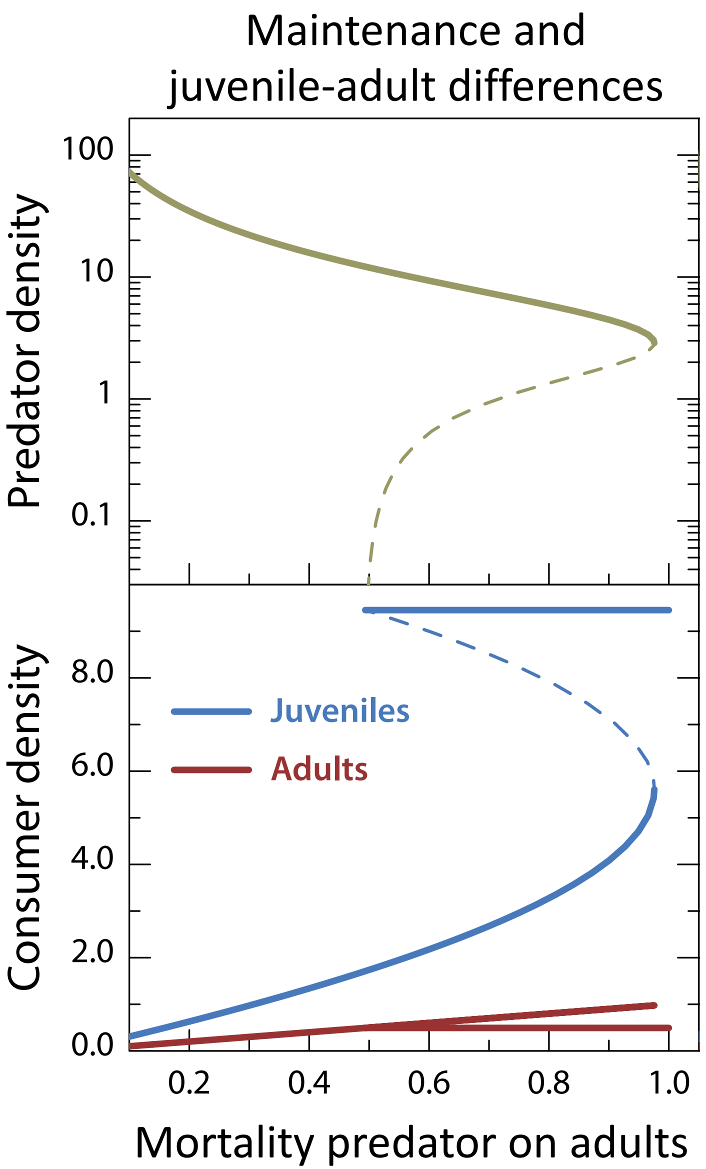
Linear food chains



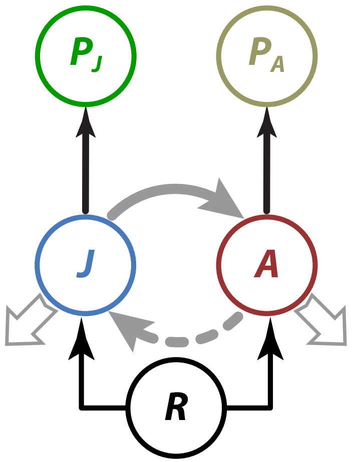


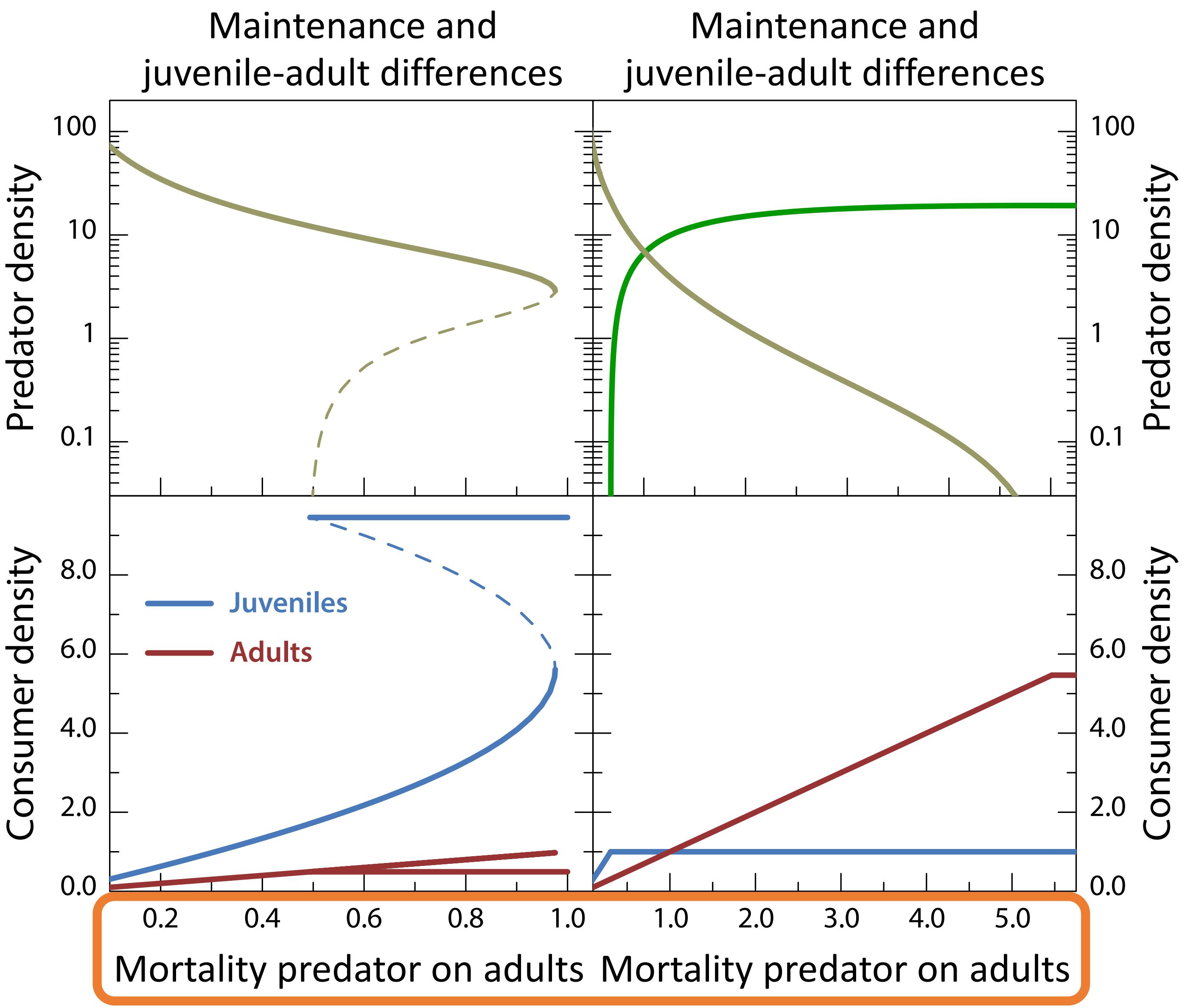
Competing size-selective predators





Competing size-selective predators





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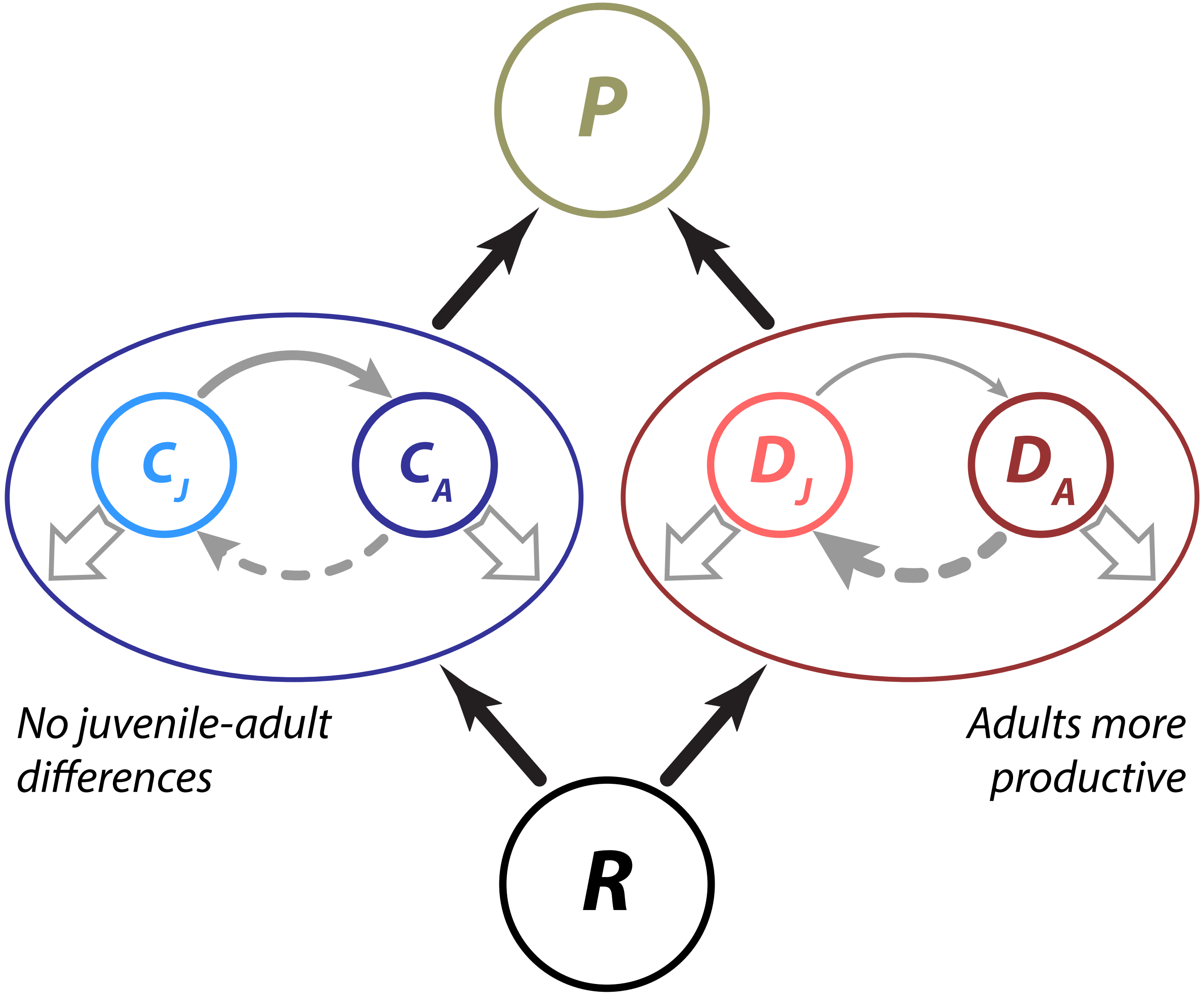
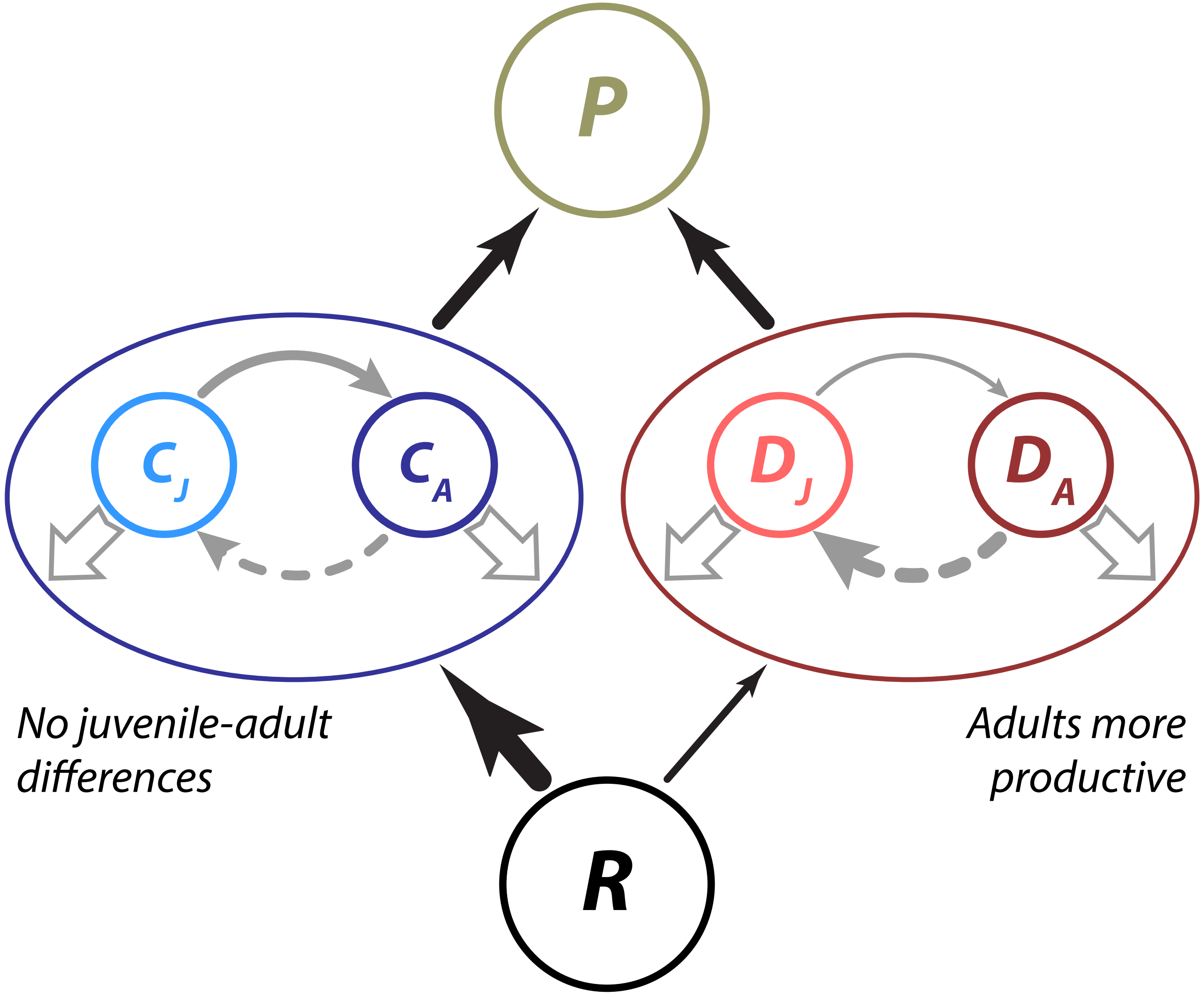
Diamond food web module



Diamond food web module



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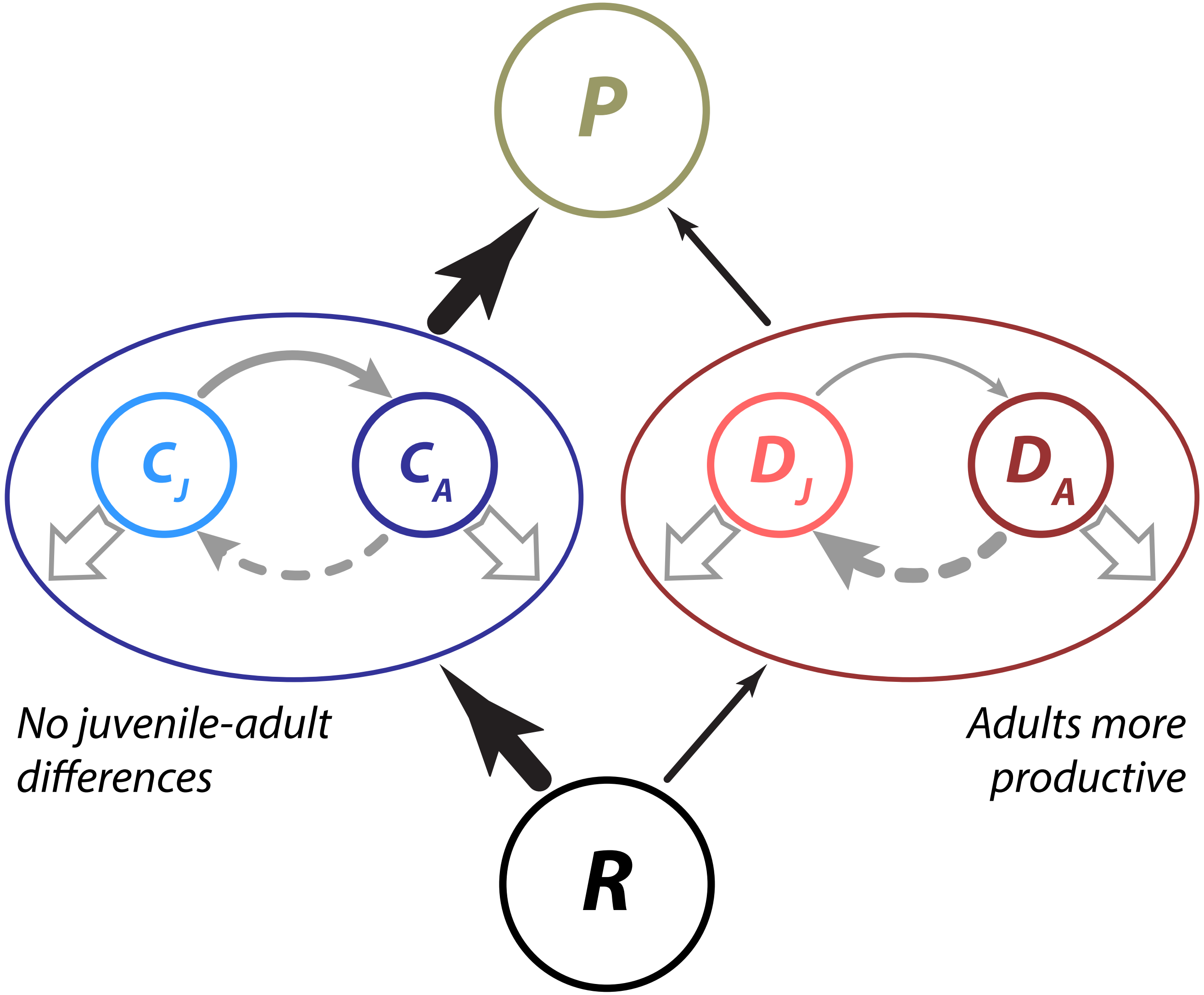
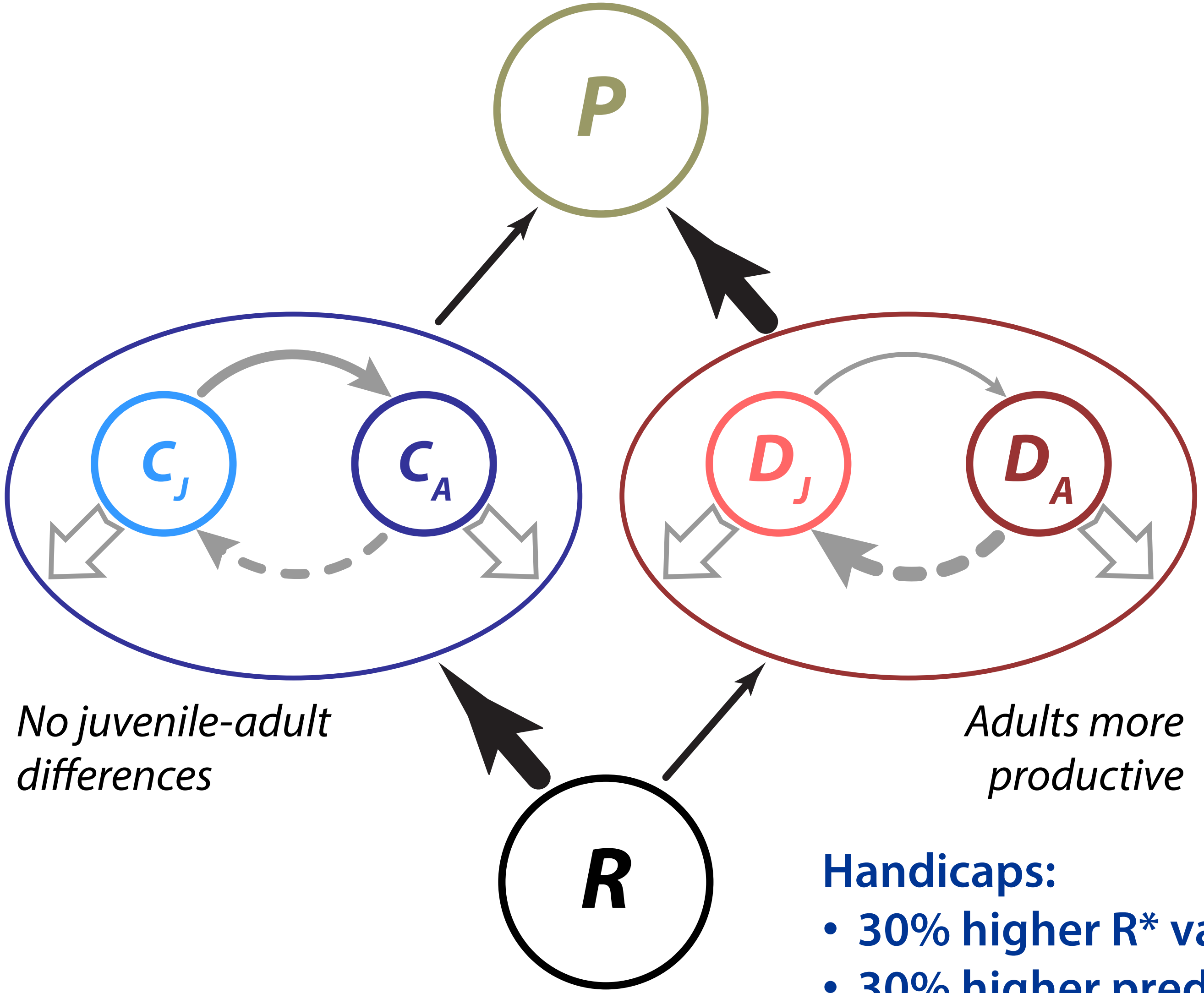
Diamond food web module

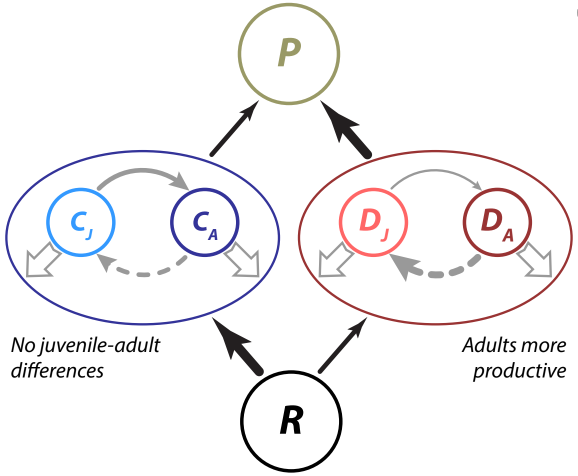


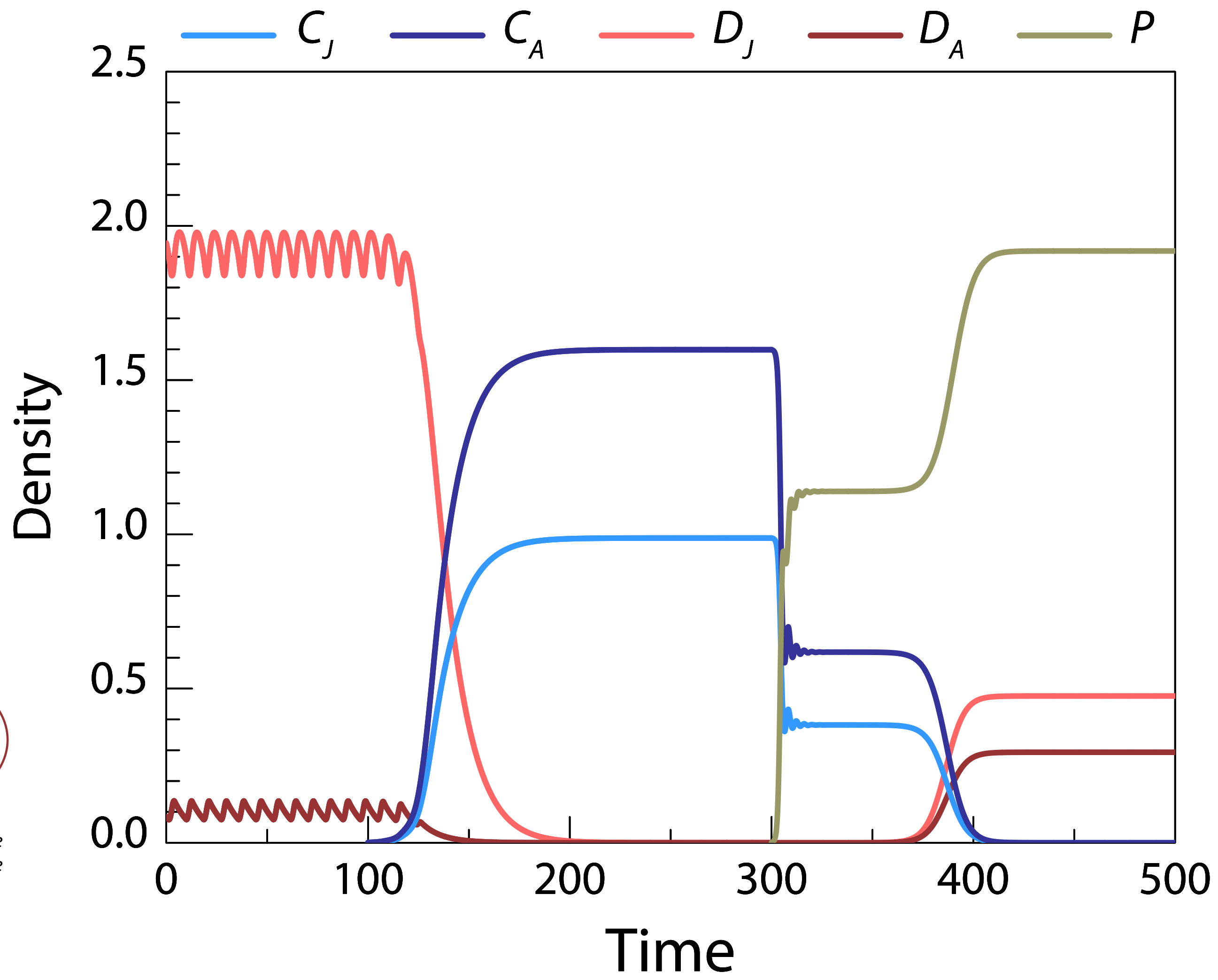
Diamond module with double-handicap loser



Handicaps:
- **30% higher R* value**
- **30% higher predation mortality**

Revenge of the double-handicap loser

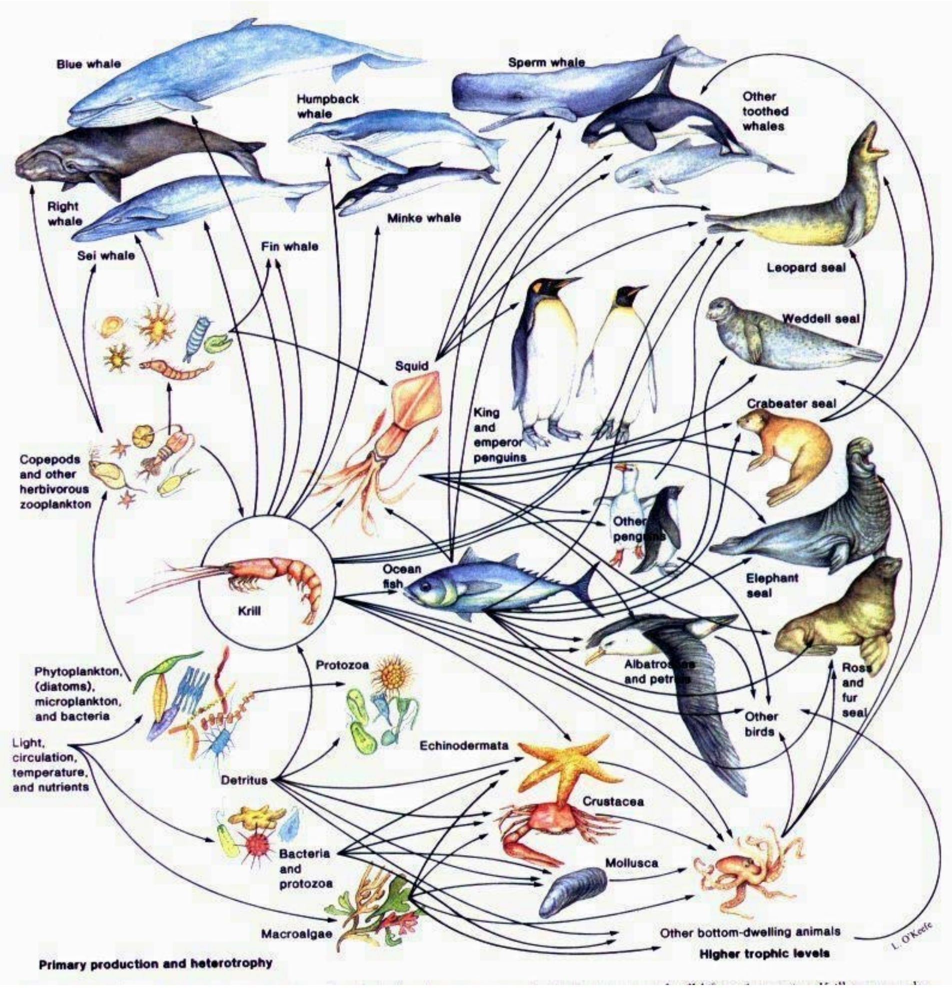




Changing stage-structure results in more efficient resource exploitation at higher mortality

What about large, diverse communities?

Communities as networks of species



Self-regulation (cannibalism, interference)

Negative effect of predator *i* on growth rate of its prey *j*

$$\boldsymbol{A_1} = \begin{pmatrix} a_{11} & a_{12} & \cdots & \cdots & a_{1N} \\ a_{21} & a_{22} & \ddots & - & a_{2N} \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & + & \ddots & \ddots & a_{MN} \\ a_{N1} & a_{N2} & \cdots & a_{NM} & a_{NN} \end{pmatrix}$$

Positive effect of prey *j* on growth rate of its predator *i*

Community (interaction) matrix (Levins, 1968):

a_{ij}: *per-capita effect of species j on population growth rate of species i*

Communities as networks of species

Will a Large Complex System be Stable?
R. M. May, Nature 238: 413-414, 1972

Robert M. May

'In short, there is no comfortable theorem assuring that increasing diversity and complexity beget enhanced community stability; rather the opposite is true. The task, therefore, is to elucidate the devious strategies which make for stability in enduring natural systems'. (R.M. May, 1974)

Self-regulation (cannibalism, interference)

Negative effect of predator *i* on growth rate of its prey *j*

$$\boldsymbol{A_1} = \begin{pmatrix} a_{11} & a_{12} & \cdots & \cdots & a_{1N} \\ a_{21} & a_{22} & \ddots & & a_{2N} \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & & \ddots & \ddots & a_{MN} \\ a_{N1} & a_{N2} & \cdots & a_{NM} & a_{NN} \end{pmatrix}$$

Positive effect of prey *j* on growth rate of its predator *i*

Community (interaction) matrix (Levins, 1968):

a_{ij} : *per-capita effect of species j on population growth rate of species i*

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Self-regulation

Exploitative competition (via interspecific interactions)

Intraspecific interference

Cannibalism

Nest site competition

Communities as networks of species

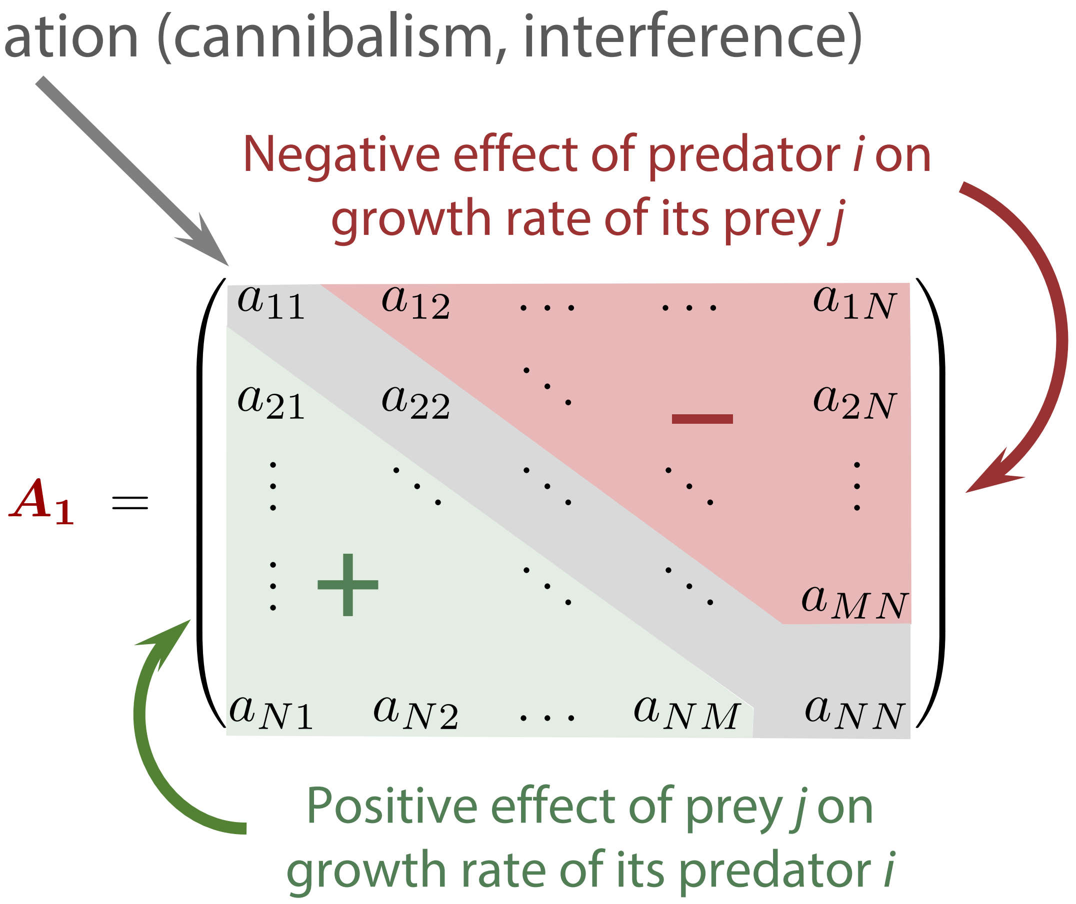
ARTICLES
https://doi.org/10.1038/s41559-017-0357-6
nature ecology & evolution

Self-regulation and the stability of large ecological networks

György Barabás [1,2*], Matthew J. Michalska-Smith [2] and Stefano Allesina [2,3,4]

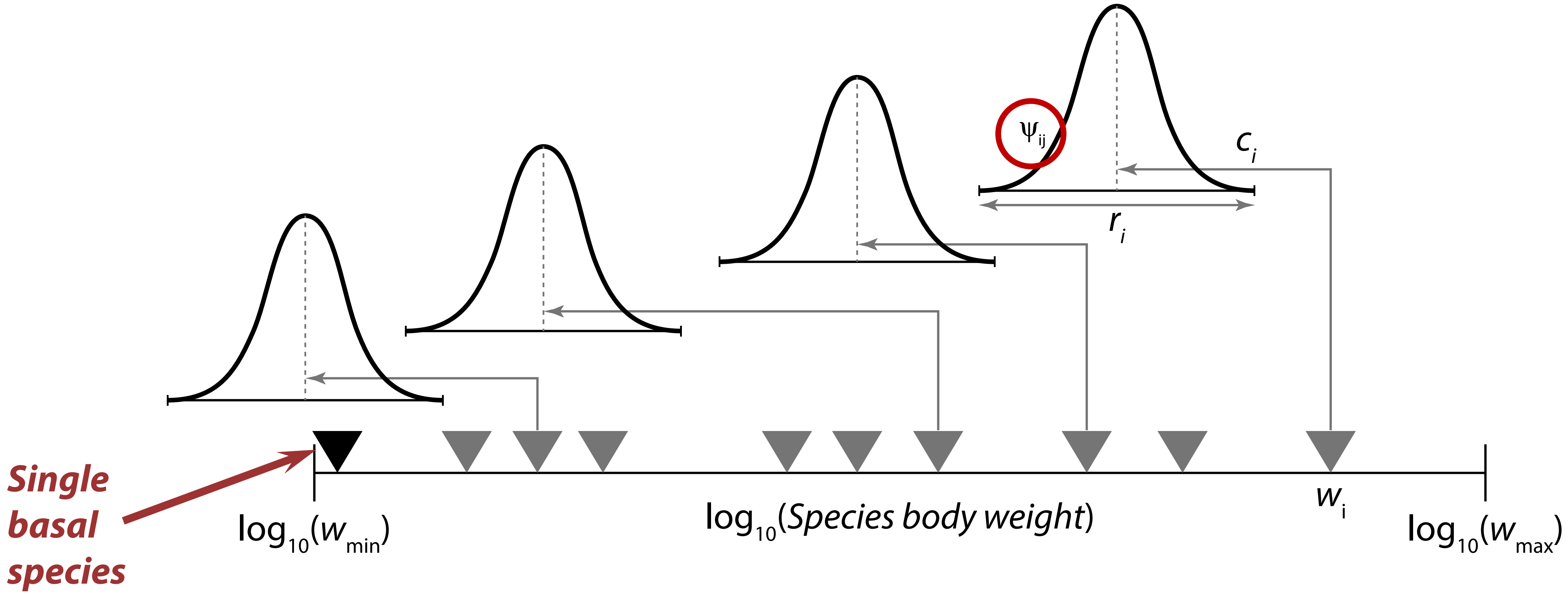
'Here, we show that empirical food web structures cannot be stabilized unless ***the majority of species exhibit substantially strong self-regulation****.'*

'Based on the results presented here, at least half—and possibly more than 90%—of species must be subject to self-regulation to a substantial degree'



➡ ***Competition and predation (inter-specific) less relevant***
Self-regulation (intra-specific) determines community stability

Food web based on prey-predator size ratio



Species dynamics without stage structure

$$\frac{dC_i}{dt} = \gamma_i F_i C_i - (\mu_i + T_i)\, C_i - \sum_{k>i} \psi_{ki}\, \alpha_k \frac{C_k}{H_k + E_k} C_i$$

Basal species (i = 1)

$$F_1 = \frac{P}{\delta + \alpha_1 C_1} \qquad \left(\frac{dR}{dt} = P - \delta R - \alpha_1 R C_1 \approx 0\right)$$

Non-basal species (i > 1)

$$F_i = \frac{E_i}{H_i + E_i}, \qquad E_i = \sum_{k<i} \psi_{ik}\, C_k$$

No self-regulation, except for the single basal species!

Simulation procedure:

- Assign 500 species a species body weight uniformly distributed over a logarithmically scaled body weight axis
- Assign species-specific parameters randomly distributed around allometric parameter-body weight relationships
- Simulate dynamics until transients have disappeared

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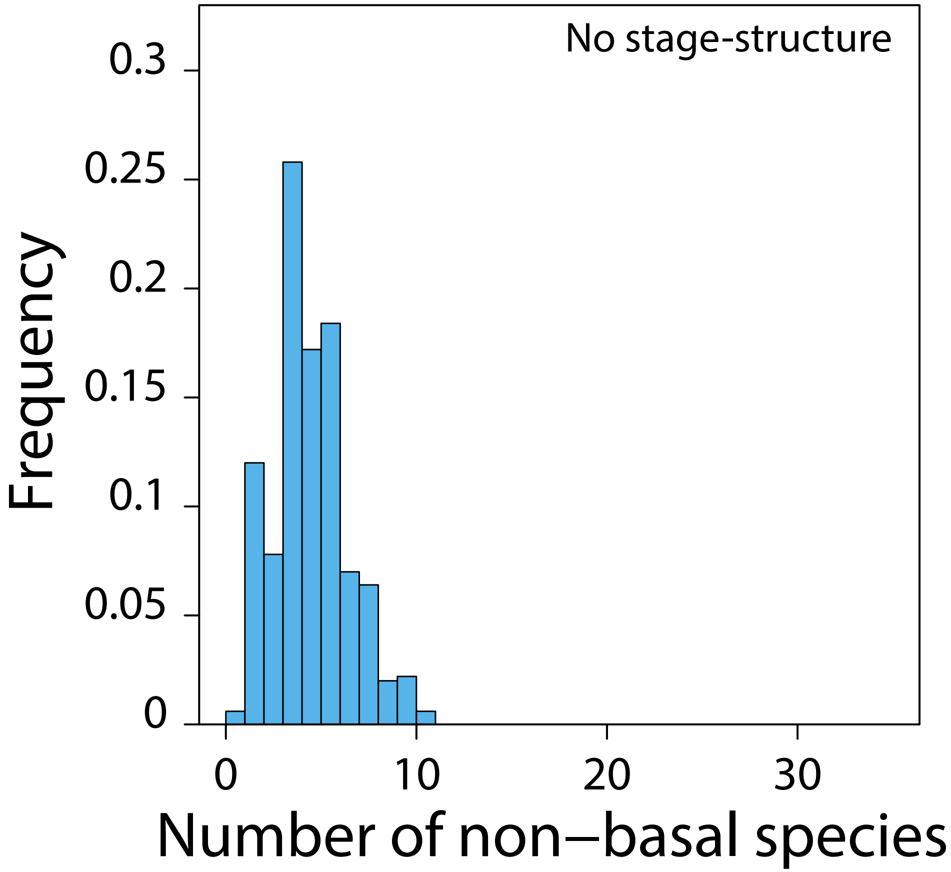
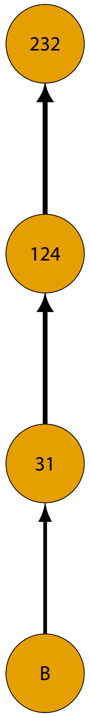
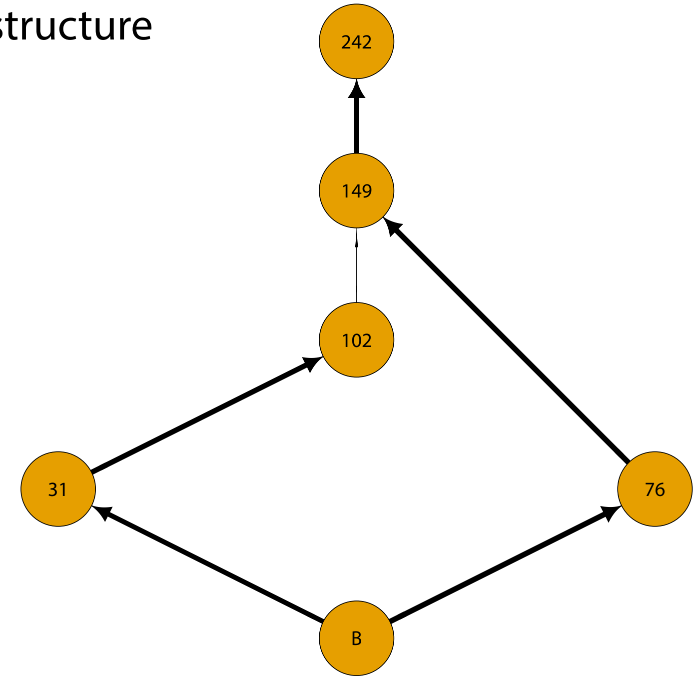
Community diversity

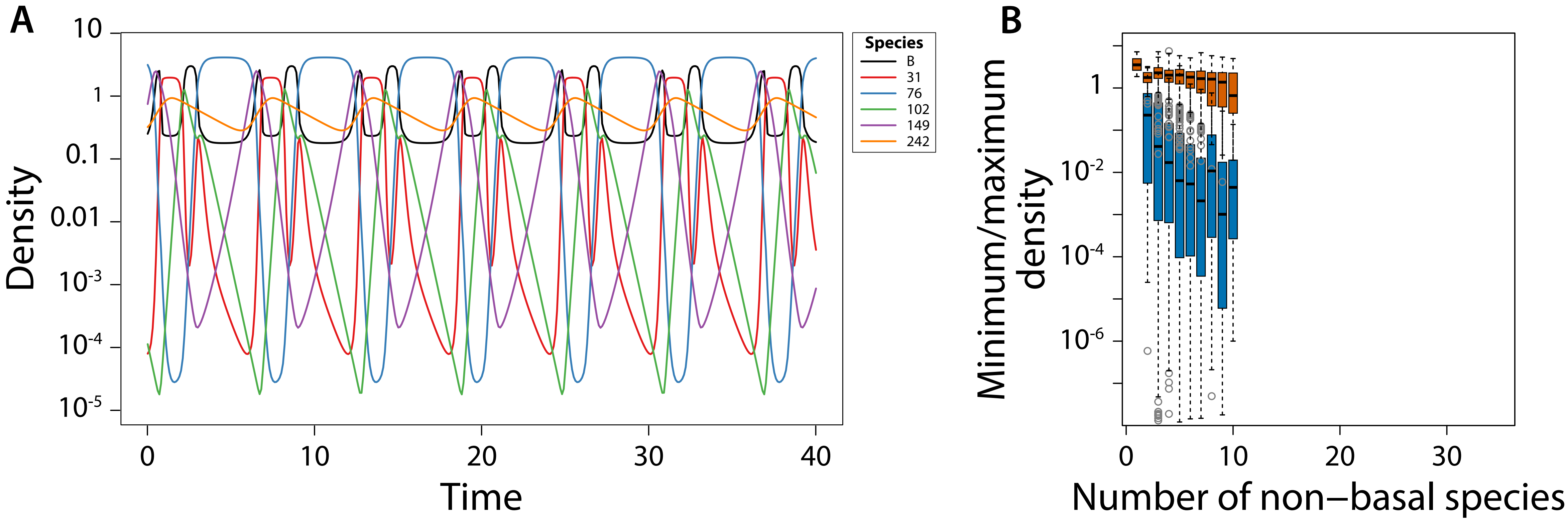






Food web dynamics without stage structure results in small communities with simple structure, in which most species exploiting a single resource and exposed to a single predator

Community dynamics



Food web dynamics without stage structure results in population oscillations, with large amplitudes that increase with community size

Three important characteristics

- **Focus on stabilization through food web properties:**
  How does the ***topology of the interaction network between species*** affect community stability
- ***Community / interaction matrix*** used to quantify interactions:
  Density effect per individual of one species on growth rate of other
- ***Self-regulation is crucial for community stability***, even though its occurrence is debated and hard to prove

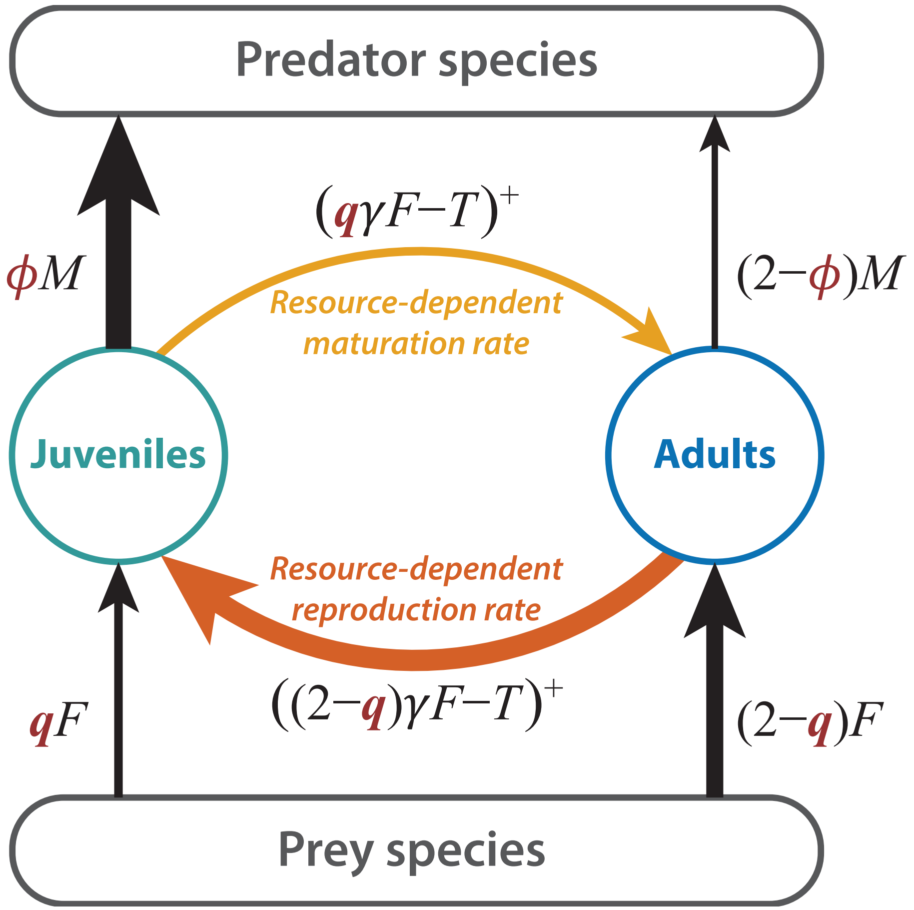
Questions

- To what extent are current insights consequences of the ***conceptualisation as a between-species interaction network?***
- What is the effect of ***differences between juveniles and adults*** on community diversity and stability?

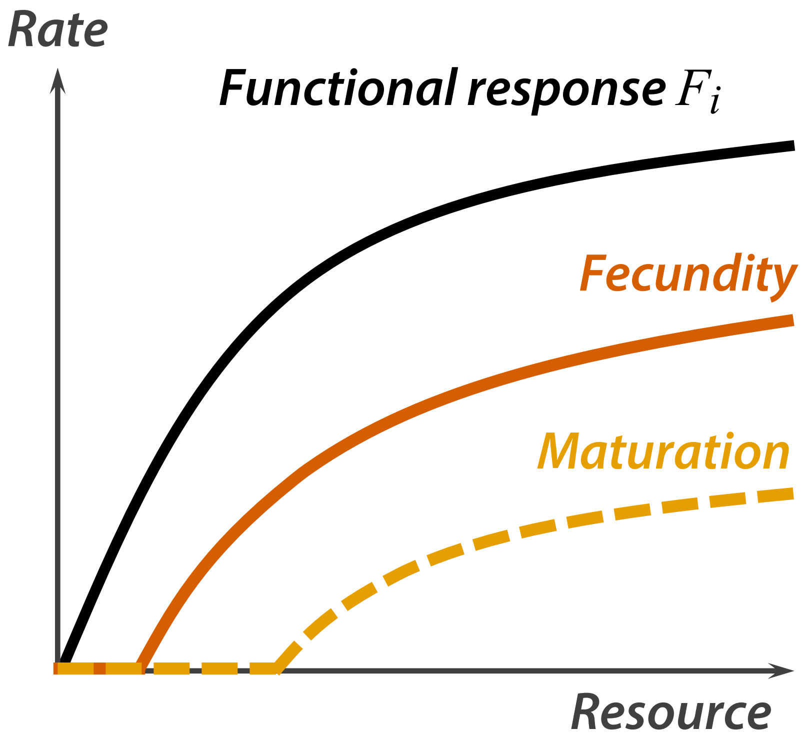
Introducing juvenile-adult stage structure

- Juvenile and adult have ***identical diets***, but their feeding rate is proportional to q and $(2-q)$, respectively:
  - *For $q<1$ maturation is more limited by food than reproduction*
- Juveniles and adults are preyed upon by the ***same predators***, but their mortality rate from predation is proportional to ϕ and $(2-\phi)$, respectively
  - *For $\phi>1$ juveniles are preyed upon more than adults*
- For $q=1$ and $\phi=1$ model is mathematically identical to model without stage structure
- *Maturation (reproduction) stops when juvenile (adult) food intake is too low to cover juvenile (adult) maintenance costs*

The effect of maintenance costs on production



$$g_J(F_i) = (\quad q \; \gamma_i \, F_i \; - \; T_i)^+$$
$$g_A(F_i) = ((2 - q)\gamma_i \, F_i \; - \; T_i)^+$$



$q < 1$

Species dynamics with stage structure

$$\frac{dJ_i}{dt} = \boxed{((2-\boldsymbol{q})\gamma_i F_i - T_i)^+} A_i - \boxed{(\boldsymbol{q}\gamma_i F_i - T_i)^+} J_i - \mu_i, J_i - \sum_{k>i} \phi\, \psi_{ki}\, \alpha_k \frac{\boldsymbol{q} J_k + (2-\boldsymbol{q}) A_k}{H_k + E_k} J_i$$

$$\frac{dA_i}{dt} = \boxed{(\boldsymbol{q}\gamma_i F_i - T_i)^+} J_i - \mu_i\, A_i - \sum_{k>i} (2-\phi)\, \psi_{ki}\, \alpha_k \frac{\boldsymbol{q} J_k + (2-\boldsymbol{q}) A_k}{H_k + E_k} A_i$$

Basal species (i = 1)

$$F_1 = \frac{P}{\delta + \alpha_1 (\boldsymbol{q} J_1 + (2-\boldsymbol{q}) A_1)} \qquad \left(\frac{dR}{dt} = P - \delta R - \alpha_1 R (\boldsymbol{q} J_1 + (2-\boldsymbol{q}) A_1) \approx 0 \right)$$

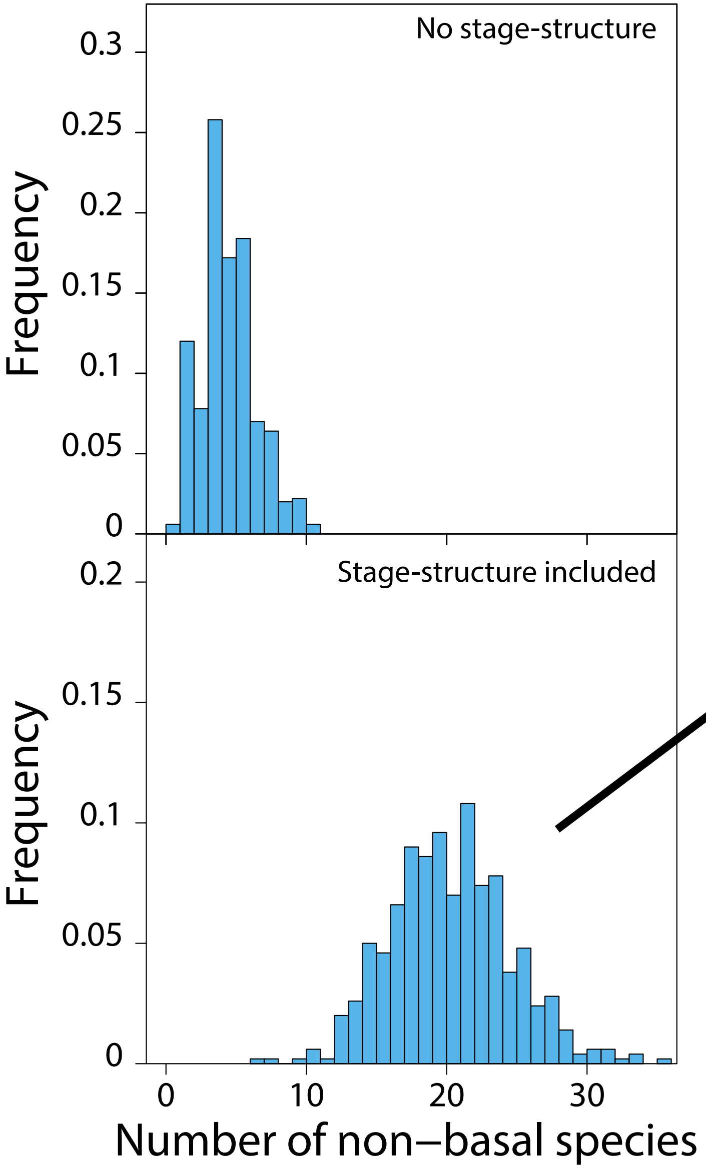
Non-basal species (i > 1)

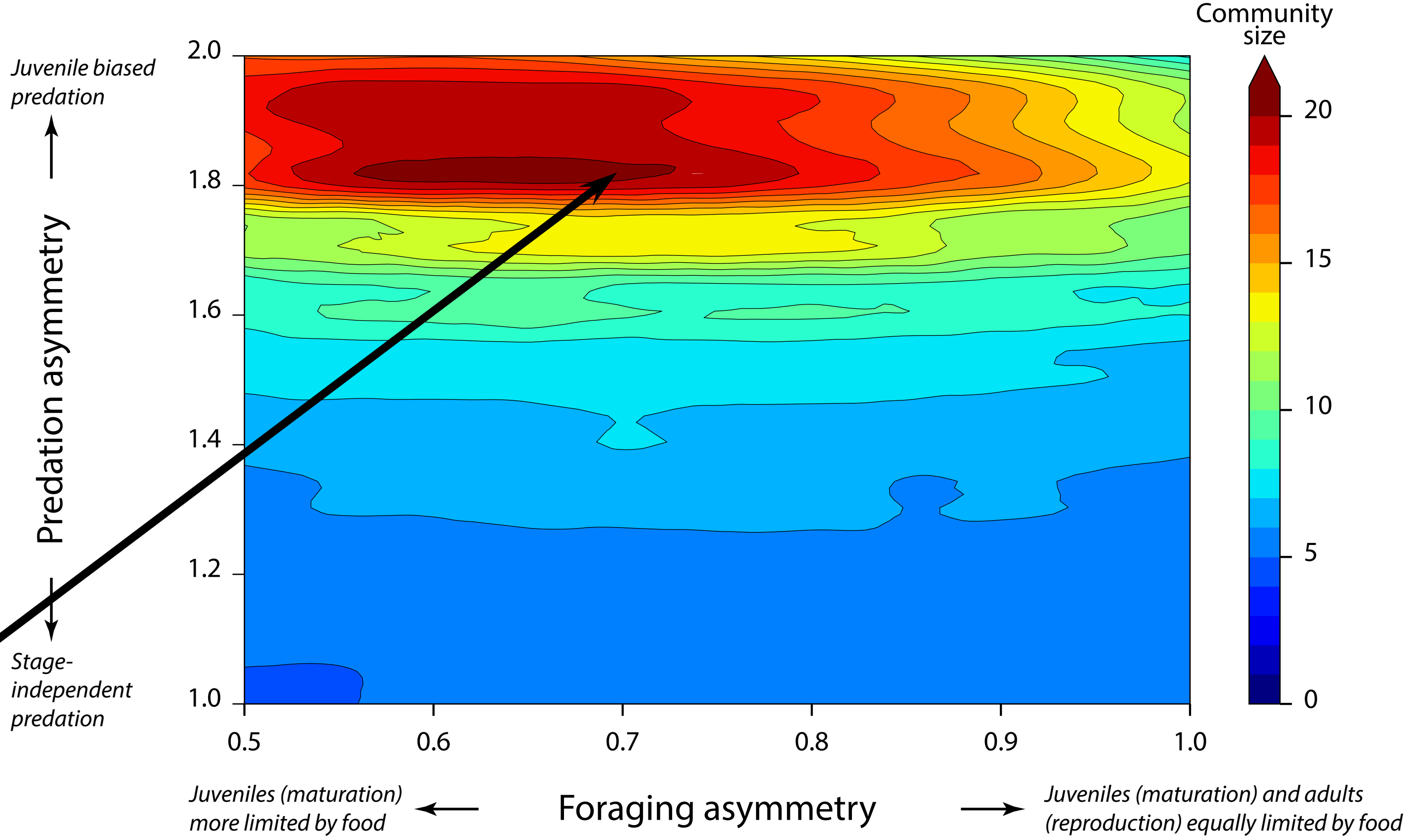
$$F_i = \frac{E_i}{H_i + E_i}, \qquad E_i = \sum_{k<i} \psi_{ik} (\phi J_k + (2-\phi) A_k)$$

$\boldsymbol{q}$ = Juvenile-adult foraging asymmetry

ϕ = Juvenile-adult predation asymmetry

Community diversity

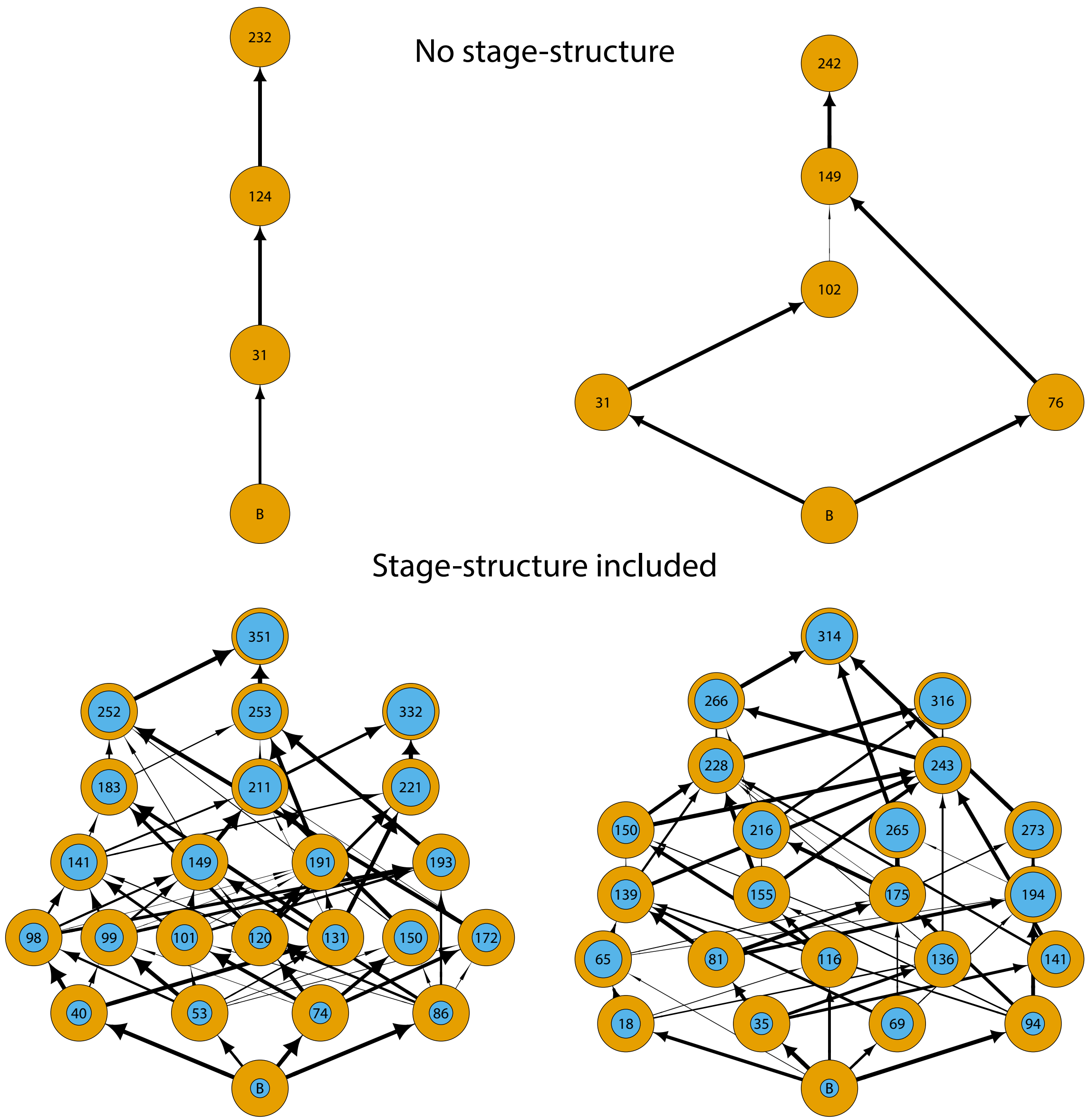




Stage-structure promotes community diversity if:

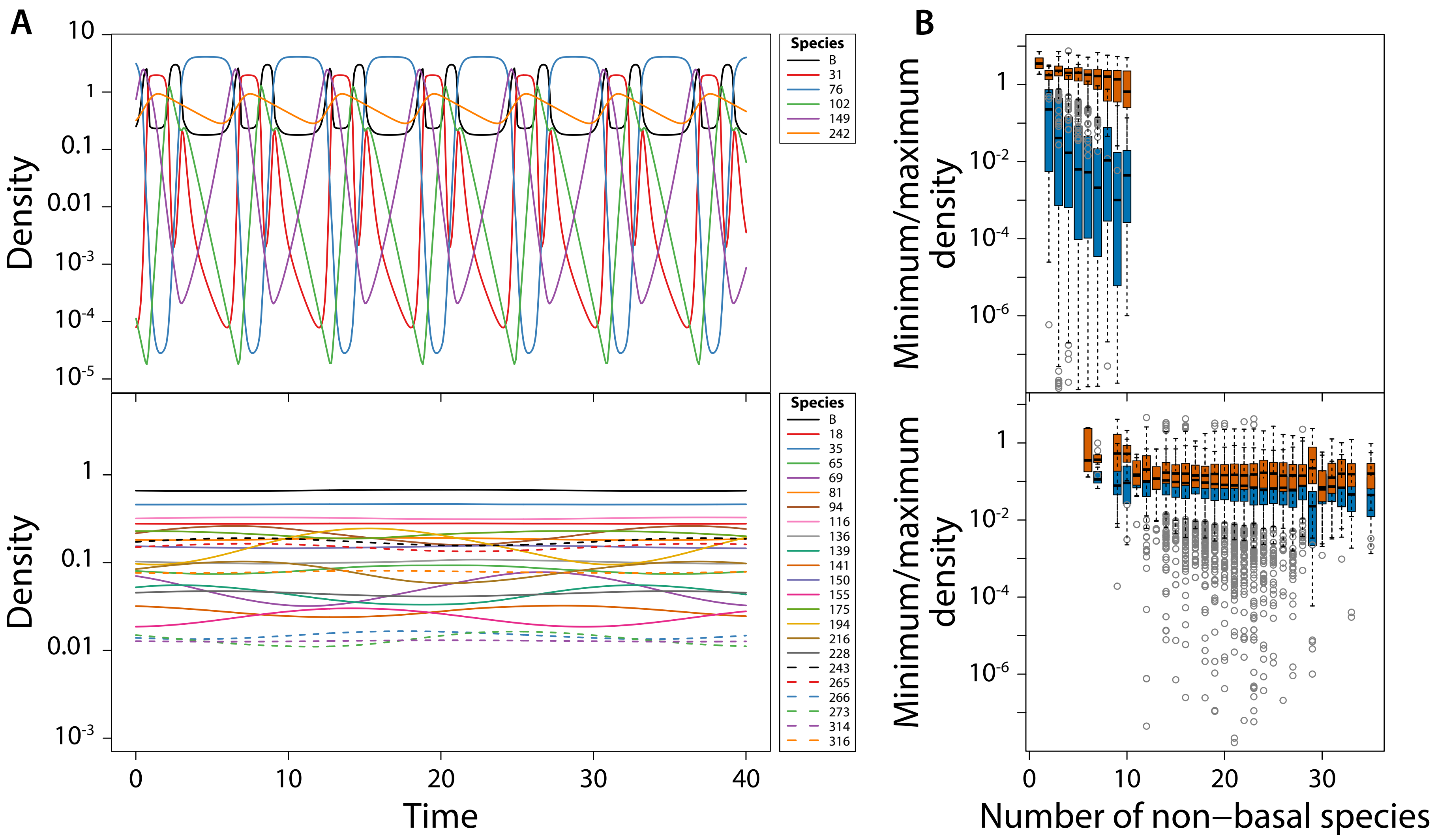
- Maturation is more limited by food than reproduction
- Juveniles are more vulnerable to fall victim to predators than adults

Community structure



Stage-structure promotes community complexity

Community dynamics



Stage-structure stabilizes community dynamics (23% of simulations converge to a stable equilibrium)

Community stability analysis

$$C_i = J_i + A_i$$: Total density of species i

$$Z_i = \frac{J_i}{J_i + A_i}$$: Fraction juveniles of species i

Stability determined by:

$$\boldsymbol{A} = \left(\begin{array}{c|c} \boldsymbol{A_1} & \boldsymbol{A_2} \\ \hline \boldsymbol{A_3} & \boldsymbol{A_4} \end{array} \right)$$

Community / Interaction matrix

Per-capita density effect of species j on population density growth rate of species i

$$\boldsymbol{A_1} = \frac{\partial}{\partial C_j}\left(\frac{dC_i}{dt}\right)\Bigg|_{\boldsymbol{C}=\tilde{\boldsymbol{C}},\boldsymbol{Z}=\tilde{\boldsymbol{Z}}}$$

Stability of network (species interaction subsystem)

$$\boldsymbol{A_2} = \frac{\partial}{\partial Z_j}\left(\frac{dC_i}{dt}\right)\Bigg|_{\boldsymbol{C}=\tilde{\boldsymbol{C}},\boldsymbol{Z}=\tilde{\boldsymbol{Z}}}$$

Dynamic effect of population structure of species j *on* population density growth rate of species i

$$\boldsymbol{A_3} = \frac{\partial}{\partial C_j}\left(\frac{dZ_i}{dt}\right)\Bigg|_{\boldsymbol{C}=\tilde{\boldsymbol{C}},\boldsymbol{Z}=\tilde{\boldsymbol{Z}}}$$

Per-capita density effect of species j *on* ***dynamics of population structure*** of species i

$$\boldsymbol{A_4} = \frac{\partial}{\partial Z_j}\left(\frac{dZ_i}{dt}\right)\Bigg|_{\boldsymbol{C}=\tilde{\boldsymbol{C}},\boldsymbol{Z}=\tilde{\boldsymbol{Z}}}$$

Dynamic effect of population structure of species j *on* ***dynamics of population structure*** of species i

Stability of population structure subsystem

Community stability analysis

$$C_i = J_i + A_i$$: Total density of species i

$$Z_i = \frac{J_i}{J_i + A_i}$$: Fraction juveniles of species i

Stability determined by:

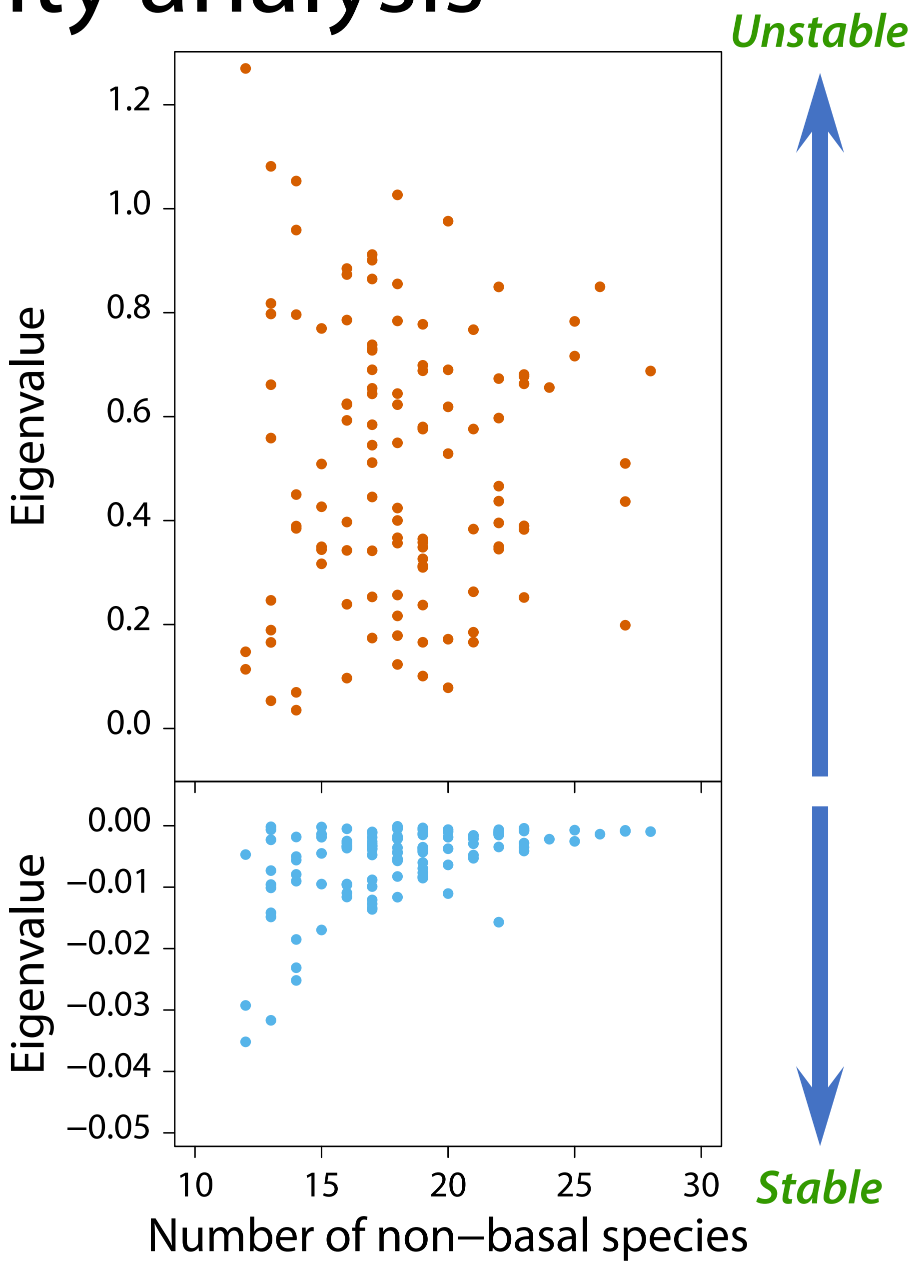
$$\boldsymbol{A} = \left(\begin{array}{c|c} \boldsymbol{A_1} & \boldsymbol{A_2} \\ \hline \boldsymbol{A_3} & \boldsymbol{A_4} \end{array}\right)$$

Community / Interaction matrix

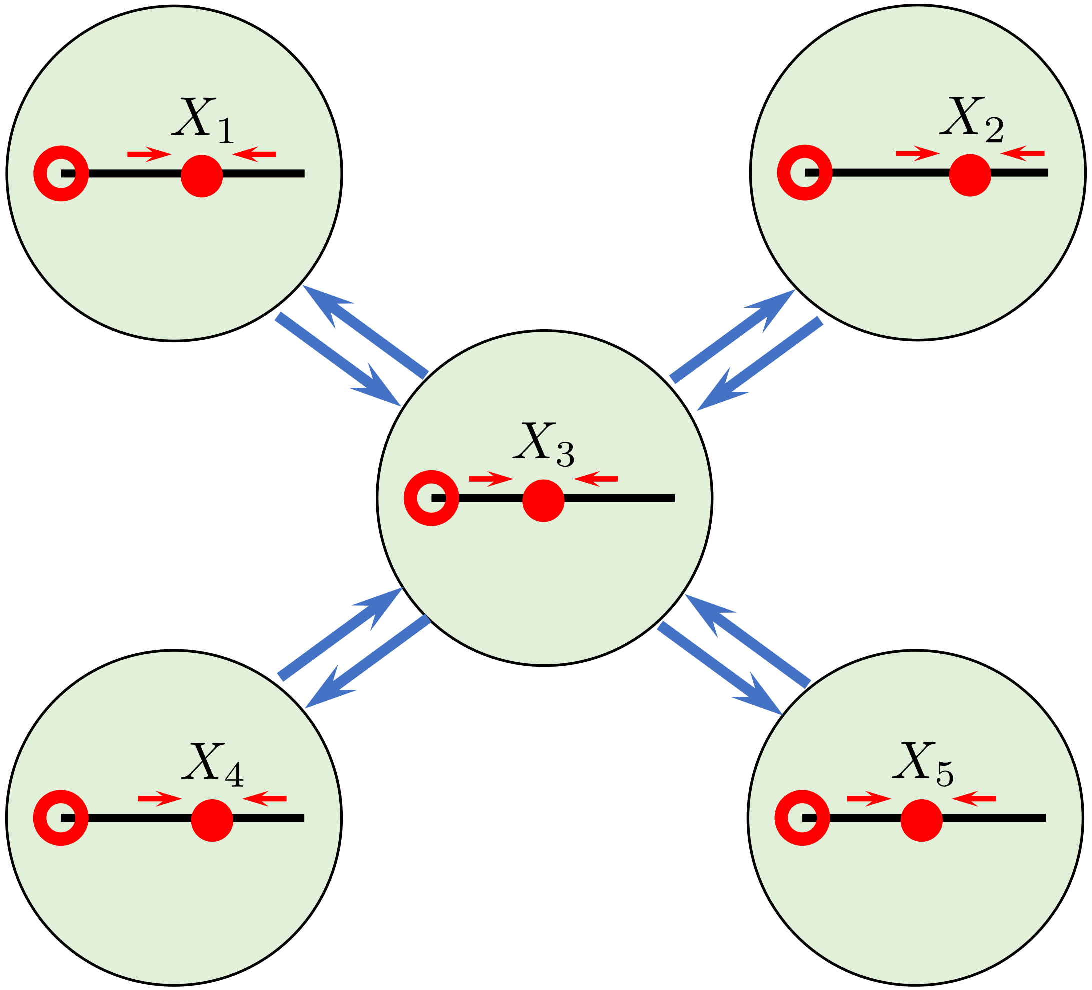
Per-capita density effect of species j on population density growth rate of species i

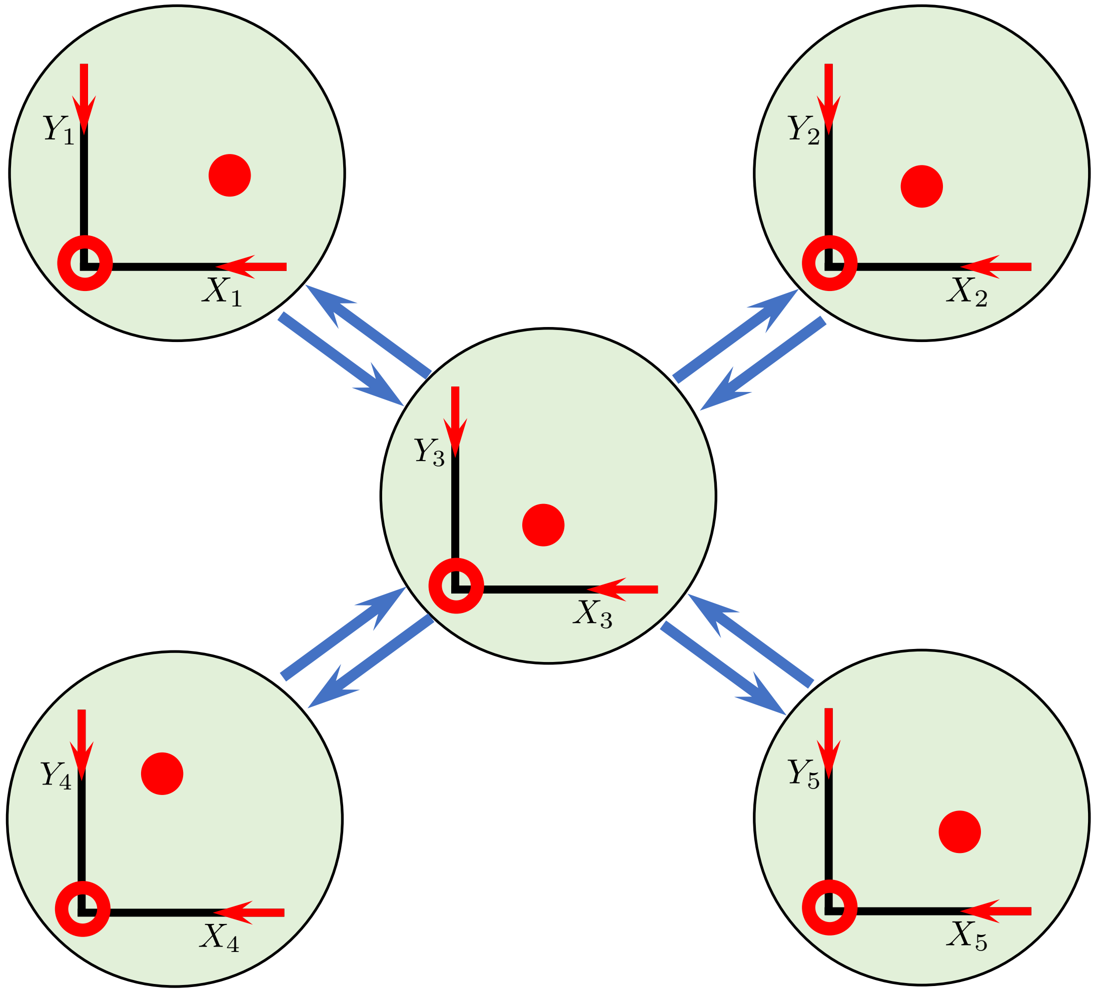
$$\boldsymbol{A_1} = \frac{\partial}{\partial C_j}\left(\frac{dC_i}{dt}\right)\Bigg|_{\boldsymbol{C}=\tilde{\boldsymbol{C}},\boldsymbol{Z}=\tilde{\boldsymbol{Z}}}$$

- Changing population structure with changing conditions stabilize dynamics
- Mechanism is different from stabilization through food web properties



Dimensionality of the state space of a node





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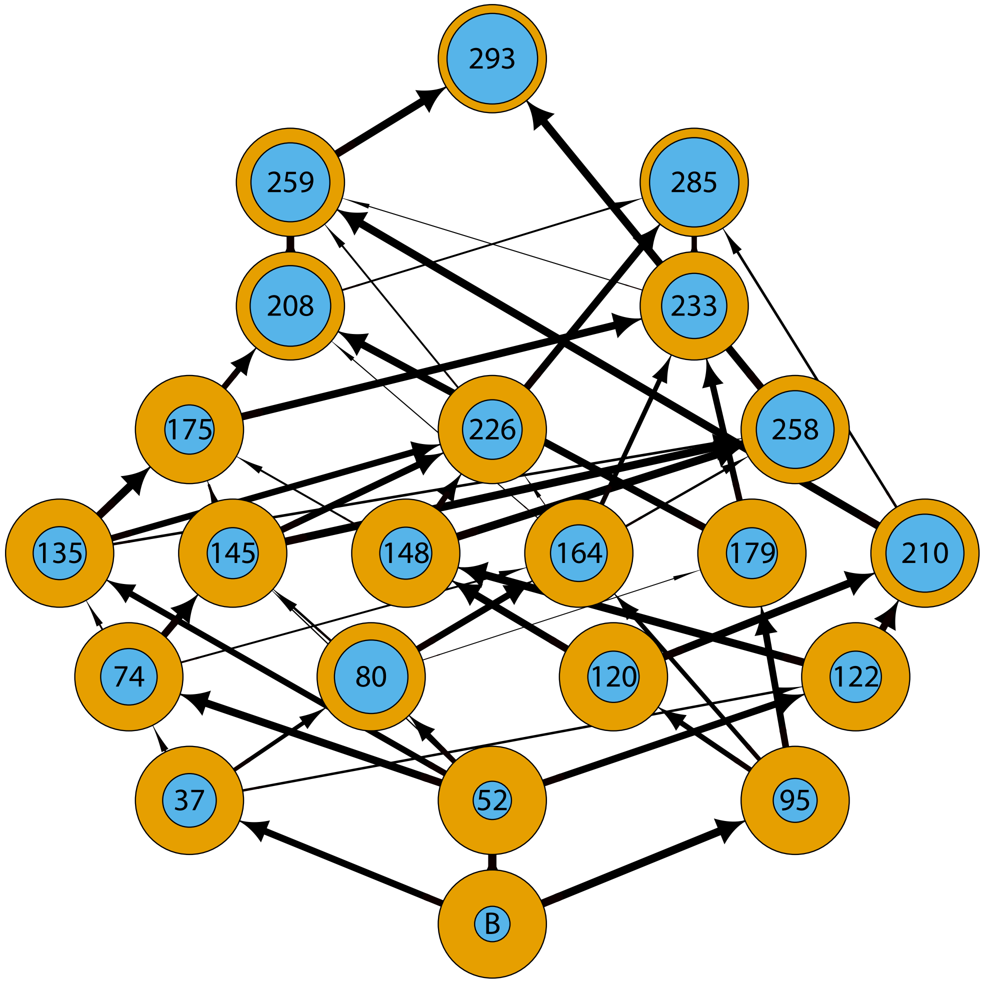
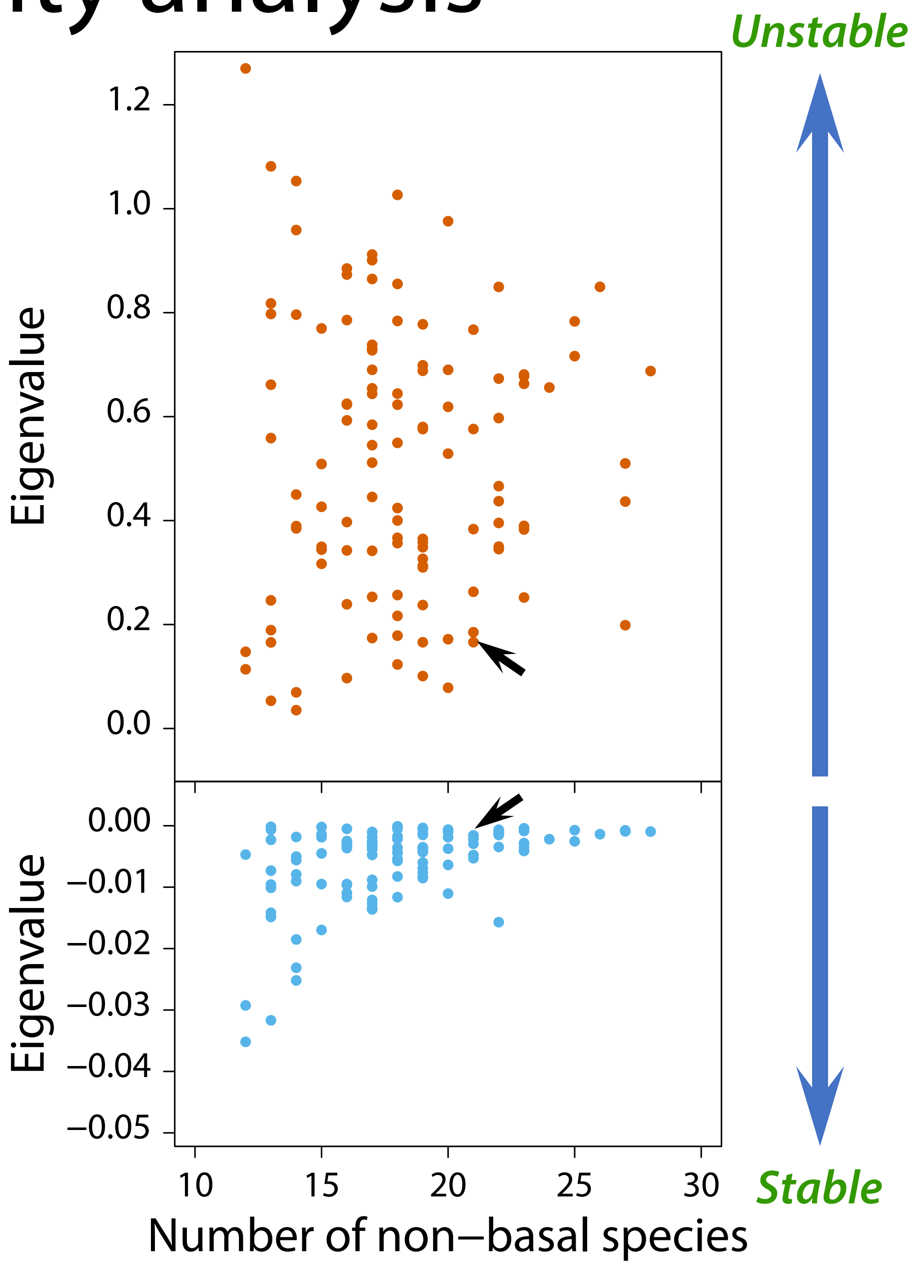
Community stability analysis





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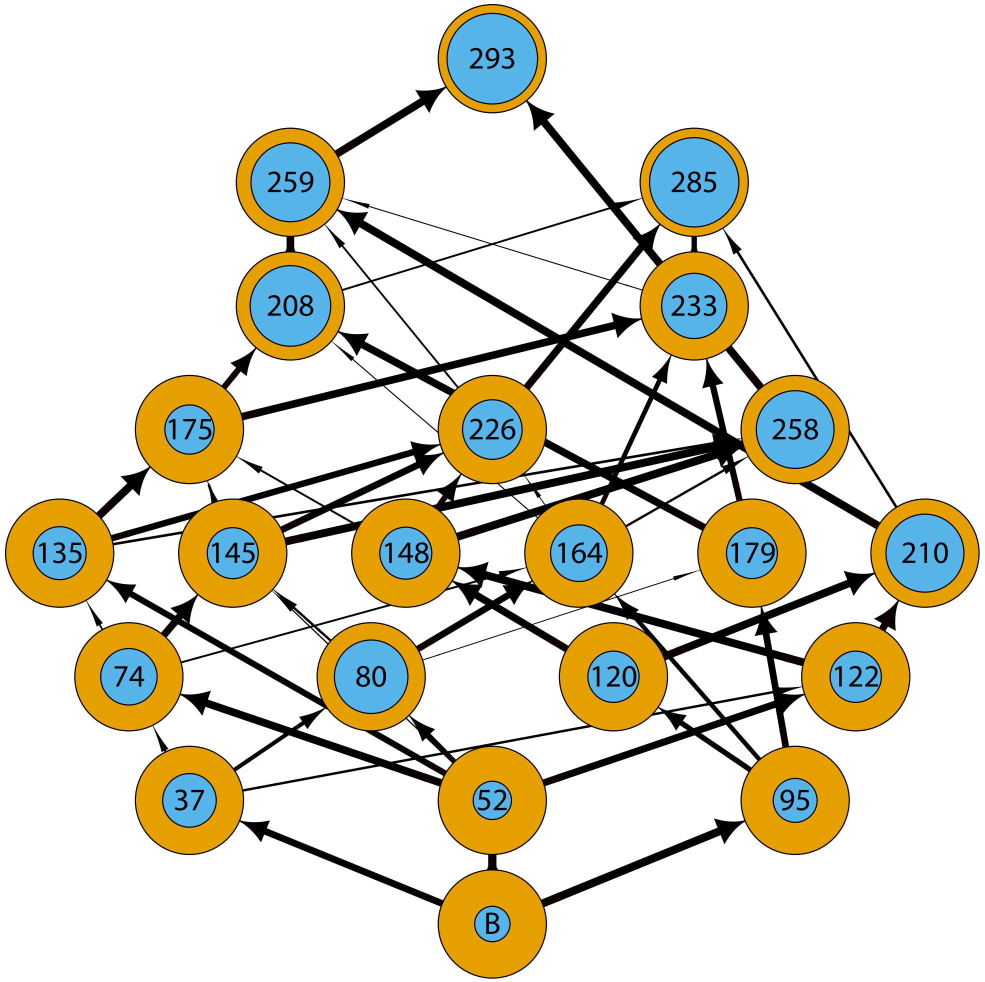
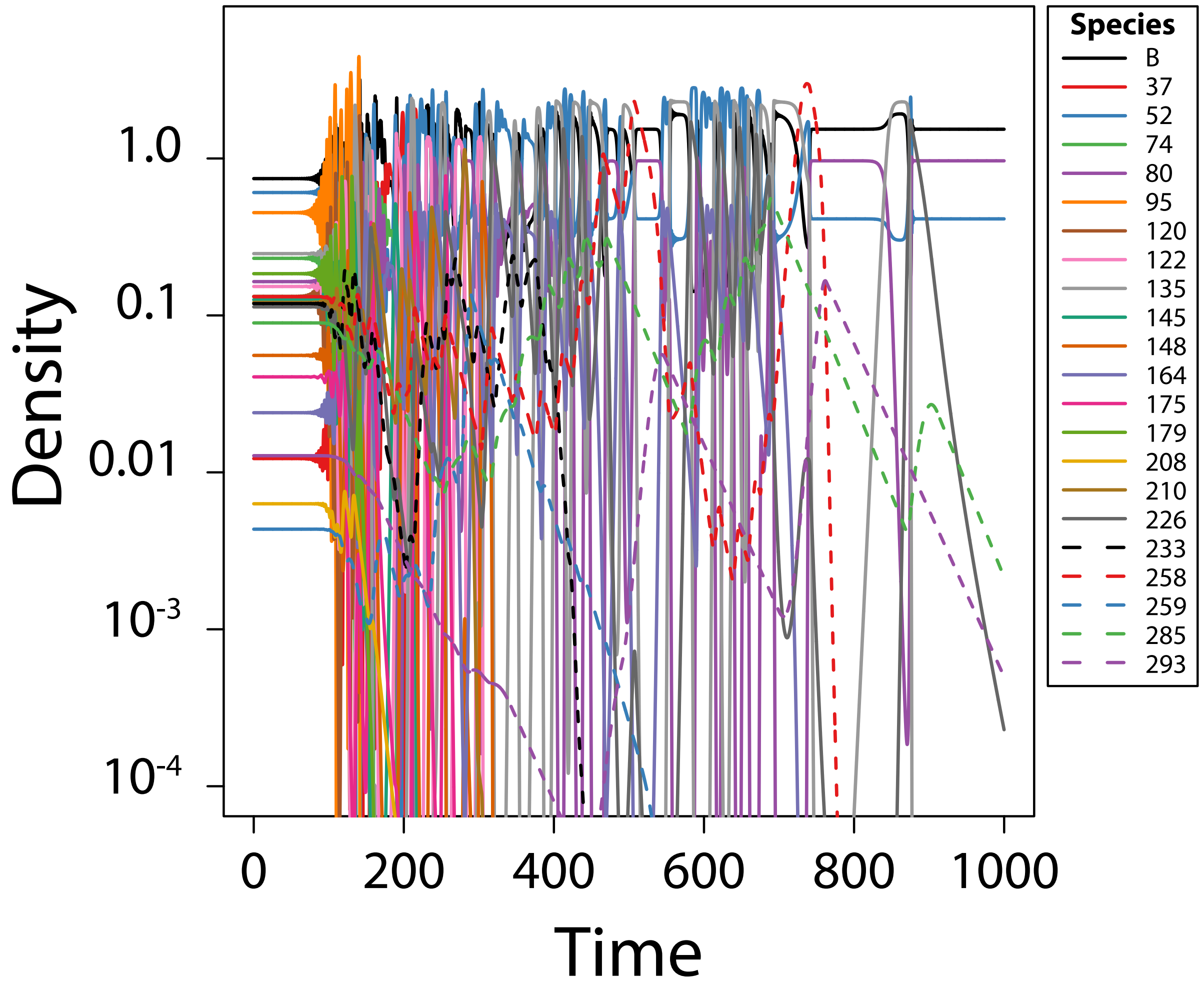
Impact of *dynamic* stage-structure



$C_i(0) = \tilde{C}_i, \quad Z_i(t) = \tilde{Z}_i$ for all $t \geq 0$



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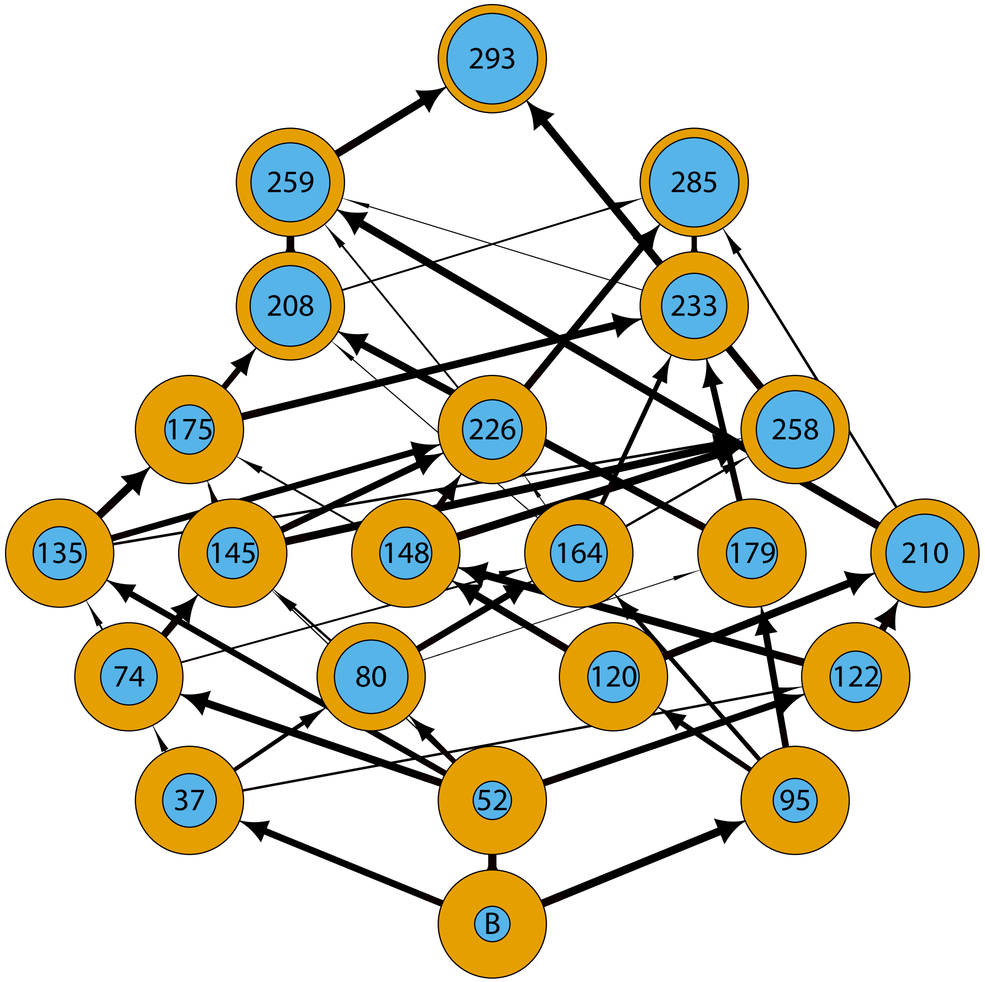
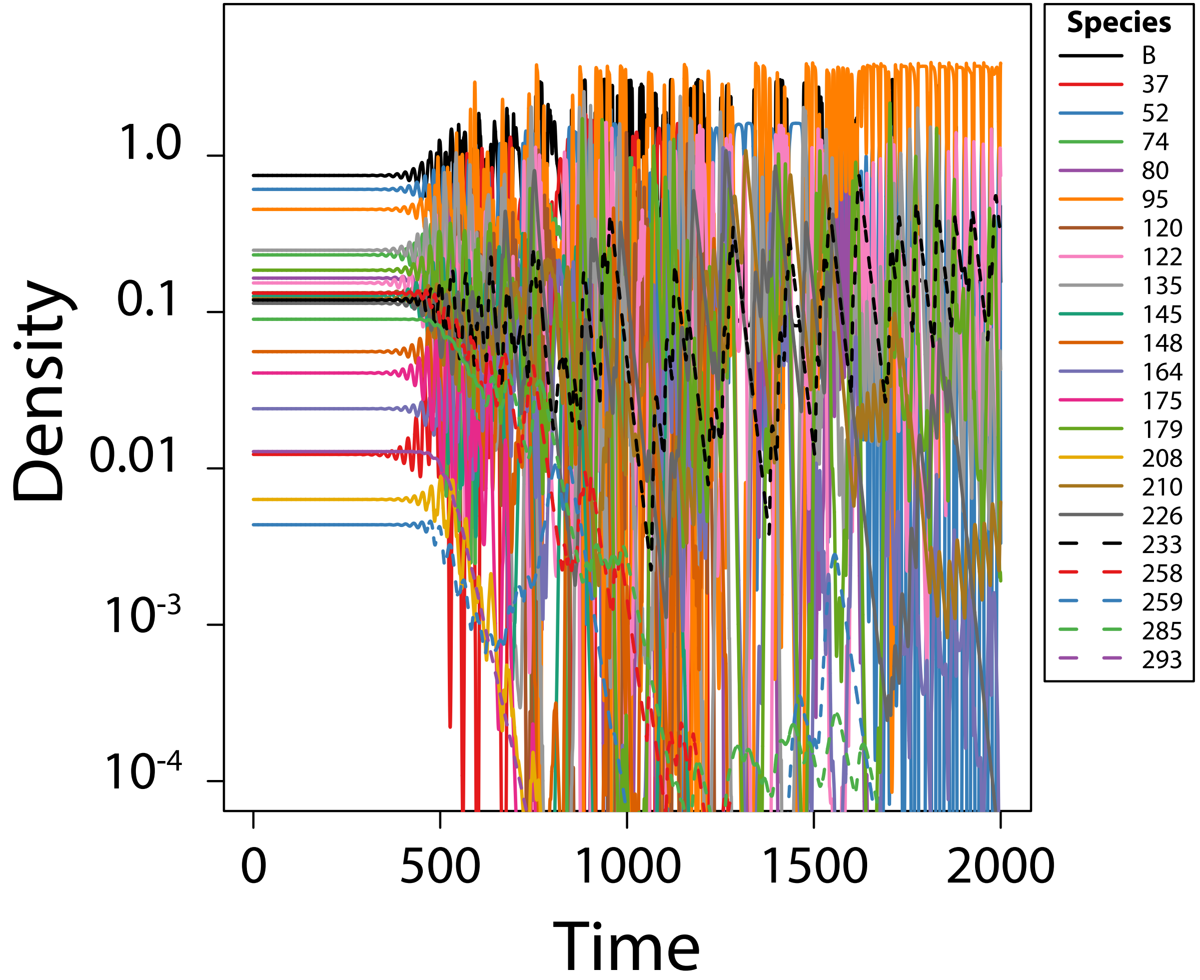
Impact of food-dependent maturation (age structure versus stage-structure)



$$C_i(0) = \tilde{C}_i \quad Z_i(0) = \tilde{Z}_i$$

$$(\boldsymbol{q}\,\gamma_i F_i(t) - T_i) = (\boldsymbol{q}\,\gamma_i \tilde{F}_i - T_i) \text{ for all } t \geq 0$$



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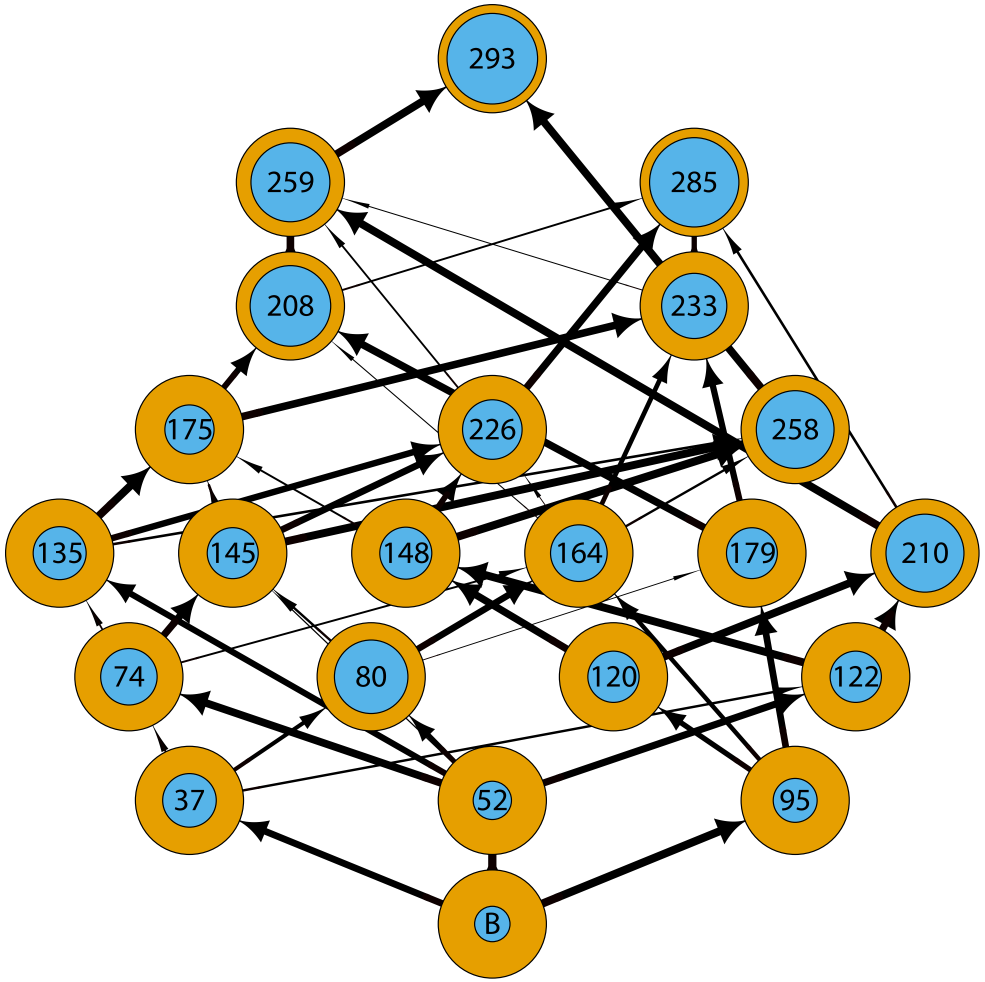
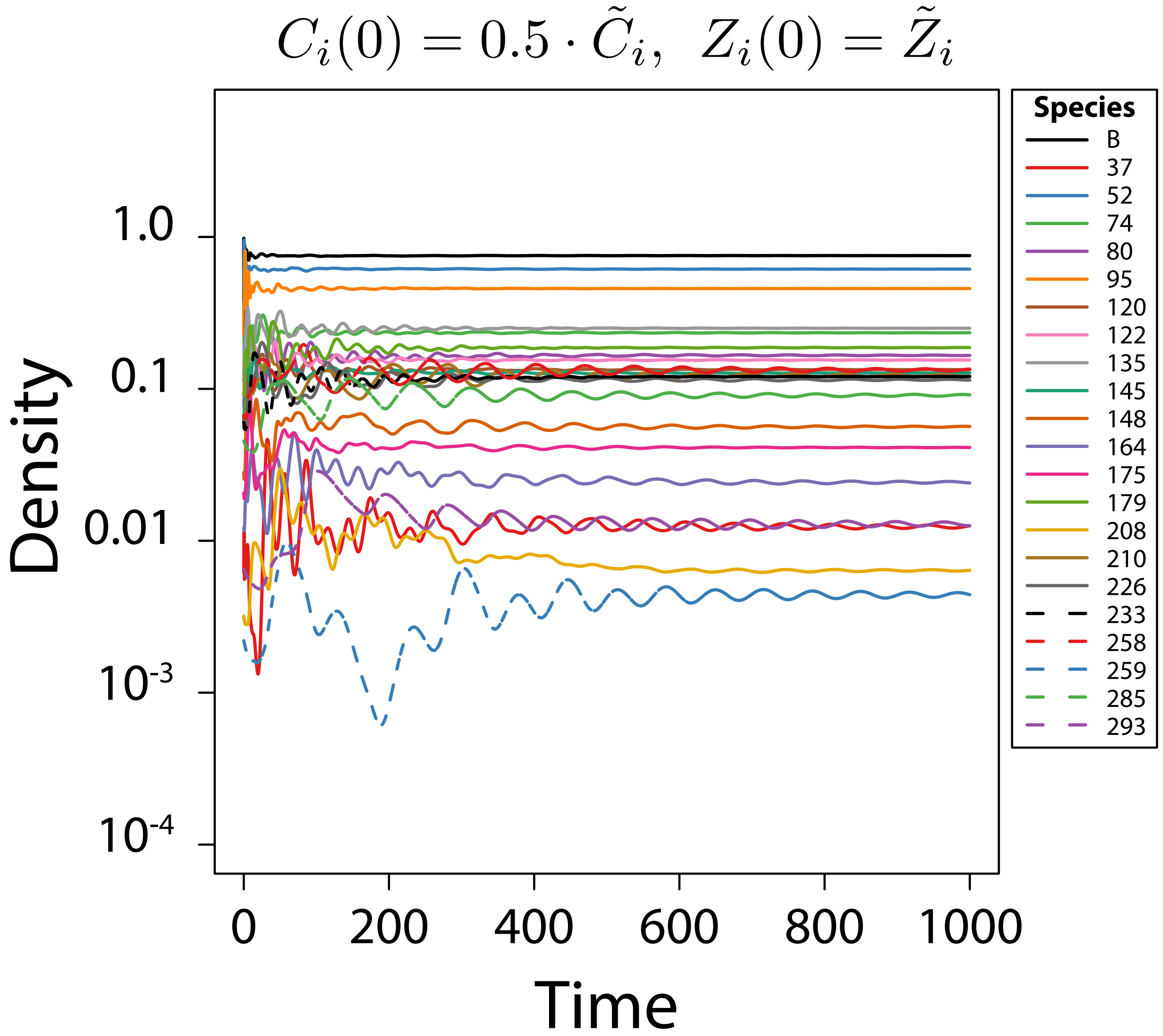
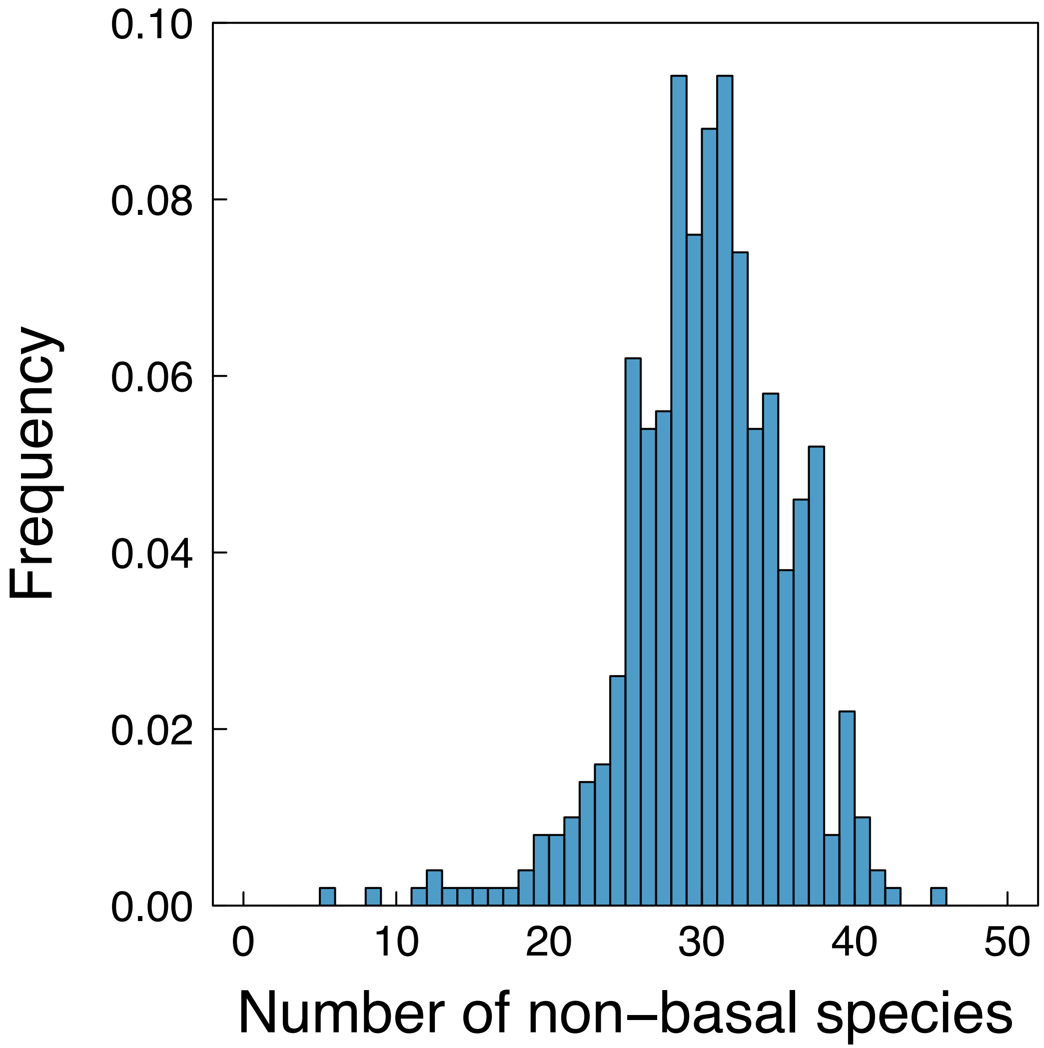
Community resilience

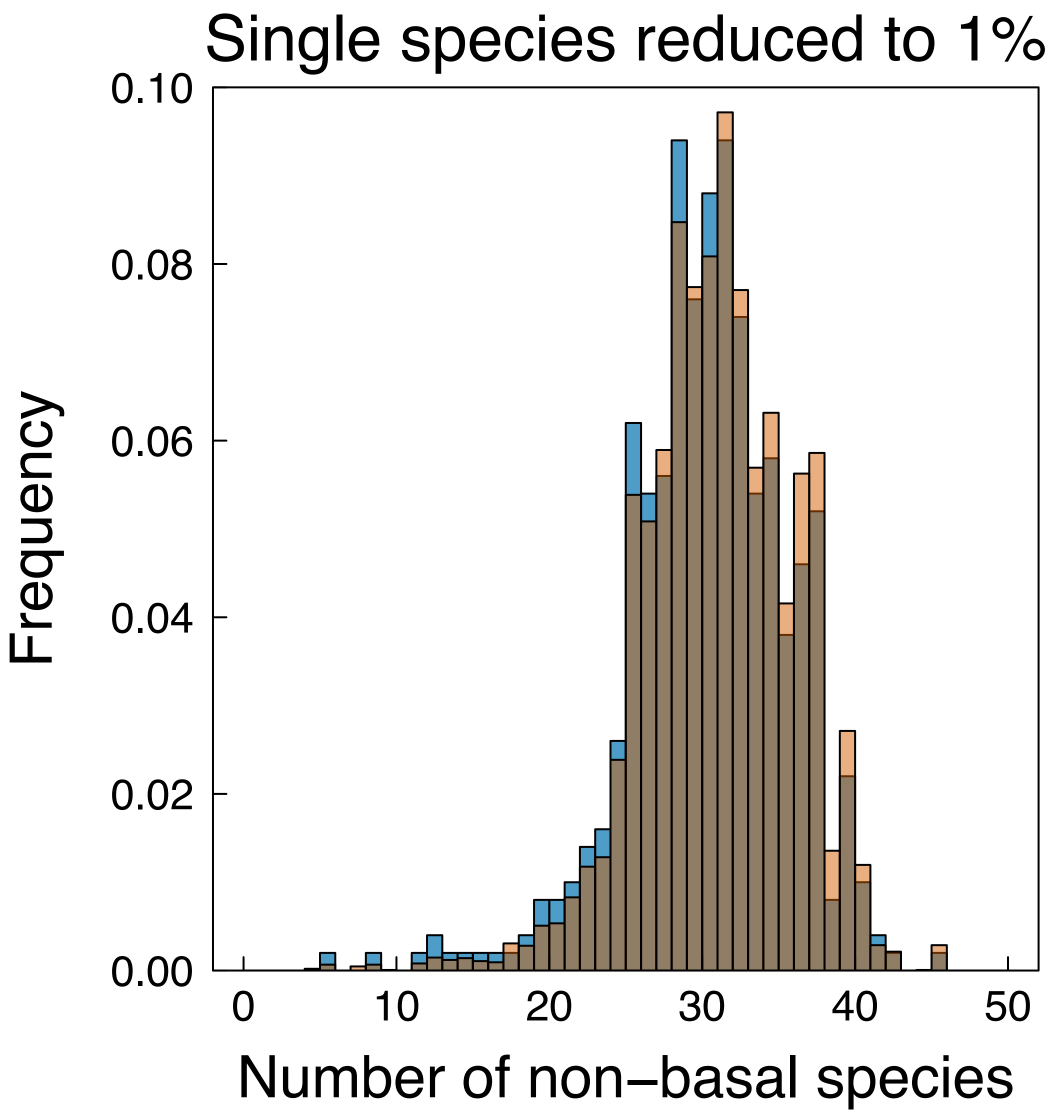




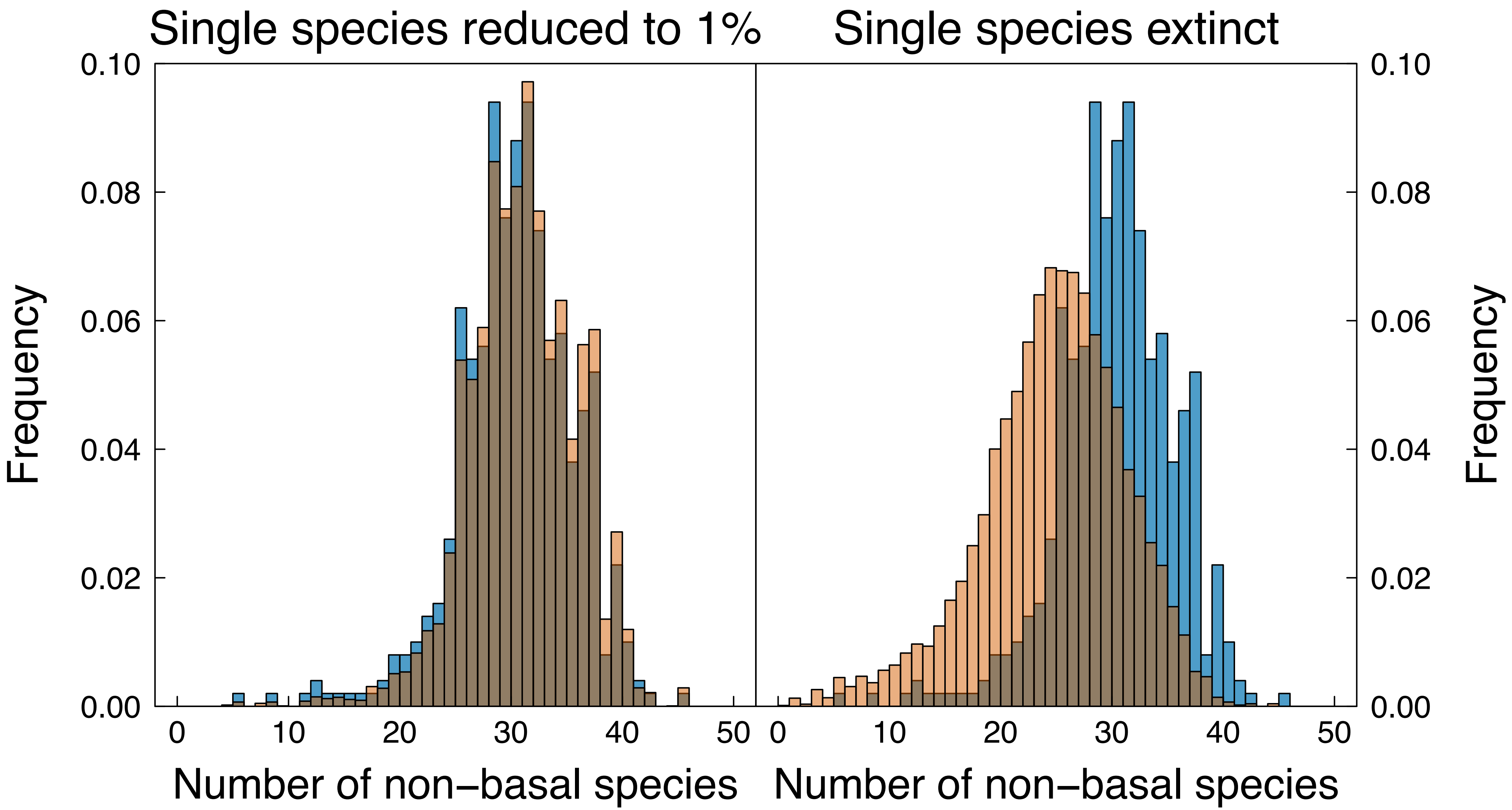
Communities are resilient to large perturbations



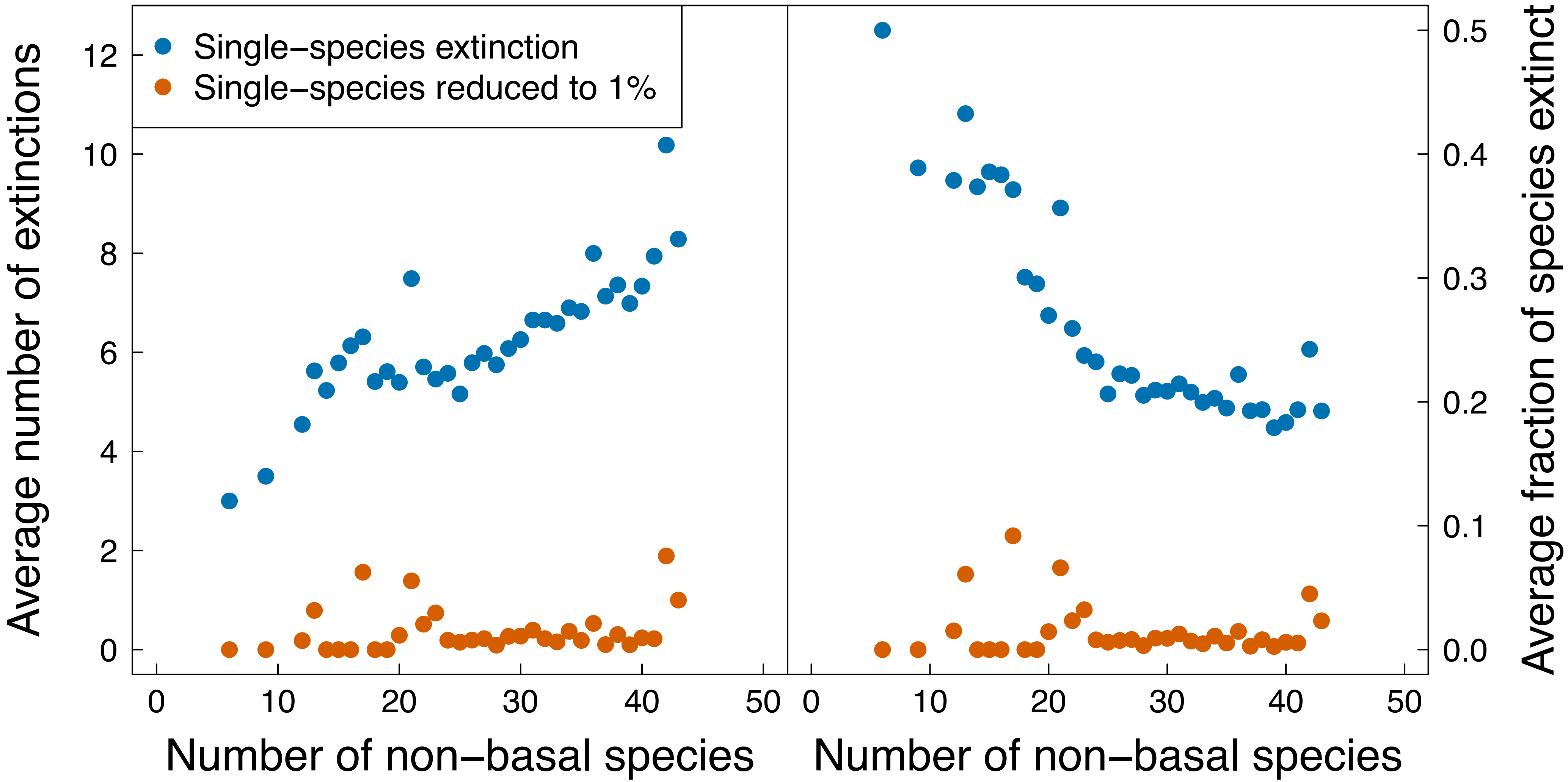
Communities are resilient to large perturbations



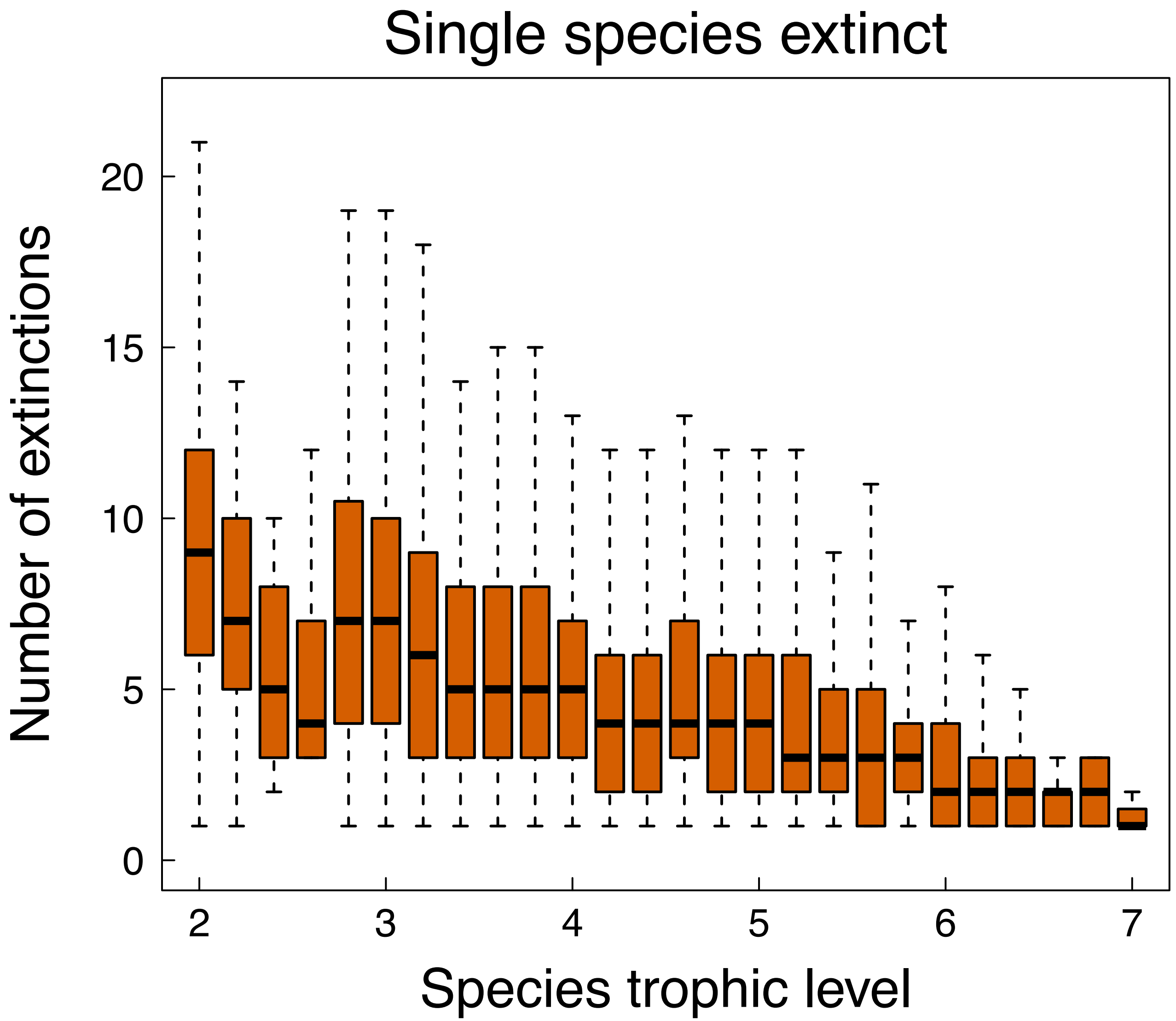
Communities are resilient to large perturbations



Communities are resilient to large perturbations



More basal species extincts have largest impact



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Conclusions

- ***Coupled changes in population structure and abundance*** alter community complexity-stability relationship:
    - Increase community diversity and complexity
    - Dampen population oscillations or stabilize community dynamics altogether
    - Annul and override destabilizing influences arising from the topology of the species interaction network

Network + Hierarchical complexity

⟹ stability & robustness

Broader implications

- Data collection:
  - Species-level data collection is and will remain the norm
  - Sometimes only data of the most conspicuous life stage (butterflies)
  - Food webs are networks between human-imposed groups that do not necessarily match dynamically relevant ecological entities
  - *To what extent do this type of data provide sufficient information for understanding, management and protection?*

- Modelling:
  - Species-level modelling on the basis of Lotka-Volterra interactions is and will remain the norm
  - *How reliable are predictions of these models and how useful are they for management purposes?*

Broader implications

- Modern ecology
  - Data revolution: large datasets, eScience, data science
  - Data-driven modelling
  - Analysis through advanced statistics or AI
  - *Conceptual thinking / theory is underrepresented*
- Science philosophy issues:
  - Data are considered "objective", despite their dependence on our conceptualization and the methods of their collection
  - The power of tradition in population / community ecology:
    When does a paradigm that considers species to be unstructured turn into a tunnel vision?

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Faculty of Science

IBED Institute for Biodiversity and Ecosystem Dynamics

Thank you!

What we observe is not nature itself, but nature exposed to our method of questioning

- Werner Heisenberg

Santa Fe Institute