

A Bioenergetic Model for Food Webs

→ Modelling population dynamics in terms of biomass flows through trophic interactions, using the principle of bioenergetics

Eva Delmas, 2019-08-21

Summer school in biodiversity modelling 2019

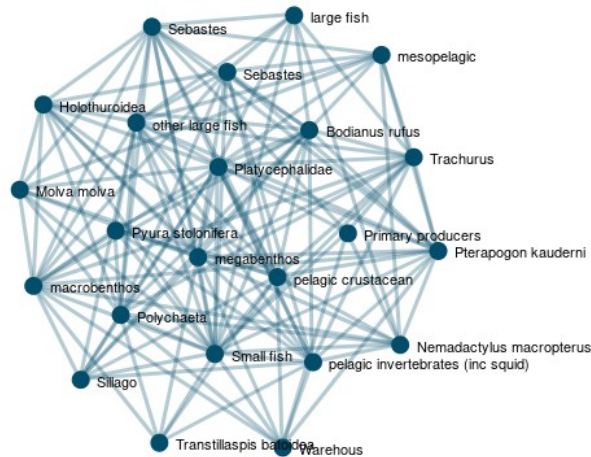
Outline

→ How to build, parameterize and use bio-energetic models to model population dynamics in food webs

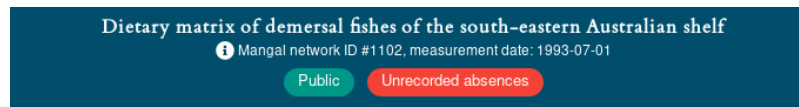
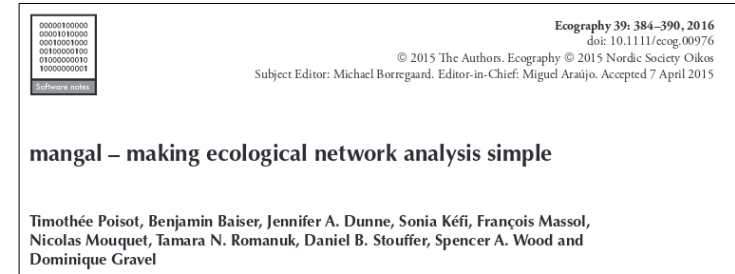
- Food webs: a useful abstraction of ecological communities
- The principle of mass balance
- Growth of basal species
 - Intro. to solving differential equation
- Consumption
- Metabolic losses
- The bio-energetic food-web model
- Setting parameters values
- Model application: food web robustness to extinctions
- A brief review and discussion

Food Webs

- Map trophic interaction => biomass routes through the community
- powerful abstraction to investigate stability / functioning of ecological communities



From mangal.io



Number of nodes
23

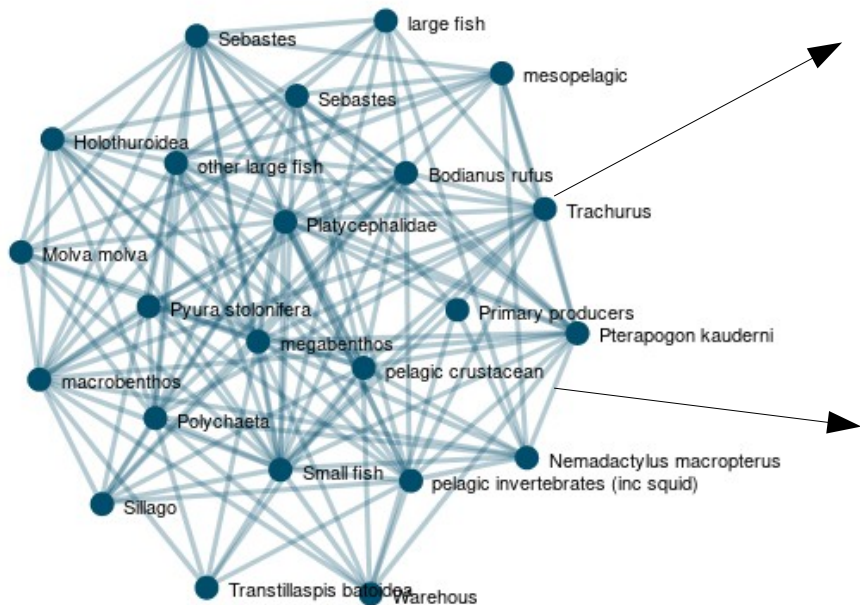
Number of interactions
141

Connectance
0.27



Food Webs

- Map trophic interaction => biomass routes through the community
- powerful abstraction to investigate stability / functioning of ecological communities

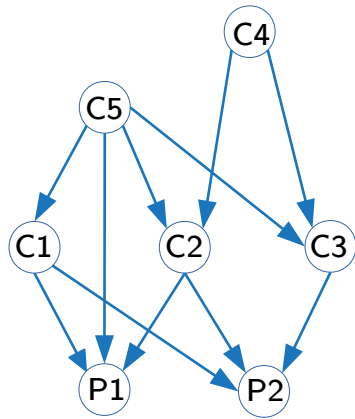


Node: population, species, trophospecies, ...
Metadata → name, traits, ...

Edge: trophic interaction
Metadata → interaction strength, direction

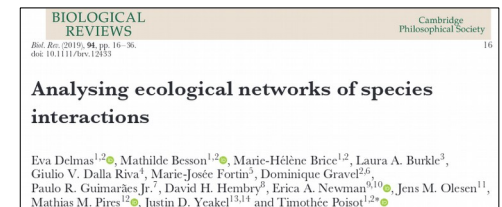
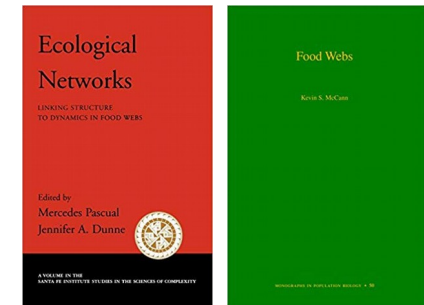
Food Webs

- Map trophic interaction => biomass routes through the community
- powerful abstraction to investigate stability / functioning of ecological communities



	P1	P2	C1	C2	C3	C4	C5
P1	0	0	0	0	0	0	0
P2	0	0	0	0	0	0	0
C1	1	1	0	0	0	0	0
C2	1	1	0	0	0	0	0
C3	0	1	0	0	0	0	0
C4	0	0	0	1	1	0	0
C5	1	0	1	1	1	0	0

Structural properties of the food web (connectance, modularity, degree distribution, etc.)



$A = S \times S$ interaction matrix
 $A[i,j] = 1$ means i eats j
 $A[i,j] = 0$ otherwise

Mass balance

→ **Conservation of mass**: in a closed physical system mass can neither be produced nor destroyed.

Mass balance is the application of the physical principle of **conservation of mass** to the analysis of systems **flux and stocks**.

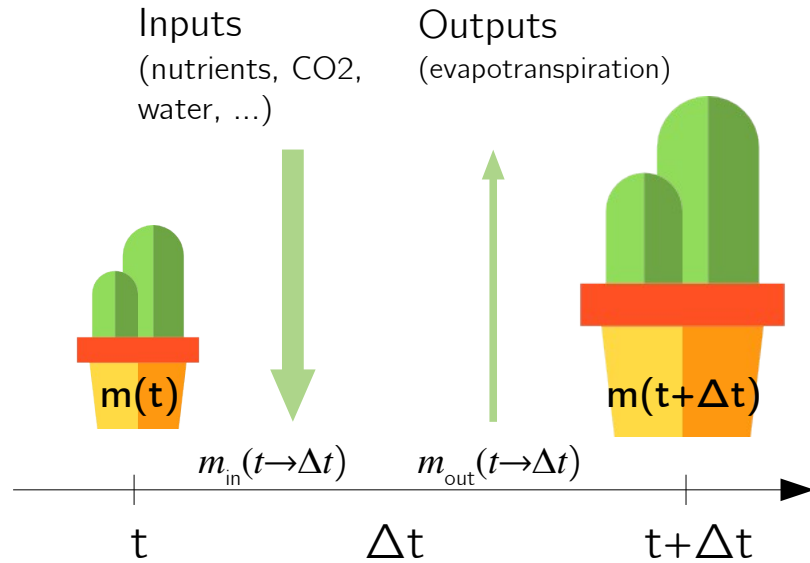
$$Storage = Inputs - Outputs$$

Mass balance

time

Storage = Inputs - Outputs

$$m(t+\Delta t) = m(t) + m_{\text{in}}(t \rightarrow \Delta t) - m_{\text{out}}(t \rightarrow \Delta t)$$



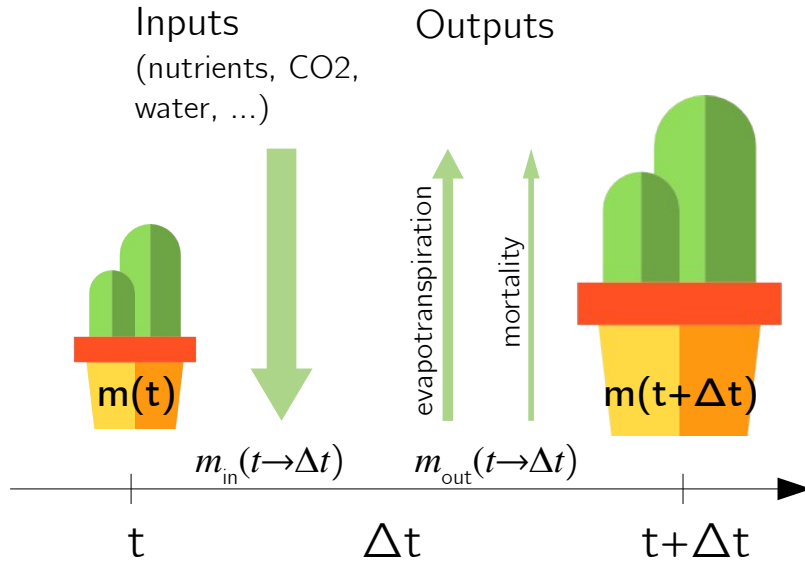
Mass balance

Each term can be decomposed to reflect the diversity of mechanisms / compartments involved

time

$$\text{Storage} = \text{Inputs} - \text{Outputs}$$

$$m(t+\Delta t) = m(t) + m_{\text{in}}(t \rightarrow \Delta t) - m_{\text{out}}(t \rightarrow \Delta t)$$



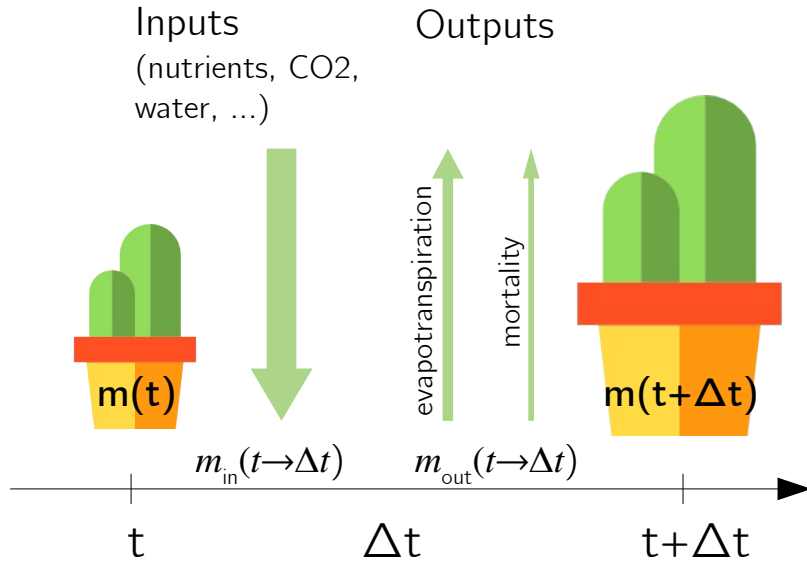
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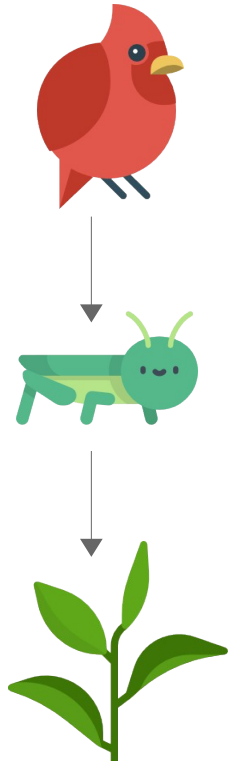
From stocks to flux: **the mass accumulation rate**

$$\frac{m(t+\Delta t) - m(t)}{\Delta t} = \frac{m_{\text{input}}(t \rightarrow \Delta t)}{\Delta t} - \frac{m_{\text{output}}(t \rightarrow \Delta t)}{\Delta t}$$

$$\frac{\Delta m}{\Delta t} = m_{\text{input}} - m_{\text{output}}$$

The bio-energetic food-web model

→ Using the principle of mass balance, we can build a general model for trophic interactions



The bio-energetic food-web model

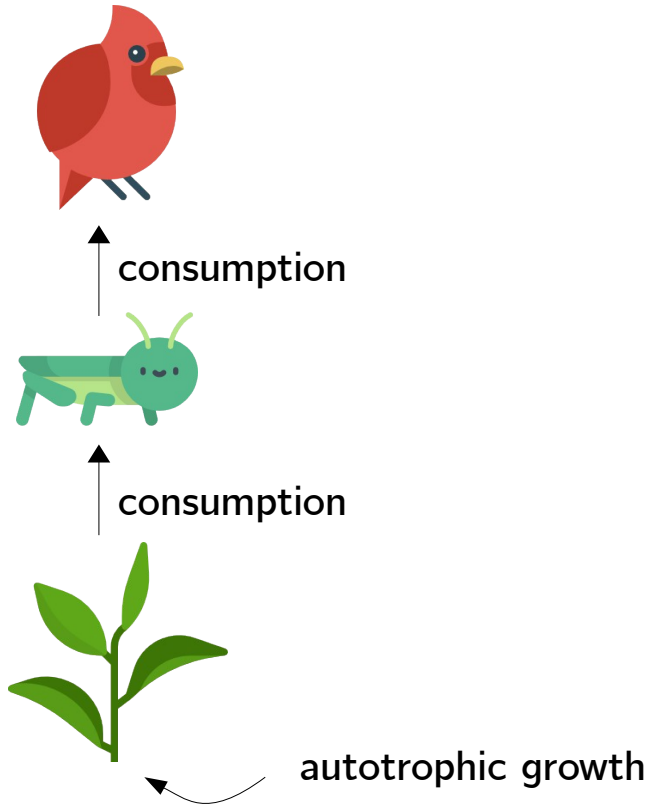
→ Using the principle of mass balance, we can build a general model for trophic interactions



autotrophic growth

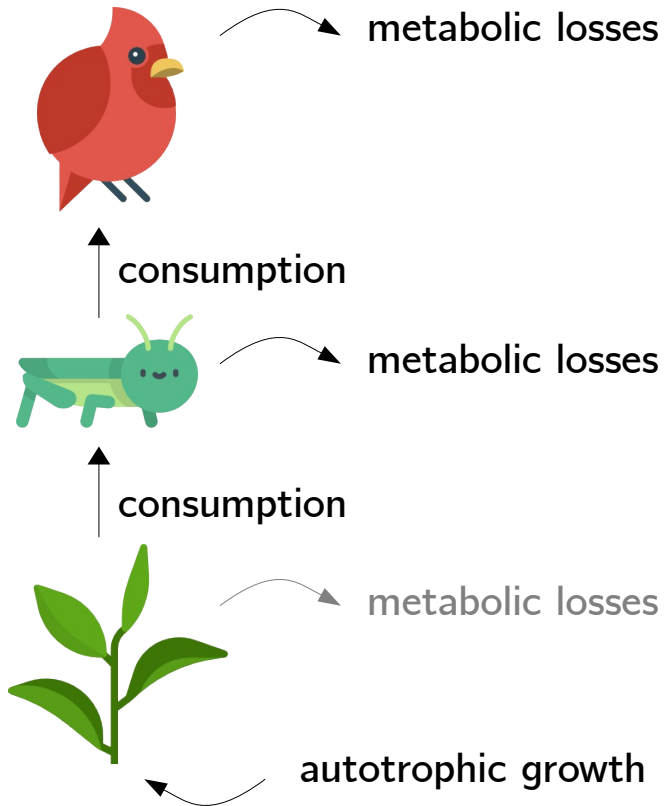
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The bio-energetic food-web model

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Mass in:

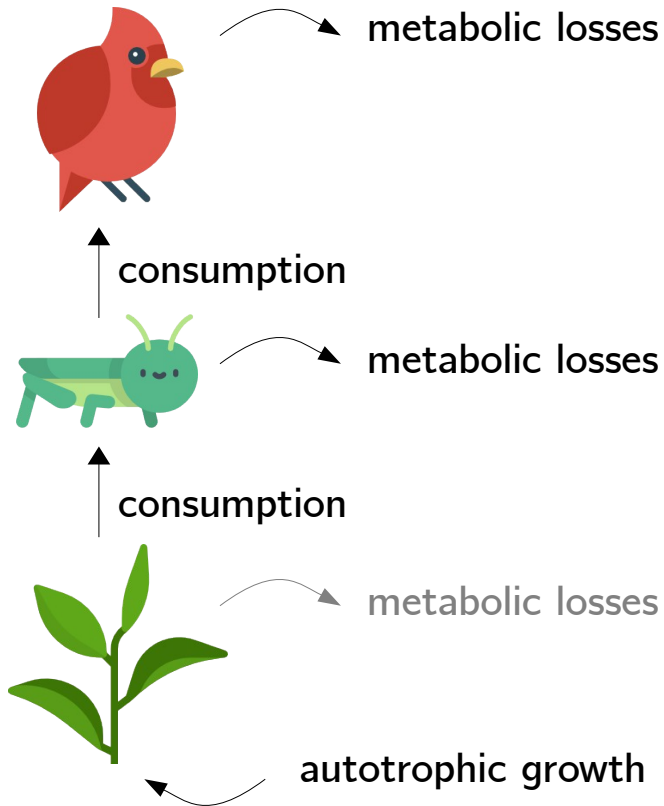
- growth
- gains from consumptions

Mass out:

- loss to consumption
- metabolic losses

The bio-energetic food-web model

→ Using the principle of mass balance, we can build a general model for trophic interactions



Mass in:

- growth
- gains from consumptions

Mass out:

- loss to consumption
- metabolic losses

For each population:

$$\Delta B / \Delta t = G + C_{in} - C_{out} - M$$

1st term: growth of basal species

$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$

→ Basic equation:

$$r_i \quad G_i(B) \quad B_i$$

Intrinsic growth rate

Net growth rate

Biomass of the focus species

$$G_i(B) = 1 - \frac{\text{Sum biomass pop. in competition for the same resources}}{\text{Carrying capacity}}$$

1st term: growth of basal species

$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$

→ General equation:

$$r_i \quad G_i(B) \quad B_i$$

Intrinsic growth rate Net growth rate Biomass of the focus species

Logistic growth

$$G_i(B_i) = 1 - B_i / K$$

Differential equations solvers in Julia and R

Julia
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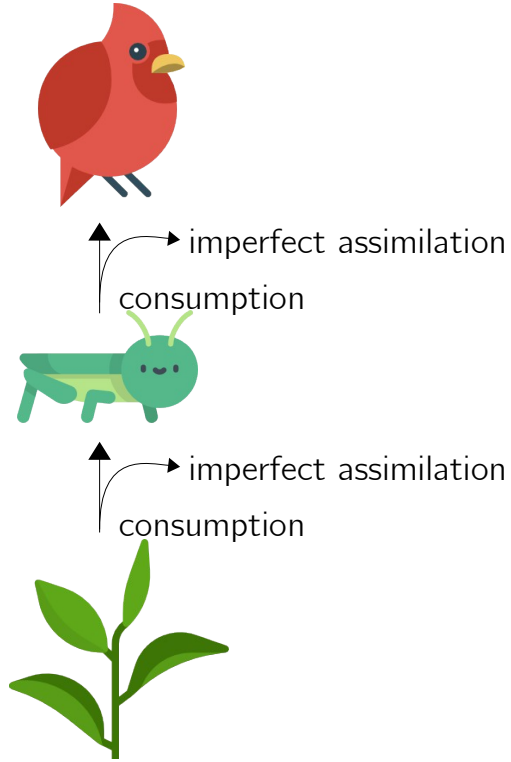
Introducing direct competition

$$G_i(B_i) = 1 - (\sum_j \alpha_{ij} B_j) / K$$

Julia
BOX

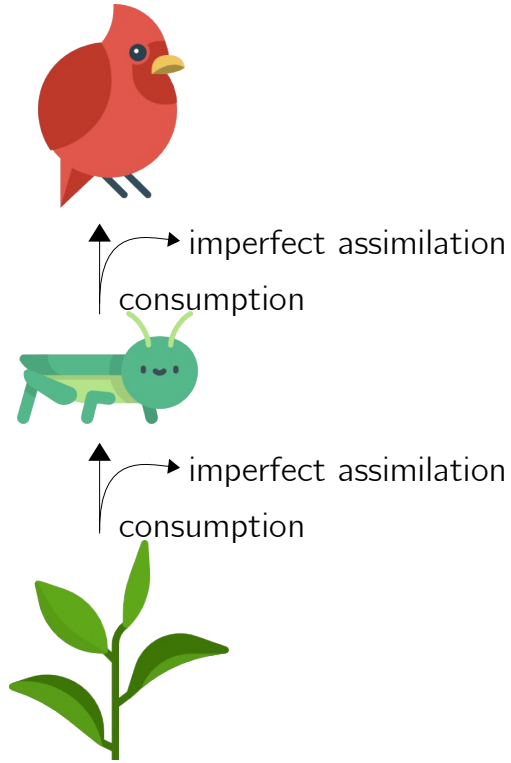
2nd and 3rd terms: consumption

$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$



2nd and 3rd terms: consumption

$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$



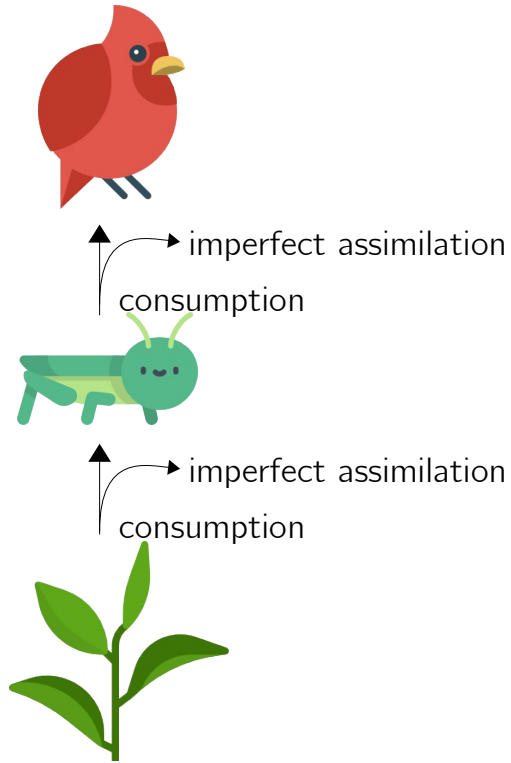
Biomass consumed / lost

Same shape for both species?

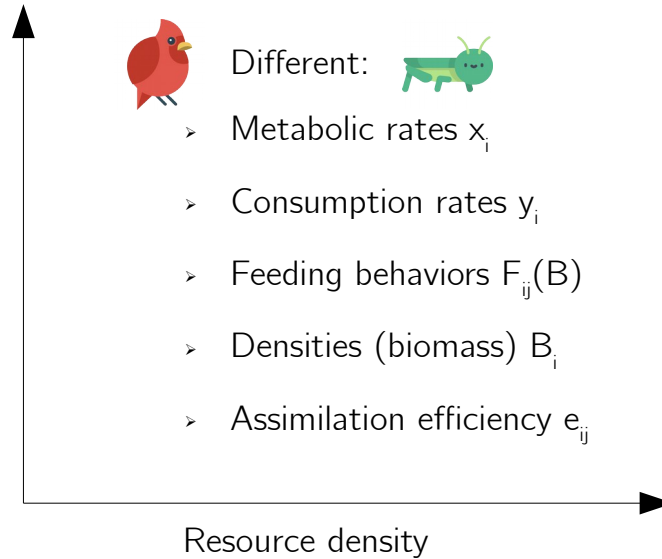
Resource density

2nd and 3rd terms: consumption

$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$

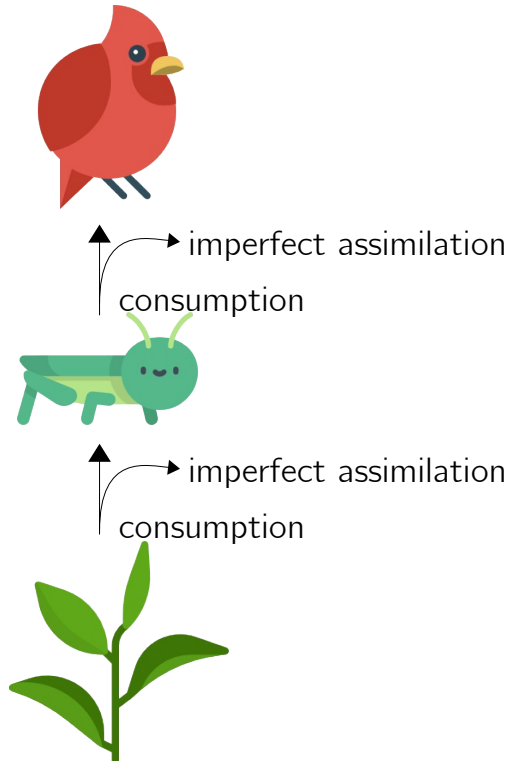


Biomass consumed / lost



2nd and 3rd terms: consumption

$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$



Biomass consumed / lost



Different:



- Metabolic rates x_i
- Consumption rates y_i
- Feeding behaviors $F_{ij}(B)$
- Densities (biomass) B_i
- Assimilation efficiency e_{ij}

$$\text{Gain} = \sum_{j=\text{pred.}} x_i y_i B_i F_{ij}$$

$$\text{Loss} = \frac{\sum_{j=\text{pred.}} x_j y_j B_j F_{ji}}{e_{ji}}$$

Resource density

2nd and 3rd terms: consumption

$$\Delta B / \Delta t = G + C_{in} - C_{out} - M$$

→ Functional response: intake rate of a consumer as a function of food density

Consumer time budget:

Consumer time = searching resources + handling and consuming

The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly¹

By C. S. HOLLING

Forest Insect Laboratory, Sault Ste. Marie, Ont.

$$f(R) = \frac{aR^{1+q}}{1+ahR^{1+q}}$$

← Max. biomass possibly captured

← Time lost searching / consuming preys

a: attack rate

h: handling time

q: holling coef. controls the shape of the curve

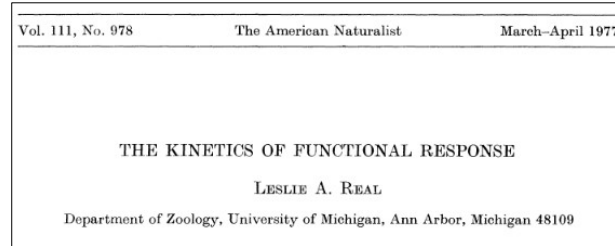
Holling type II and III functional responses

Compare type II and type III functional response and the associated resource mortality rates.

2nd and 3rd terms: consumption

$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$

→ Multi-species functional response



$$F_{ij}(B_j) = \frac{a_{ij} B_j^{1+q}}{1 + \sum_{k=\text{resources}} a_{ik} B_k^{1+q}}$$



$$F_{ij}(B_j) = \frac{\alpha_{ij} B_j^{1+q}}{B0_i + \sum_{k=\text{resources}} \alpha_{ik} B_k^{1+q}}$$

Multi-species functional response

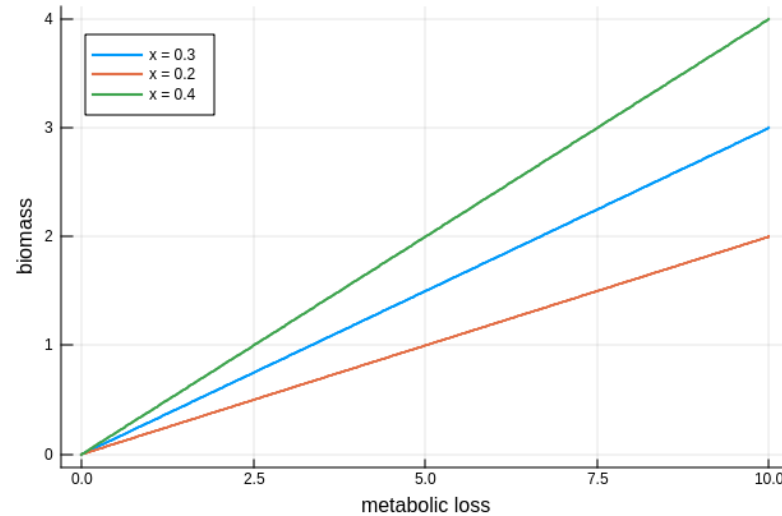
Implementation and analysis of the multi-species functional response

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4th term: metabolic losses

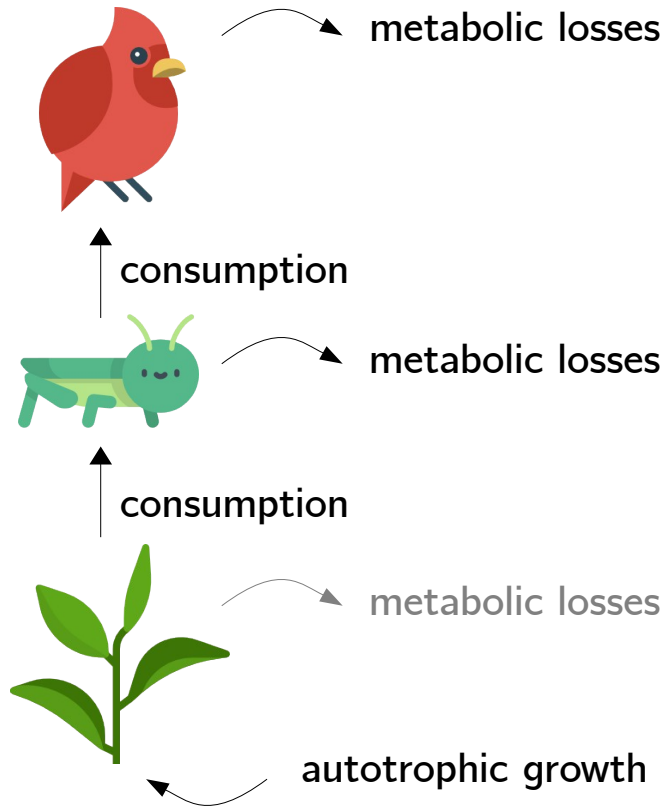
$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$

$$\rightarrow M = x_i B_i$$



The bio-energetic food-web model

→ Using the principle of mass balance, we can build a general model for trophic interactions

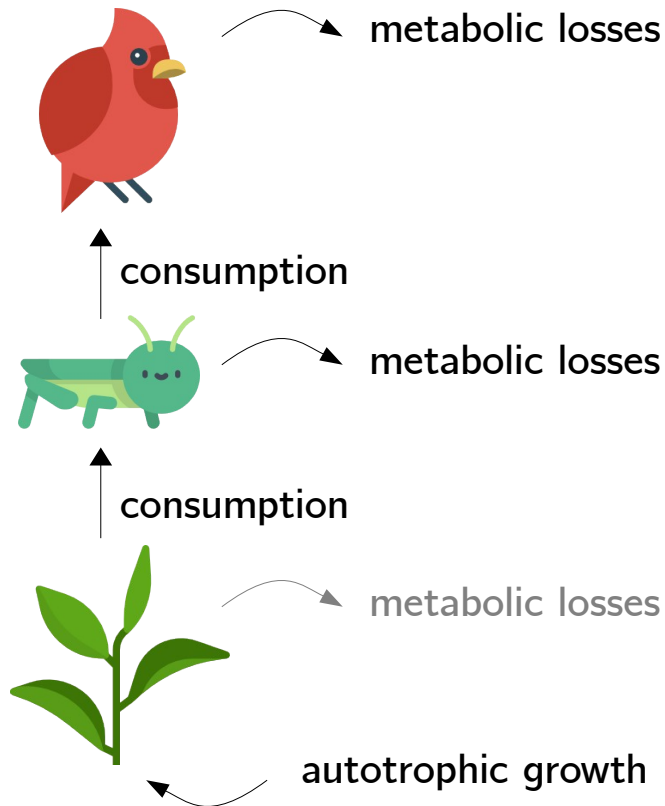


$$\Delta B / \Delta t = G + C_{\text{in}} - C_{\text{out}} - M$$

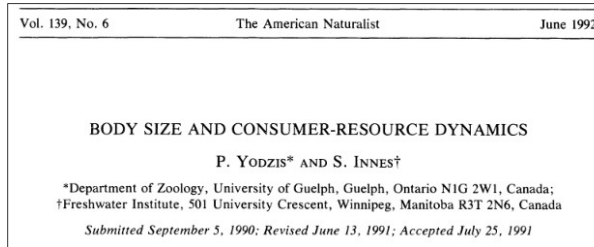
$$\frac{\Delta B_i}{\Delta t} = r_i G_i(B) B_i + \sum_{j=\text{resources}} x_i y_i F_{ij} B_j - \sum_{j=\text{consumers}} \frac{x_j y_j F_{ji} B_j}{e_{ij}} - x_i B_i$$

The bio-energetic food-web model

→ Using the principle of mass balance, we can build a general model for trophic interactions



$$\frac{\Delta B_i}{\Delta t} = r_i G_i(B) B_i + \sum_{j=\text{resources}} x_i y_i F_{ij} B_i - \sum_{j=\text{consumers}} \frac{x_j y_j F_{ji} B_j}{e_{ij}} - x_i B_i$$



CHAPTER 2

HOMAGE TO YODZIS AND INNES 1992: SCALING UP FEEDING-BASED POPULATION DYNAMICS TO COMPLEX ECOLOGICAL NETWORKS

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 Germany*

NEO D. MARTINEZ

Pacific Ecoinformatics and Computational Ecology Lab, PO Box 10106, Berkeley, CA 94709, USA

Rooney, N., McCann, K. S., & Noakes, D. L. (Eds.).
 (2006). *From energetics to ecosystems: the dynamics
 and structure of ecological systems* (Vol. 1).

Allometric scaling of biological rates

→ Almost all organisms biological rates vary predictably with body sizes

Whole organism

$$Y = Y_0 M^{0.75}$$

Mass specific

$$rate = a M^{-0.25}$$

Ecology, 85(7), 2004, pp. 1771–1789
© 2004 by the Ecological Society of America

TOWARD A METABOLIC THEORY OF ECOLOGY

JAMES H. BROWN,^{1,2,4}

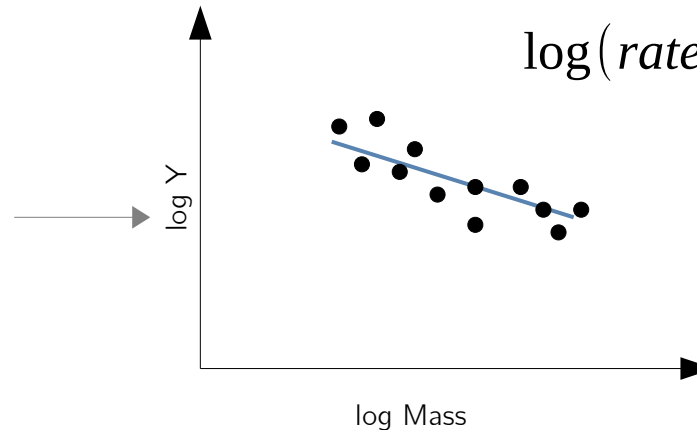
with JAMES F. GILLOOLY,¹ ANDREW P. ALLEN,¹ VAN M. SAVAGE,^{2,3} AND GEOFFREY B. WEST^{2,3}

¹Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA

²Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501 USA

³Theoretical Division, MS B285, Los Alamos National Laboratory, Los Alamos, New Mexico 87545 USA

Oxygen consumption,
resource consumption,
heat loss, ...



$$\log(rate) = intercept - 0.25 \log(M)$$

Choosing parameters values

→ Empirically measured parameters

Maximum consumption rate

Use the data from Yodzis and Innes (1992) paper to find y_i value



→ Sensitivity analysis: how the uncertainty in the output of a mathematical model can be divided and allocated to different sources of uncertainty in its inputs (model parameters).

1. Define output (e.g. total biomass)
2. Fix all parameters values except for one (e.g. y_i)
3. Run the model
4. Calculate the percentage change in both output (%B) and input (%y)
5. The model sensitivity to this parameter is $\%B / \%y$

Choosing parameters values

Sensitivity analysis

Perform a sensitivity analysis: how a food web total biomass varies when changing herbivores assimilation efficiency



→ Should we use this type of sensitivity analysis on non-linear dynamical systems?

Choosing parameters values

Sensitivity analysis

Perform a sensitivity analysis: how a food web total biomass varies when changing herbivores assimilation efficiency

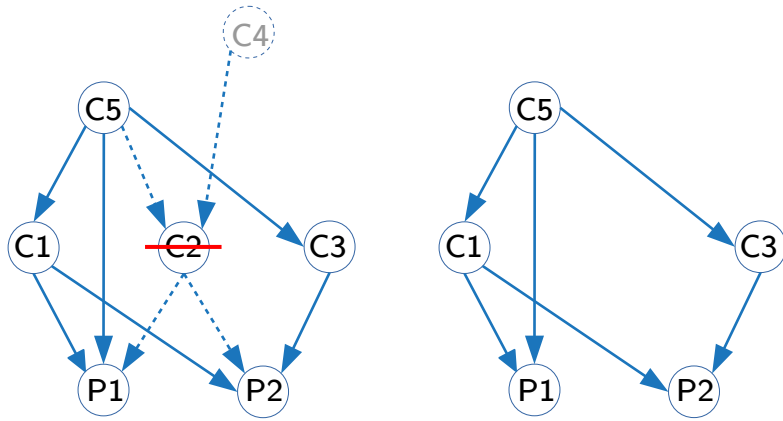


- Should we use this type of sensitivity analysis on non-linear dynamical systems?
- Variance-based sensitivity analysis: decomposes the variance of the output of the model into fractions which can be attributed to inputs (or sets of inputs).
 - Parameter optimization: finding the best set of parameters to optimize output (robustness, temporal stability...)
 - Visual inspection: are the shape of the focus relationship sensitive to changes in parameters?

Application: Robustness analysis

→ Simulate primary extinction and analyze secondary loss of species

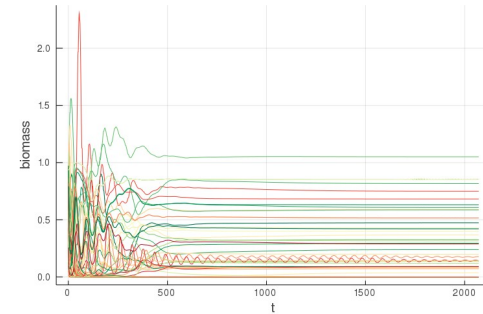
Topological



Only bottom-up secondary extinctions

Dynamical

Meso-predator release after extinction of a top-predator can lead to overexploitation



Bottom-up **and** Top-down secondary extinctions

Application: Robustness analysis

→ Simulate primary extinction and analyze secondary loss of species

1. Simulate the food web dynamics without primary extinctions to remove transient dynamics
2. Choose a deletion sequence (highest to lowest body mass, generality, ...)
3. Remove the first species of the sequence
4. Simulate the food web dynamics and record secondary extinctions
5. Repeat 3 and 4 until end of sequence
6. Calculate R50: number of primary extinctions necessary to remove 50% of the species

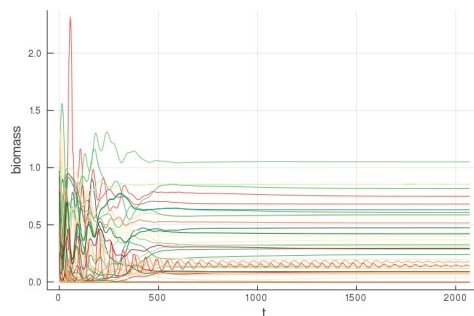
Robustness analysis

Perform a robustness analysis using the BioEnergeticFoodWebs model

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Dynamical

Meso-predator release after extinction of a top-predator can lead to overexploitation



Bottom-up **and** Top-down secondary extinctions

Brief review and discussion

Letter | Published: 20 December 2007

Allometric degree distributions facilitate food-web stability

Sonja B. Otto , Björn C. Rall & Ulrich Brose

Oikos / Volume 117, Issue 2


 Full Access

Food-web connectance and predator interference dampen the paradox of enrichment



Björn C. Rall, Christian Guill, Ulrich Brose

Effects of network and dynamical model structure on species persistence in large model food webs

Authors Authors and affiliations

Richard J. Williams 

How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience

Sonia Kéfi  , Vincent Miele , Evie A. Wieters, Sergio A. Navarrete, Eric L. Berlow

Animal diversity and ecosystem functioning in dynamic food webs

Florian D. Schneider , Ulrich Brose, Björn C. Rall & Christian Guill

Ecology Letters / Volume 13, Issue 2

 Full Access

Understanding food-web persistence from local to global scales

Daniel B. Stouffer , Jordi Bascompte

Research article

Complex food webs prevent competitive exclusion among producer species

Ulrich Brose

Published: 22 July 2008 | <https://doi.org/10.1098/rspb.2008.0718>

Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs

Alva Curtsdotter ^a , Amrei Binzer ^b, Ulrich Brose ^b, Francisco de Castro ^c, Bo Ebenman ^a, Anna Eklöf ^d, Jens O. Riede ^b, Aaron Thierry ^{e,f}, Björn C. Rall ^b

Complexity Increases Predictability in Allometrically Constrained Food Webs

Alison C. Iles ^{*} and Mark Novak [†]

Department of Integrative Biology, Oregon State University, Corvallis, Oregon 97331

Compartmentalization increases food-web persistence



Daniel B. Stouffer and Jordi Bascompte

PNAS March 1, 2011 108 (9) 3648–3652; <https://doi.org/10.1073/pnas.1014353108>

Edited ^{*} by Robert May, University of Oxford, Oxford, United Kingdom, and approved January 7, 2011 (received for review September 24, 2010)

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Effects of network and dynamical model structure on species persistence in model food webs

Authors

Authors and affiliations

Richard J. Williams 

→ Theoretical work

→ Mostly used to study food webs stability/resistance/resilience

What are the model limits? Why is it not used to do empirical studies, like predicting the future of a community under different scenarios?

Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs

Alva Curtsdotter ^a , Amrei Binzer ^b, Ulrich Brose ^b, Francisco de Castro ^c, Bo Ebenman ^a, ^d , Björn C. Rall ^b

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