Food webs made simple: The role of body mass in structuring natural communities

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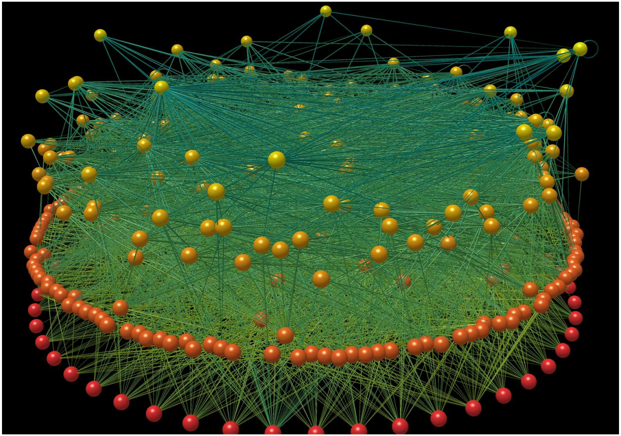
Complexity and stability of ecosystems

Lough Hyne, Ireland

- Natural ecological communities: highly diverse and complex systems
- What structures these communities (and how)?
- What are the mechanisms that stabilise the communities?

Food webs: Networks of predator-prey interactions

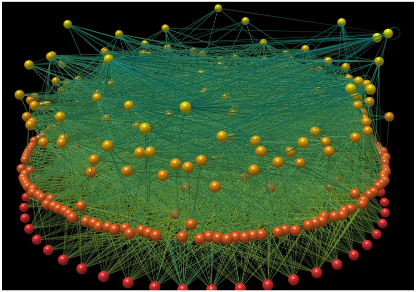


Lough Hyne food web (picture: econetlab)

Overview

- Introduction: Stability of food webs
- Relation between predator-prey size ratio and food-web stability
- How dynamic effects of body size structure food webs

Network structure of food webs



- S nodes (populations)
- L links (trophic interactions) $\rightarrow C = L/S^2$ connectance (network complexity)
- trophic levels, trophic similarity, degree distributions,...

Dynamical system

simplest case: one variable per species, e.g. biomass density B_i

$$\begin{aligned} \frac{dB_i(t)}{dt} &= \text{intrinsic growth (only for basal species)} \\ &+ \text{consumption of other species } (\mathbf{B}) \\ &- \text{being preyed upon by other species } (\mathbf{B}) \\ &- \text{respiration and mortality} \end{aligned}$$

(R. MacArthur, Ecology, 1955)

Dynamical system

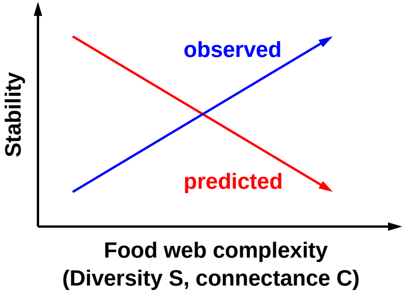
simplest case: one variable per species, e.g. biomass density B_i

$$\frac{dB_i(t)}{dt} = \text{intrinsic growth (only for basal species)}$$
$$+ \text{ consumption of other species } (\mathbf{B})$$
$$- \text{ being preyed upon by other species } (\mathbf{B})$$
$$- \text{ respiration and mortality}$$

(R. May, Nature, 1972)

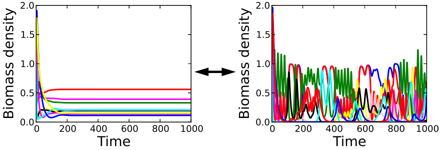
(at least if $a\sqrt{SC} > 1$)

Stability of model food webs



Stability:

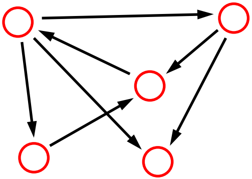
linear stability of fixed points



persistence of species

$$P = \frac{S_{fin}}{S_{ini}}$$

Structure of networks



Random networks:

no restrictions on interactions

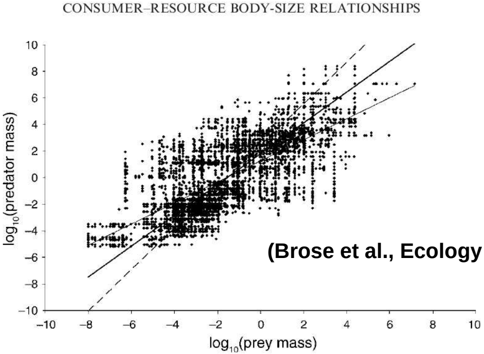
all types of interactions

(exploitation, competition, mutualism)

Structure of networks

Real networks:

feeding hierarchy



(Brose et al., Ecology 2006)

Population dynamics

$$\frac{dB_i(t)}{dt} = \sum_{j\in R_i} e_{ij} g_{ij}(\mathbf{B}) B_i - \sum_{k\in P_i} g_{ki}(\mathbf{B}) B_k - x_i B_i$$

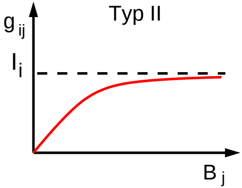
g_{ij} : consumption on prey j

g_{ki} : consumption by predator k

x_i : mass-specific metabolic rate

consumption rate:

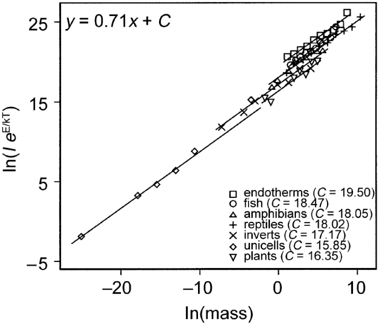
$$g_{ij}(\mathbf{B}) = I_i \frac{f_{ij} B_j}{B_0 + \sum_l f_{il} B_l}$$



I_i: max. mass-specific consumption rate

Mass-specific rates are not constant!

Allometric scaling of physiological rates



(Brown et al., Ecology, 2004)

whole−body metabolism:

$X \sim m^{3/4}$

mass−specific metabolism:

$x \sim m^{-1/4}$

mass−specific max. ingestion:

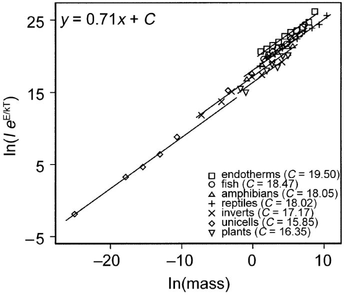
$I = y\,x \rightarrow I \sim m^{-1/4}$

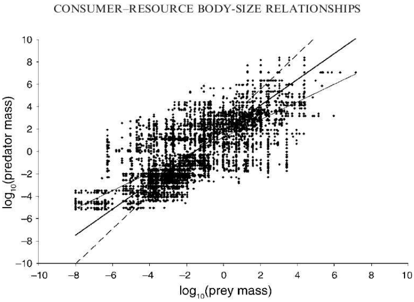
Allometric scaling of physiological rates

$$\frac{dB_i(t)}{dt} = \sum_{j \in R_i} e_{ij} g_{ij}(\mathbf{B}, m_i) B_i - \sum_{k \in P_i} g_{ki}(\mathbf{B}, m_k) B_k - x_i(m_i) B_i$$

$$\max(g_{ij}) \propto m_i^{-1/4} \qquad x_i \propto m_i^{-1/4} \qquad \max(g_{ki}) \propto m_k^{-1/4}$$

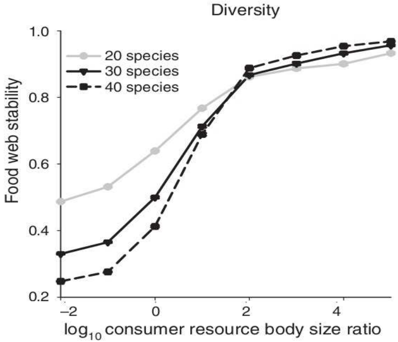
Allometric scaling enhances stability in complex food webs



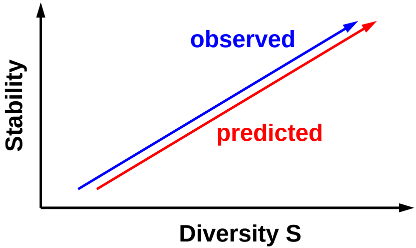


$$\frac{dB_i(t)}{dt} = \sum_{j \in R_i} e_{ij} g_{ij}(\mathbf{B}, m_i) B_i - \sum_{k \in P_i} g_{ki}(\mathbf{B}, m_k) B_k - x_i(m_i) B_i$$

Allometric scaling enhances stability in complex food webs



(Brose et al., Eco. Lett. 2006)



How does it work?

$$\frac{dB_i(t)}{dt} = \sum_{j\in R_i} e_{ij} y x_0 m_i^{-\frac{1}{4}} \frac{f_{ij}B_j}{B_0 + \sum_{l\in R_i} f_{il}B_l} B_i - \sum_{k\in P_i} y x_0 m_k^{-\frac{1}{4}} \frac{f_{ki}B_i}{B_0 + \sum_{l\in R_k}} B_k - x_0 m_i^{-\frac{1}{4}} B_i$$

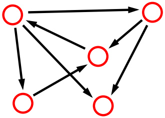
divide by $m_i^{-\frac{1}{4}}$:

$$\frac{dB_i(t)}{m_i^{-\frac{1}{4}} dt} = \sum_{j\in R_i} e_{ij} y x_0 \frac{f_{ij}B_j}{B_0 + \sum_{l\in R_i} f_{il}B_l} B_i - \sum_{k\in P_i} y x_0 \left(\frac{m_k}{m_i}\right)^{-\frac{1}{4}} \frac{f_{ki}B_i}{B_0 + \sum_{l\in R_k}} B_k - x_0 B_i$$

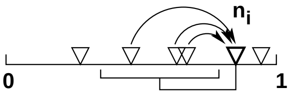
time scale effect: large species have slower dynamics

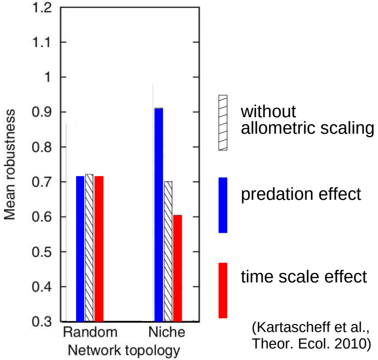
predation effect: reduction of predation pressure if predator is larger than prey network structure:

random model



niche model





(Kartascheff et al., Theor. Ecol. 2010)

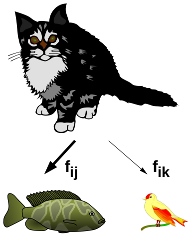
- time scale effect
  negative or neutral
- predation effect
  neutral in random model, positive in niche model

Allometric scaling enhances stability of food webs

Predation effect: release of prey from top-down control

Required: network structure imposing feeding hierarchy

Variable network structure: adaptive foraging dynamics



per capita growth rate:

$$\frac{dB_i(t)}{dt} = G_i(\mathbf{B})B_i$$

consumption rate:

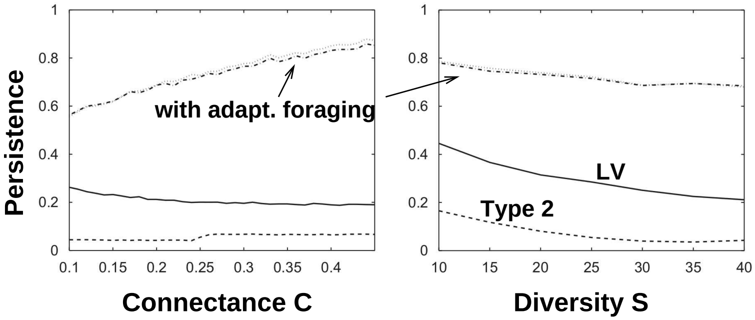
$$g_{ij}(\mathbf{B}) = y_i x_i \frac{f_{ij}B_j}{B_0 + \sum_k f_{ik}B_k}$$

adaptation: replicator dynamics

$$\frac{df_{ij}}{dt} = \kappa f_{ij}\left(\frac{\partial G_i}{\partial f_{ij}} - \sum_k f_{ik}\frac{\partial G_i}{\partial f_{ik}}\right)$$

- evolutioary stable strategy
- time budget constrained: $\sum_j f_{ij} = 1$

Variable network structure: adaptive foraging dynamics



(Uchida and Drossel, J. Theor. Biol. 2007)

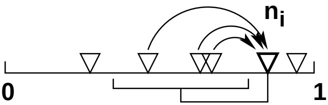
“Positive complexity-stability relation, if complexity means more potential prey species.”

Interactive effects of body-size structure and adaptive foraging

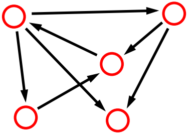
(Heckmann et al., Ecol. Lett. 2012)

network structure:

niche model



random model



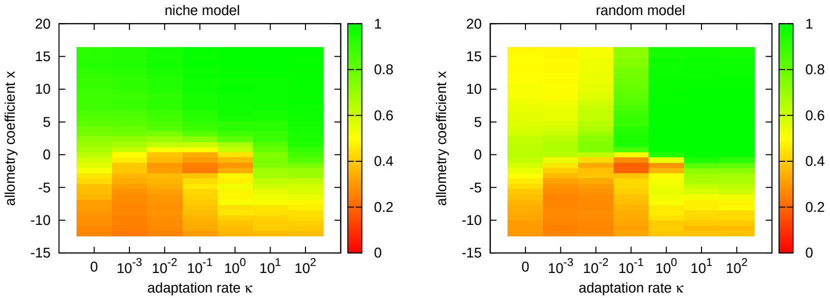
body masses: $m_i = 10^{xn_i}$,   basal species: $m_0 = 1$

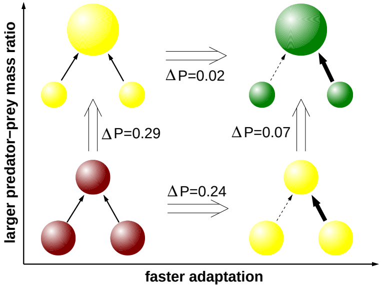
diversity: $S = 30$,   connectance: $C = 0.15$

$$\frac{dB_i(t)}{dt} = \sum_{j \in R_i} e_{ij} g_{ij}(\mathbf{B}, m_i) B_i - \sum_{k \in P_i} g_{ki}(\mathbf{B}, m_k) B_k - x_i(m_i) B_i - \mu_i(B_i, m_i) B_i$$

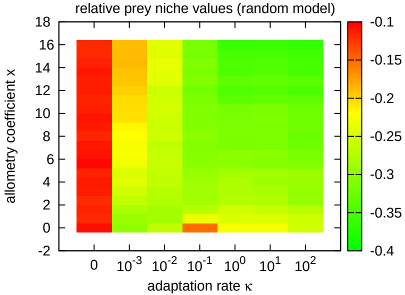
$$\mu_i(B_i, m_i) B_i = \mu_0 m_i^{-1/4} B_i^2$$

Results I: Persistence





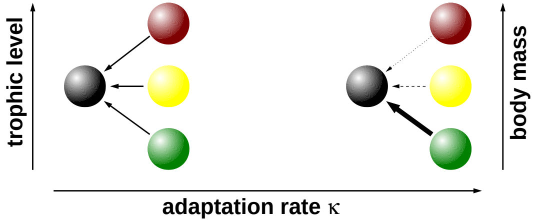
Results II: Network structure



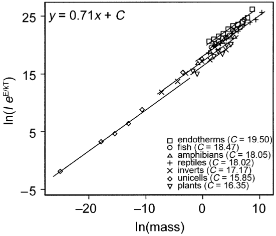
$$\langle n_{\text{prey}} \rangle = \frac{1}{S' - Z'} \sum_{i=Z'+1}^{S'} \sum_{j \in p(i)} f_{ij}(n_j - n_i)$$

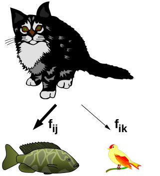
$$\sim \log_{10} \left\langle \frac{m_{\text{prey}}}{m_{\text{pred}}} \right\rangle$$

$$\langle n_{\text{prey}} \rangle^{\text{ini}} \approx 0 \qquad \left\langle \frac{m_{\text{prey}}}{m_{\text{pred}}} \right\rangle^{\text{ini}} \approx 1$$



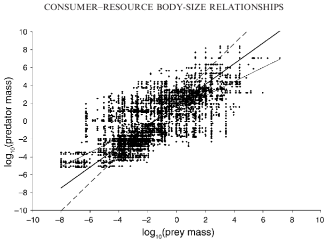
Dynamics explains structure





$$\frac{df_{ij}}{dt} = \kappa f_{ij}\left(\frac{\partial G_i}{\partial f_{ij}} - \sum_k f_{ik}\frac{\partial G_i}{\partial f_{ik}}\right)$$

$$\frac{dB_i(t)}{dt} = \sum_j e_{ij} g_{ij}(\mathbf{B}, m_i) B_i - \sum_k g_{ki}(\mathbf{B}, m_k) B_k - x_i(m_i) B_i - \mu_i(B_i, m_i) B_i$$



Summary

- In size-structured food webs (predators are larger than their prey):
  allometric scaling of physiological rates stabilises the network
- due to a release of the prey from top-down pressure
- interactive effect of foraging adaptation and allometric scaling
- adaptive ordering of random networks
- stable size structure as an emergent phenomenon

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