Evolution of body-size

Eric Edeline: edeline@biologie.ens.fr
Introduction: correlates of body size

Body size variation and covariation with life history traits

Among animals

Rotifers
Size: 0.1-0.5 mm
Lifespan: 10 days

Molluscs (*Arctica islandica*)
Size: 13 cm
Lifespan: 400 years
Introduction: correlates of body size

Body size variation and covariation with life history traits

Among animals

N = 1700 species (http://genomics.senescence.info/species/)
Introduction: correlates of body size

Body size variation and covariation with life history traits

Among plants

**Sequoia sempervirens**
Height: 115 m
Lifespan: 2,200 y

**Chlamydomonas**
Size: 10 μm
Lifespan: minutes to days (sexual and asexual reproduction)
White-toothed pygmy shrew (*Suncus etruscus*)
- 6 cm, 2 g
- Gestation: 27 d
- Clutch size: 6
- Weaning: 17d
- Maturity: 2y
- Lifespan: 3y

Blue whale (*Balaenoptera musculus*)
- 20 to 34 m, 100 to 190 t
- Gestation: 12 mo
- Clutch size: 1 every 3 years
- Weaning:
- Maturity: ~5 y
- Lifespan: >100 y
Body size variation and covariation with life history traits

Among fish

**Gasterosteus aculeatus**
Length: 5-14 cm
Maturity: 1y
Lifespan: 1-8y
Clutch size: 60-400 eggs

**Whale shark *Rhincodon typus***
Size: 20 m, 34 t
Clutch size: few hundreds (ovoviviparity)
Maturity: 30y
Lifespan: 100-150y
Body size variation and covariation with life history traits

**Intraspecific variability**

Southern France:
- Body size: 3-6 cm
- Lifespan: 1 year

Most of the range:
- Body size: 4-7 cm
- Lifespan: 2-4 year

Drizzle Lake in Queen Charlotte Islands:
- Body size: 7-10 cm
- Lifespan: 8 year
Introduction: correlates of body size

Body size variation and covariation with life history traits

Intraspecific variability

*Hippoglossoides platessoides*

Scotland:
- Max size: 25 cm
- Max age: 6 years
- Maturity: 20 cm and 3 years

Grand banks of Newfoundland:
- Max size: 60 cm
- Max age: >20 years
- Maturity at 40 cm and 15 years
Body size is crucial to a number of physiological and ecological processes

\[ Y = Y_0 M^b \]
\[ \log(Y) = \log(Y_0) + b \log(M) \]
Body size is crucial to a number of physiological and ecological processes

Table 1. Examples of relationships between body size and ecological traits, and the potential implications for the structure and/or dynamics of ecological networks

<table>
<thead>
<tr>
<th>Trait and relationship with body size [+/-]</th>
<th>Within nodes</th>
<th>Between nodes</th>
<th>Network</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of size-classes (~cohorts) [+]</td>
<td>Potential for cannibalism and/or cohort dominance</td>
<td>Potential ontogenetic reversals of trophic status</td>
<td>Potential for intraguild predation, self-damping and feeding loops increases towards top of the web</td>
<td>[15,24]</td>
</tr>
<tr>
<td>Numerical abundance [-]</td>
<td>More small than large individuals</td>
<td>Prey are more abundant and are smaller than predators</td>
<td>Trophic pyramid of abundance</td>
<td>[2,9,10,15,23]</td>
</tr>
<tr>
<td>Trophic status [+ ]</td>
<td>Larger individuals are more carnivorous</td>
<td>Prey are smaller than predators</td>
<td>Assimilation efficiency increases towards top of the web</td>
<td>[10,15]</td>
</tr>
<tr>
<td>Diet width [+(-)]</td>
<td>Diet widths expand during ontogeny</td>
<td>High diet overlap among similar-sized species; size constraints on feeding links</td>
<td>Nested vertical hierarchy of feeding niches; size-delimited ‘subwebs’ within the community web</td>
<td>[15]</td>
</tr>
<tr>
<td>Secondary production [+]</td>
<td>Larger individuals are more productive</td>
<td>Production:biomass (PB) ratios are lower for predators than prey</td>
<td>PB ratios decline towards the top of the web</td>
<td>[10]</td>
</tr>
<tr>
<td>Nutrient cycling rate [-]</td>
<td>Larger individuals immobilize nutrients for longer</td>
<td>Larger species have slower return times for nutrients; consumer-driven resource dynamics</td>
<td>Stoichiometric imbalances between resources and consumers</td>
<td>[5,33]</td>
</tr>
<tr>
<td>Species richness [-]</td>
<td>n/a</td>
<td>Small species have more potential competitors and predators</td>
<td>Triangular food webs; greater redundancy at lower trophic levels</td>
<td>[22,70]</td>
</tr>
</tbody>
</table>

*Examples of some of the consequences of these relationships are given in order of increasing scale of organization, from intraspecific (within-node) effects, to effects on pairwise consumer-resource feeding links (between-nodes), to effects that are manifested at the scale of the entire food web (network).*
Introduction: body size and eco-evolutionary feedbacks

Individual body-sizes

Food-web structure

Ecosystem function and stability

Niche construction

Selection
Cope's rule is the tendency of lineages to increase in size over macroevolutionary time.

While the rule has been demonstrated in many instances, it does not hold true at all taxonomic levels, or in all clades.

Cope's rule necessitates that a directional selection favoring a larger size constantly operates on organisms.
Kingsolver & Pfennig (Evolution 2004): a meta-analysis of selection (linear selection gradient $\beta$) on individual body size (plant and animal) and other morphological traits (wingspan, flower size...) supports the view that selection is positive on body size while other traits are at equilibrium.

(n=854, 32 species, 49 studies)
1. Evolutionary benefits to being large

Cope's rule (1896)

- **a. survival**
  - body size
  - other morphological traits

- **b. fecundity**

- **c. mating success**

Frequency

Linear selection gradient
Survival increases with body size in invertebrates, fish, birds, mammals and reptiles (Effects of predation?)

Table 5.1. Allometric relationship between survival and body size in birds, mammals, and reptiles

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Trait</th>
<th>a</th>
<th>b</th>
<th>n</th>
<th>r</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eutherian mammals</td>
<td>Life-span in captivity</td>
<td>2.96</td>
<td>0.20</td>
<td>63</td>
<td>0.77</td>
<td></td>
</tr>
<tr>
<td>Eutherian mammals</td>
<td>Life expectancy at birth</td>
<td>0.23</td>
<td>0.24</td>
<td>29</td>
<td>0.87</td>
<td></td>
</tr>
<tr>
<td>Eutherian mammals</td>
<td>Life expectancy at maturity</td>
<td>0.36</td>
<td>0.24</td>
<td>29</td>
<td>0.87</td>
<td></td>
</tr>
<tr>
<td>Artiodactyls</td>
<td>Life-span</td>
<td>1.33</td>
<td>0.22</td>
<td>14</td>
<td>0.92</td>
<td></td>
</tr>
<tr>
<td>Primates</td>
<td>Life-span</td>
<td>2.45</td>
<td>0.24</td>
<td>14</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td>Carnivores</td>
<td>Life-span</td>
<td>2.85</td>
<td>0.17</td>
<td>17</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td>Heteromyids</td>
<td>Life-span</td>
<td>5.04</td>
<td>-0.15</td>
<td>7</td>
<td>0.46</td>
<td></td>
</tr>
<tr>
<td>Birds</td>
<td>Life-span in captivity</td>
<td>7.62</td>
<td>0.19</td>
<td>58</td>
<td>NG</td>
<td></td>
</tr>
<tr>
<td>Passeriformes</td>
<td>Life-span</td>
<td>3.58</td>
<td>0.26</td>
<td>71</td>
<td>NG</td>
<td></td>
</tr>
<tr>
<td>Nonpasseriformes</td>
<td>Life-span</td>
<td>4.79</td>
<td>0.18</td>
<td>81</td>
<td>NG</td>
<td></td>
</tr>
<tr>
<td>Birds</td>
<td>Adult mortality rate</td>
<td>6.60</td>
<td>0.18</td>
<td>14</td>
<td>0.70</td>
<td></td>
</tr>
<tr>
<td>European birds</td>
<td>Juvenile survival rate</td>
<td>0.27</td>
<td>0.07</td>
<td>56</td>
<td>0.39</td>
<td></td>
</tr>
<tr>
<td>European birds</td>
<td>Adult survival rate</td>
<td>0.38</td>
<td>0.09</td>
<td>107</td>
<td>0.58</td>
<td></td>
</tr>
<tr>
<td>Anseriformes</td>
<td>Adult survival rate</td>
<td>0.24</td>
<td>0.14</td>
<td>18</td>
<td>0.60</td>
<td></td>
</tr>
<tr>
<td>Passeriformes</td>
<td>Adult survival rate</td>
<td>0.34</td>
<td>0.10</td>
<td>32</td>
<td>0.52</td>
<td></td>
</tr>
<tr>
<td>Charadriiformes</td>
<td>Adult survival rate</td>
<td>0.51</td>
<td>0.07</td>
<td>27</td>
<td>0.45</td>
<td></td>
</tr>
<tr>
<td>Reptiles</td>
<td>Life-span</td>
<td>2.99</td>
<td>0.23</td>
<td>NG</td>
<td>NG</td>
<td></td>
</tr>
</tbody>
</table>

Relationships are given in the format $y = ax^b$, where $y$ is survival measured on a scale and $x$ is body weight in grams.


NG: not given.

Roff 1992, p118
Survival increases with body size in invertebrates, fish, birds, mammals and reptiles

**Figure 2** The number of mammal carnivore species that prey upon the savannah ungulates of different body sizes in Serengeti. Adult female body sizes are from published sources\(^{26}\) and provided in Supplementary Information.

(Sinclair et al. 2003 Nature)
Survival increases with body size in invertebrates, fish, birds, mammals and reptiles

Figure 3 The proportion of annual adult mortality accounted for by predation in ten non-migratory ungulate populations for which data were available in the Serengeti ecosystem. There is a threshold in body size of about 150 kg above which predator limitation switches to food limitation. Error bars are 95% confidence limits. Species are: O, oribi; I, impala; T, topi; W, wildebeest; Z, zebra; B, African buffalo; G, giraffe; R, black rhino; H, hippo; E, African elephant. Data are provided in Supplementary Information.

(Sinclair et al. 2003 Nature)
1. Evolutionary benefits to being large

Diet width increases with body size

**Figure 1** The range of weights of mammal prey consumed by carnivores of different sizes in the Serengeti ecosystem. There is a large overlap in diet at small prey sizes. Data are from our unpublished observations and published sources\(^{17,26}\).

(Sinclair et al. 2003 Nature)
1. Evolutionary benefits to being large

Diet width increases with body size

(Claessen et al. 2004, PRSB)
1. Evolutionary benefits to being large

Increased predator attack rate (from speed and range) and decreased handling time (from larger manipulation and digestion capacities)
1. Evolutionary benefits to being large

Fecundity increases with body size in plants and ectotherms

Sexual size-dimorphism and fecundity selection in spiders.
1. Evolutionary benefits to being large

Sexual selection for a larger male size

The “good genes” hypothesis
Benefits from being larger:

- Increased defense against predation (not always true) → reduced mortality selecting for longer life span (positive feedback).
- Increased predation success (not always true).
- Larger diet breadth.
- Increased success in mating and intraspecific competition (contest sexual selection and competition).
- Increased success in interference competition.
- Increased resistance to starvation.
2. Evolutionary costs to being larger

But... Small species are more abundant (EER)

Global size–density relationship plot combining mammals (red circles) and assorted ectotherms (blue squares)
2. Evolutionary costs to being larger

Energy requirements increase with body size

![Graph showing the relationship between ln(metabolic rate $+ e^{E/kT}$) and ln(body mass), with different data points for fish, invertebrates, and unicells. The equations for the lines are $y = 0.70x + 18.24$, $r^2 = 0.97$ for fish; $y = 0.73x + 19.74$, $r^2 = 0.97$ for invertebrates; and $y = 0.74x + 20.89$, $r^2 = 0.79$ for unicells.]

**Figure 1.1** The relationship between temperature-corrected metabolic rate, measured in watts, and the natural logarithm of body mass, measured in grams. Metabolic rate is temperature corrected using the Boltzmann factor, $e^{-E/kT}$, following Eq. (1.2). Data and analyses from Gillooly *et al.* (2001).
2. Evolutionary costs to being larger

Energy requirements increase with body size

Food-chain length is predicted to increase with increasing nutrient level

(Oksanen et al. 1982)
Energy allocation trade-offs

Development time to maturity increases with body size

Resources

Survival for future reproduction

Immediate reproduction

Where does body size come into play here?
2. Evolutionary costs to being larger

Development time to maturity increases with body size

- The trade-off between growth and (immediate) reproduction is "the best confirmed broad-sense phenotypic trade-off" (Stearns 1992)
- Increased body size increases survival and future fitness at the cost of reducing present fitness.
2. Evolutionary costs to being larger

Development time to maturity increases with body size

(a) ![Graph](image1)
(b) ![Graph](image2)

**Figure 1.3** The relationship between temperature-corrected hatching rate, measured in 1/days, and the natural logarithm of body mass, measured in grams, for zooplankton eggs in the laboratory (panel A) and fishes in the field (panel B). Hatching rate is temperature-corrected using the Boltzmann factor, \( e^{-E/kT} \), following Eq. (1.2). Data and analyses from Gillooly et al. (2002).

- Longer generation times.
- Reduced ability of populations to persist if mortality increases.
- Slower rate of evolution and, consequently, a reduced ability to adapt to sudden change.
- Extinction risk increases with body size.
2. Evolutionary costs to being larger

Extinction risk increases with body size

Diffusion vs. increased extinction trade-off fits mammal body size distribution

A schematic illustrating a simple cladogenetic diffusion model of species body-size evolution, where the size of a descendant species $x_D$ is related to its ancestor's size $x_A$ by a multiplicative factor $\lambda > 0$ (reflecting Cope's rule).

The model reproduces the distribution of 4002 mammal species from the late Quaternary.

Clauset & Erwin 2008 Science
Bergmann's rule: smaller is better in warm habitats
Karl Georg Lucas Christian Bergmann (1814 – 1865)

- Heat loss of an organism is proportional to its surface-to-volume ratio.
- There is a **selective advantage to a smaller size and associated higher body surface-to-volume ratio in warm areas**, and *vice versa*.
- Works fine for endotherms (mammals and birds)...

Latitudinal Variation in White-Tailed Deer
(*Odocoileus virginianus*) (Cervidae)
2. Evolutionary costs to being larger

Bergmann's rule: smaller is better in warm habitats
Karl Georg Lucas Christian Bergmann (1814 – 1865)

… but also applies well to **ectotherms** (99% of species on earth): temperature-size rule.

![Bar chart showing thermal effect on body size](Angiletta 2009, after Atkinson 1994.)
2. Evolutionary costs to being larger

Temperature-size rule and the thermal dependency of metabolic rates

\[
\begin{align*}
I &= f_I a_I(T_0) m_c^{-0.25} e^{E_I(T-T_0)/kTT_0} \\
M &= a_M(T_0) m_c^{-0.25} e^{E_M(T-T_0)/kTT_0}
\end{align*}
\]

\(I\) = ingestion  \\
\(M\) = maintenance  \\
\(f\) = realized fraction of the maximal rates  \\
\(a(T_0)\) = intercepts of the allometric relationships, maximum sustainable rates (physiological maxima) measured at \(T_0\).  \\
\(E\) = activation energies  \\
\(k\) = Boltzmann constant

From Vasseur & McCann Am Nat 2005
2. Evolutionary costs to being larger

Temperature-size rule and the thermal dependency of metabolic rates

![Graph showing the relationship between temperature and metabolic rates.](image)
2. Evolutionary costs to being larger

Other costs

 Increased parasitism with increased growth rate (well documented trade-off).

Reduced agility:

Reduced swimming efficiency in faster growing individuals
2. Evolutionary costs to being larger

Costs from being larger:

• Increased energy requirements → reduced population densities (EER) → higher demographic stochasticity and extinction risk.

• Increased development time → reduced population growth rate and ability to tolerate increased mortality (increased extinction risk).

• Lower energetic efficiency under warming climate (see also below)

• Increased energy allocation to somatic growth and decreased allocation to maintenance (immunity, see below).
Increased mortality from predation selects for increased investment and reproduction at a smaller size.

Increased mortality from predators induces earlier maturity and reduced body size in guppies (Reznick & Ghalambor CJFAS 2005)
3. Body size evolution in food webs: predation

Wild-caught guppies (Reznick & Ghalambor CJFAS 2005)

Fig. 2. Modified from Fig. 2 in Reznick et al. (1996b). Least squares means (±1 SE) of life history traits from high- and low-predation sites on the north slope (solid line) and south slope (broken line) of the Northern Range Mountains. (a) Number of developing offspring per female adjusted for the females’ somatic dry weight; (b) dry weight of developing offspring adjusted for their stage of development; (c) average size of mature males; (d) reproductive allotment of females with developing offspring adjusted for the stage of development of the offspring.
Fishery for cod (*Gadus morhua*) in Newfoundland and Labrador

Stock collapse was concomitant with a drop in size at maturity.

The addition of a top predator (human) at the top of the food-web induces a drop in body sizes of the (former) top predator.
Reinforcement feedback between life history evolution and the trophic position

Instantaneous rate of natural mortality (M) of cod in the southern Gulf of St. Lawrence. Heavy horizontal line is an assumed value; circles are estimates for the periods delimited by light horizontal lines. Vertical lines are ±2 SE. Grey lines show the trend in length at 50% maturity for females (solid line) and males (dashed line).

"The current high natural mortality of SGSL cod appears to be primarily a cause, rather than a consequence, of the continued early maturation in this population, now replacing fishing mortality as the agent of selection favouring early maturity."

Swain 2011
Small size ↔ low trophic level: cause and consequence?

Results on cod suggest a positive feedback loop between life history evolution and the trophic position:

Evolutionary response to predation tends to increase predation mortality and thus further lower the trophic position.
3. Body size evolution in food webs: predation

When predators select for a smaller body size by preying on immature prey: fast growth to size refuge

Crenicichla alta

Occasionally feeds on juvenile guppy and tends to select for fast growth, but confounding effects of habitat productivity (see work by Reznick et al.)

Rivulus hartii

Feeds on any guppy and induces reduced growth and increased reproduction in guppies
3. Body size evolution in food webs: predation

Antagonistic selection from two predators in Windermere

Cannibals and fishermen in Windermere pike

**Cannibals** select against small body size (preying on immature fish), while **gillnets** select against large body size (preying on mature fish)  
(Carlson et al. Ecol Lett 2007)
3. Body size evolution in food webs: predation

Antagonistic selection from two predators in Windermere

(FISHERY) directional selection for being smaller and growing slower

(NATURAL) directional selection for being larger and growing faster (CANNIBALISM)

(Carlson et al. Ecol. Lett. 2007)
Presumably increased cannibalism

At the start of the time series fishery selection was likely dominant

At the end of the time series natural selection was likely dominant

→ Expectation of nonlinear changes in pike somatic growth rate with first a decrease and then an increase in somatic growth rate
Growth rate responded to the dominant selective force

Antagonistic selection from two predators in Windermere

Nonlinear trend in individual lifetime somatic growth corrected for the effects of basin productivity, sex, temperature, pike numbers and perch abundance [estimated from back-calculated length-at-age for ~14,000 individual pike using a generalized additive mixed-effects model, GAMM, mgcv library of R (Wood, 2006)]

Growth rate responded to the dominant selective force

(Edeline et al. PNAS 2007)
3. Body size evolution in food webs: predation

Antagonistic selection from two predators in Windermere

Reproductive investment decreased in proportion to the relaxation of fishing pressure

(Edeline et al. PNAS 2007)
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere

INTRAGUILD PREDATION + cannibalism
Antagonistic selection from predators and parasites in Windermere

INTRAGUILD PREDATION + cannibalism

+ antagonistic selection from pike and pathogen on perch

(1963) 1976
10^6 perch killed
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere

By 1977, perch showed no external sign of the disease
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere

The pike/perch ratio has increased before pathogen expansion
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere

Raw age and size data support the prediction that predators and pathogens induced antagonistic selection on perch body size and life history.
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere

\[ BL_{i}^{\text{wc}} = \beta_0 + f_1(A_i) + \beta_1 \text{Bas}_i + \beta_2 S_i + \beta_3 T_i + \beta_4 P_h + \beta_5 P_i + \beta_6 P_h \times T_i + \beta_7 P_i \times T_i + f_2(YC) + \varepsilon_i \]
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere

What may be the consequences in terms of food-web interactions?
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere.

![Graph showing perch numbers over time in North and South basins.](image)

- North basin
  - Small perch
  - Large perch
- South basin

Perch numbers (x10^5)

Year: 1950 to 1990
Antagonistic selection from predators and parasites in Windermere

Paradoxically, pathogen expansion favored pike
Pike recruitment rate increased after pathogen expansion, and the effect of perch on juvenile pike changed from – to +
Pathogen expansion coincided with a peak in the predation pressure in both basins.

Pike might have favored pathogen expansion by increasing the proportion of large, fast-growing but pathogen-sensitive perch!
3. Body size evolution in food webs: predation

Antagonistic selection from predators and parasites in Windermere

Perch body size and life history

Niche construction

2

Food-web structure

1

Selection

3

Trophic interactions

Population dynamics
Modeling antagonistic selection from predators and parasites: Non-evolutionary, competition-mediated effects
Case 1: competition among juvenile prey only

Invasion of an adult-specialized predator (Pa) is only successful after establishment of a juvenile-specialized predator (Pj). Pj reduces competition in J and allows increased growth and reproduction (increased A): predator-induced density-dependent life-history change in prey generates mutualism among specialized predators.
3. Body size evolution in food webs: predation

Modeling antagonistic selection from predators and parasites: Non-evolutionary, competition-mediated effects

Left panels (competition for resources among J): Pj mortality influences the extent to which Pj facilitates A and Pa.
Right panel: competition for resources among A.
3. Body size evolution in food webs: predation

Modeling antagonistic selection from predators and parasites: Non-evolutionary, competition-mediated effects

![Graph showing death rate of predators and juveniles](image)

**Fig. 3.** Equilibrium community composition depending on death rates of juvenile- and adult-specialized predators when juvenile and adult consumers occupy different feeding niches. *(Left)* Adult consumers have unlimited food supply, whereas juveniles compete for limiting resource (model I). *(Right)* Juvenile consumers have unlimited food supply, whereas adults compete for limiting resource (model II). $RC$, consumer-resource equilibrium; $RCP_J$, juvenile specialized predator-consumer-resource equilibrium; $RCP_A$, adult specialized predator-consumer-resource equilibrium; $RCP_JP_A$, all species equilibrium.
3. Body size evolution in food webs: predation

Modeling antagonistic selection from predators and parasites: Non-evolutionary, competition-mediated effects

Coexistence of 3 stage-specific predators on a 4-stage prey species. Conclusions are not sensitive to the number of prey stages and specialized predators.
3. Body size evolution in food webs: predation

Modeling antagonistic selection from predators and parasites:
Non-evolutionary, competition-mediated effects

• Predators specializing on prey developmental stages that experience little competition may be able to persist only in the presence of another predator species that attacks and reduces the food limitation in the prey life stage which suffers most from scramble competition.

• Coexistence of two predator species is then possible for considerable ranges of their background mortalities for which one of them could not survive on its own.

• Just as in the Windermere example, negative effects of density-dependent competition are overwhelmed by the positive effects of size-dependent selection.
Interspecific competition induces character displacement and favors constant size ratios.

Large niche overlap

Small niche overlap
Interspecific competition induces character displacement and favors constant size ratios.
4. Body size evolution in food webs: exploitative competition

Interspecific competition induces character displacement and favors constant size ratios.

![Graph showing body mass of different species](image_url)
Interaction between temperature and competition on body size

A test using 50 river fish species
Interaction between temperature and competition on body size

\[ I = f_I a_I(T_0) m_c^{-0.25} e^{E_I(T - T_0)/kT_0} \]
\[ M = a_M(T_0) m_c^{-0.25} e^{E_M(T - T_0)/kT_0} \]

4. Body size evolution in food webs: exploitative competition
Interaction between temperature and competition on body size
Interaction between temperature and competition on body size
Interaction between temperature and competition on body size
5. Evolutionary emergence of size-structured food-webs

Evolutionary emergence of size-structured food webs
(Loeuille & Loreau 2005)

Can we explain the emergence of size-structured food webs from simple, size-dependent processes?

Body size-dependent components of the model

Predation rate from species of size 10 on species in the interval 6-10

Interference competition rate between a species of size 10 and other species

Predation rate from species in the interval 10-14 on a species of size 10

Production rate per unit mass $f$

Mortality rate per unit mass $m$

\[
f(x) = f_0 x^{-0.25}
\]

\[
m(x) = m_0 x^{-0.25}
\]
5. Evolutionary emergence of size-structured food-webs

Evolutionary emergence of size-structured food webs
(Loeuille & Loreau 2005)

• The initial population consumes inorganic nutrient.

• At each time step, a mutation (new species) is produced at rate $10^{-6}$ per unit mass.

• The newly created species has a body size drawn randomly in the interval $[0.8x, 1.2x]$, where $x$ is the body size of the mother population.

• The initial biomass of the mutant is $10^{-20}$, which is also the threshold biomass below which any population is assumed to go extinct.

• Mutants are eliminated if they have a low fitness or through demographic stochasticity. If a mutant invades, it may coexist with other populations or eliminate some other population(s).

• The trophic position is defined as the average trophic position of prey weighted by their nutrient proportion in the diet, plus one.

• Niche width $nw$ is defined as $s^2/d$, ranging from 0.5 to 5. This is the degree of predator generalism.
• Competition intensity is given by $\alpha_0$, ranging from 0 to 0.5.
The evolution of simulated food webs during $10^8$ time steps for three values of niche width ($nw$) and competition intensity ($\alpha_0$). Community structure rapidly emerges and stabilizes.
5. Evolutionary emergence of size-structured food-webs

Evolutionary emergence of size-structured food webs
(Loeuille & Loreau 2005)

- Competition strength ($\alpha_0$) and niche width (nw, degree of generalism of predators) are key parameters to the final community structure.

- Predation favors the emergence vertical diversity (chain length), while competition favors the emergence of horizontal diversity (omnivory and connectance).
5. Evolutionary emergence of size-structured food-webs

Evolutionary emergence of size-structured food webs
(Loeuille & Loreau 2005)

- The variety of emerging structures is comparable with empirical observations of real ecosystems.

- Food webs with distinct trophic levels are commonly found in freshwater ecosystems.

- Food webs with a more continuous trophic structure may be more common in soil terrestrial or marine ecosystems.

Comparisons with documented food webs. Niche width and competition intensity that lead to food-web properties (chain length, connectance, ominovory...) that best fit those of seven well documented food webs (BB, Bridge Brook Lake; CB, Chesapeake Bay; CD, Coachella Desert; LR, Little Rock Lake; SM, St. Martin Island; SP, Skipwith Pond; and YE, Ythan Estuary).