Structural sensitivity:

predator-prey models to food webs, through Dynamic Energy Budget theory

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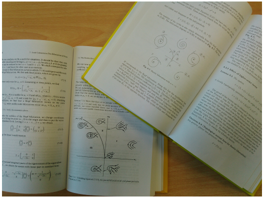
[2] Vrije Universiteit, Amsterdam, Netherlands

6th September 2016, MPDE'16, Marseille

credit : G.C.

assumptions



validation

predictions

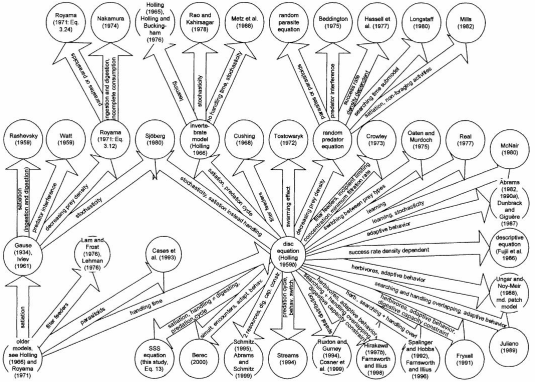
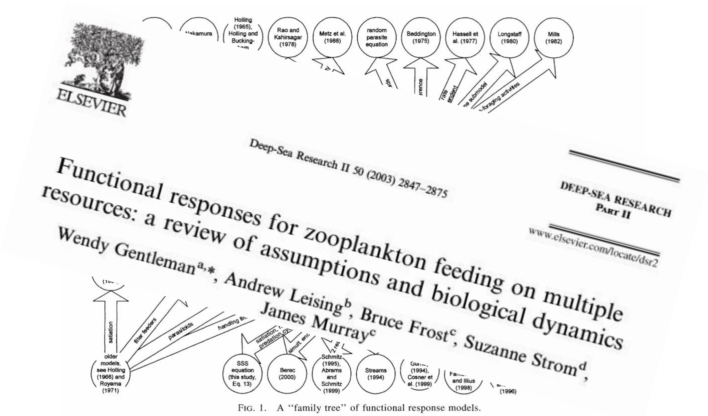


FIG. 1. A "family tree" of functional response models.

(Jeschke et al., 2002)

encounter / attack, handling, digestion / metabolism, spatial heterogeneity, individual variability, collective behaviour, ...

Assumptions ⇒ simplifications (e.g. : predation)



(Jeschke et al., 2002)

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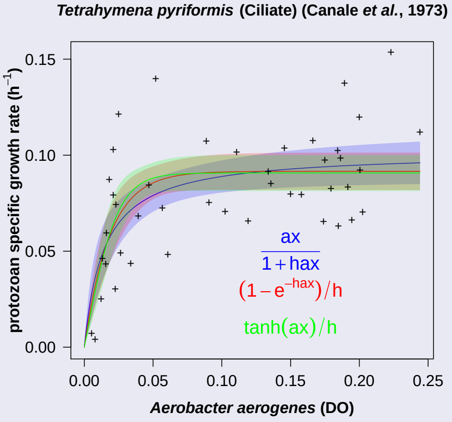
Modelling predation at population scale



functional response

- amount of prey eaten / unit of predator / time unit

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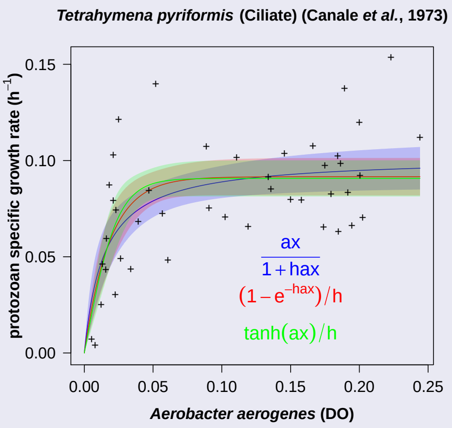
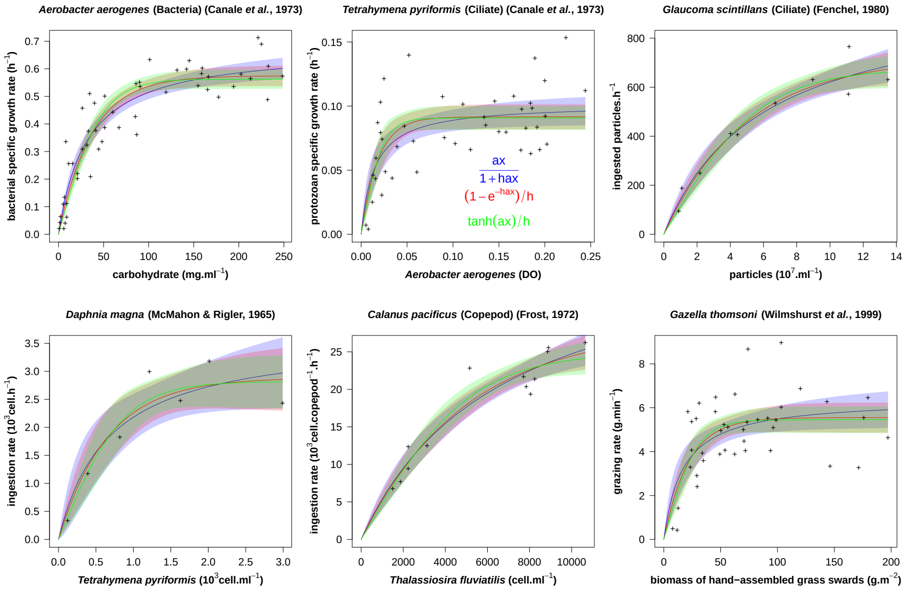


functional response

- amount of prey eaten / unit of predator / time unit
- 3 functions with the same mathematical properties ⇒ same assumptions on **process shape**
- different assumptions on **underlying mecanisms**

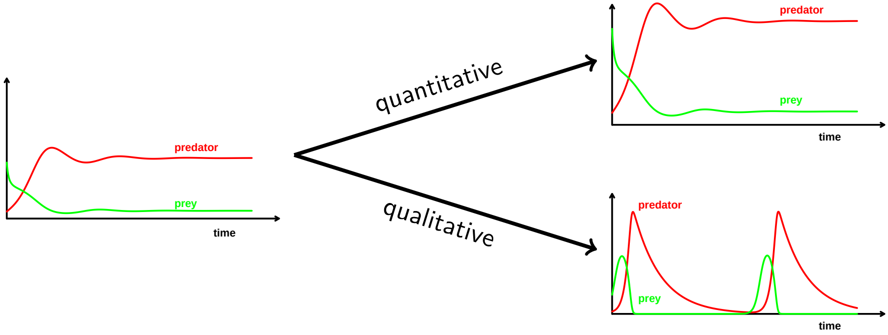
Modelling predation at population scale



Structural sensitivity

model change ⇒ change in predicted dynamics

- quantitative change (e.g. equilibrium value)
- qualitative change in dynamics (bifurcation) *(Kuznetsov, 2004)*



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what is the problem ?

- functions having the same mathematical properties, fit data, with biological justification ⇒ different predictions

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- **functional response** in predator-prey, food chain and biogeochemical models

  (Myerscough et al., 1996, Gross et al., 2004, Fussmann & Blasius, 2005, Anderson et al., 2010, Cordoleani et al., 2011, M. Baklouti, pers. comm.)
- infection in a host-pathogen model *(Wood & Thomas, 1999)*
- co-limitation in a multi-nutrient model *(Poggiale et al., 2010)*

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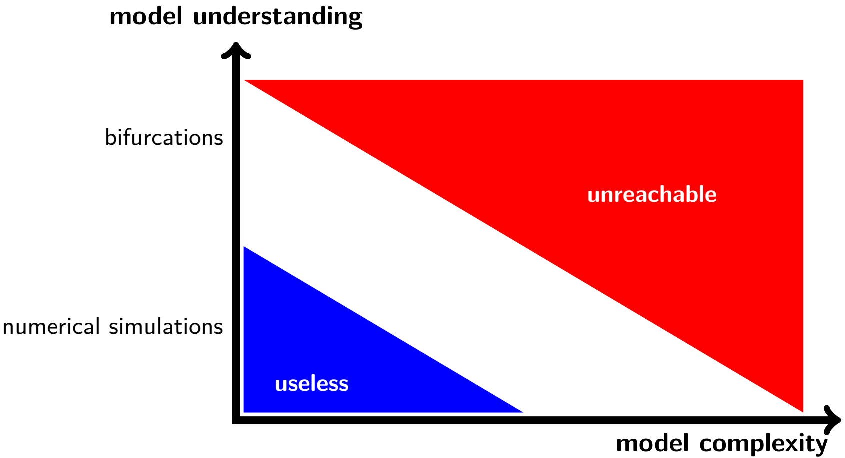
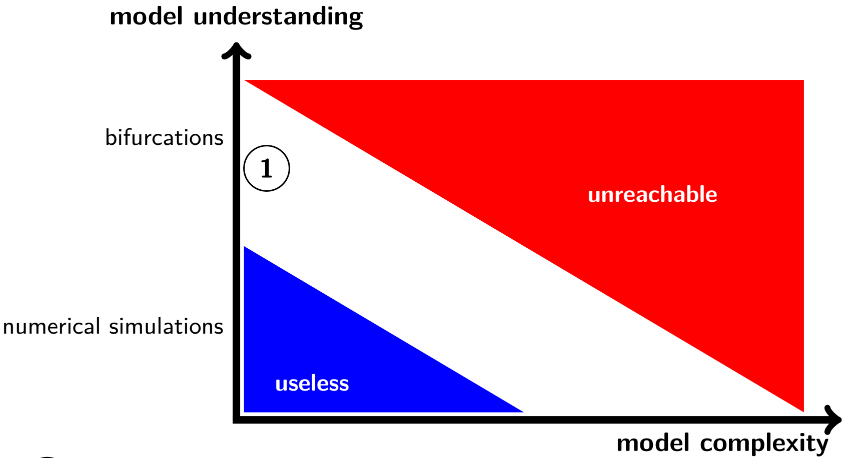
previous studies : few state variables, “simple” dynamics (one stable state)

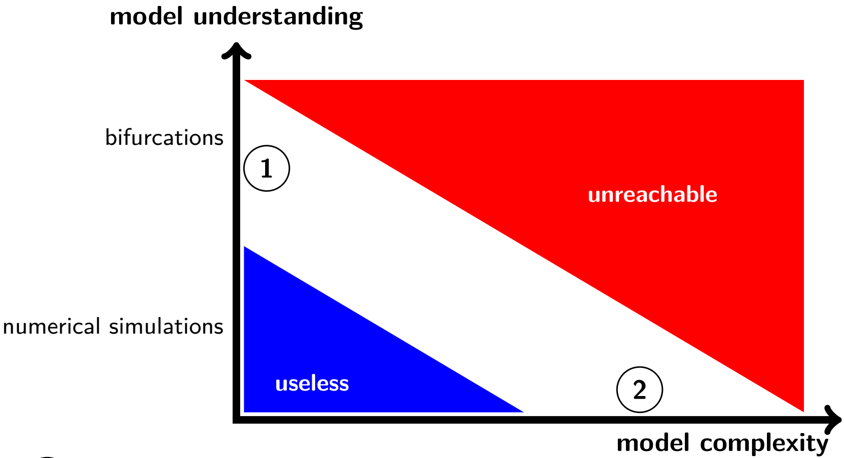

model understanding
bifurcations
numerical simulations
unreachable
useless
model complexity

Structural sensitivity : ± complex models



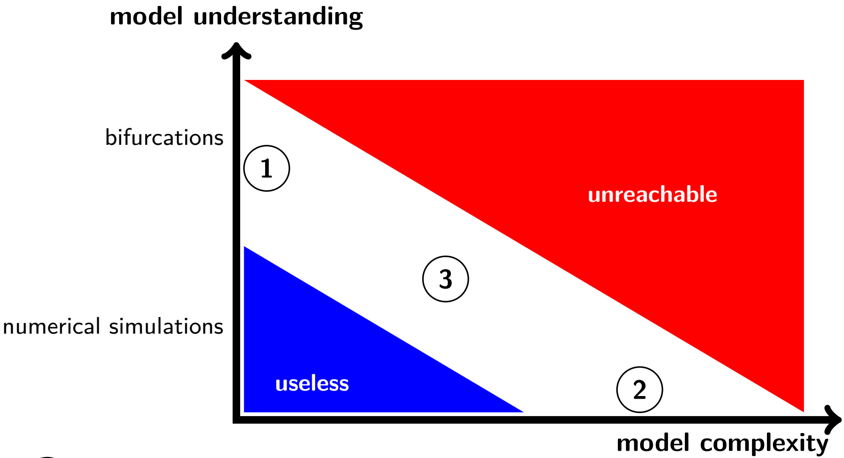
1 predator-prey system : multiple stable states & **resilience**

Structural sensitivity : ± complex models



1. predator-prey system : multiple stable states & **resilience**
2. food webs : predation vs **trophic complexity**

Structural sensitivity : ± complex models



1. predator-prey system : multiple stable states & **resilience**
2. food webs : predation vs **trophic complexity**
3. predator-prey system : predation vs details on **metabolism**

Predator-prey model : Bazykin (1998)

$$
\begin{cases}
\dfrac{dB_{prey}}{d\bar{t}} = \left[\lambda \bar{q}^{\xi} - \alpha - \beta\omega B_{prey}\right] B_{prey} - \bar{G}^{\xi}(B_{prey}) B_{pred} \left(\dfrac{M_{pred}}{M_{prey}}\right)^{-0.25} \\[2em]
\dfrac{dB_{pred}}{d\bar{t}} = \left[\lambda \bar{G}^{\xi}(B_{prey}) - \alpha - \beta B_{pred}\right] B_{pred} \left(\dfrac{M_{pred}}{M_{prey}}\right)^{-0.25}
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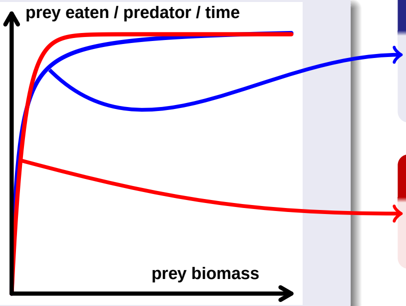


Holling (1959) : handling

$$\bar{G}^H = \frac{a^H B_{prey}}{1 + h^H a^H B_{prey}}$$

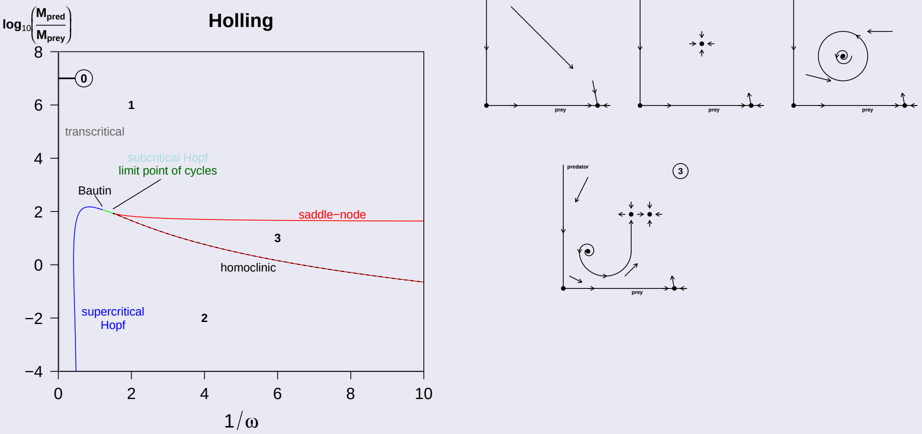
Ivlev (1955) : satiation

$$\bar{G}^I = \left(1 - e^{-h^I a^I B_{prey}}\right) / h^I$$

(Aldebert et al., in press a)

Bifurcation diagram with Holling

body mass ratio



⟶ prey's carrying capacity ⟶

(modified from Aldebert et al., in press a)

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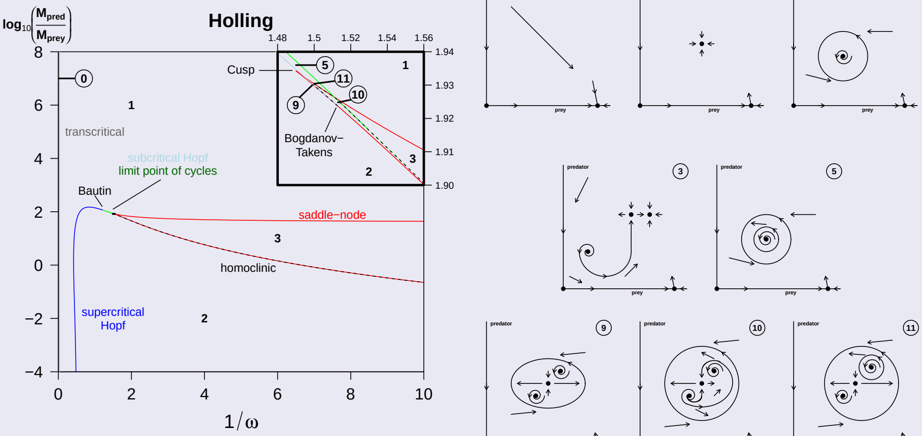

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Bifurcation diagram with Ivlev

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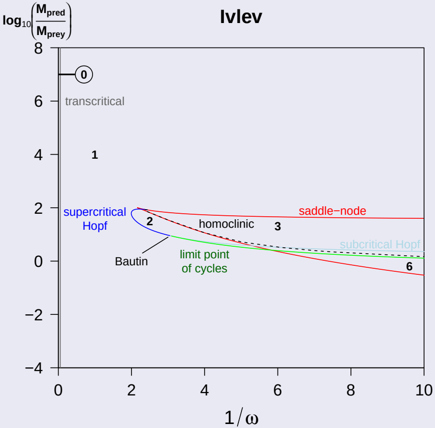

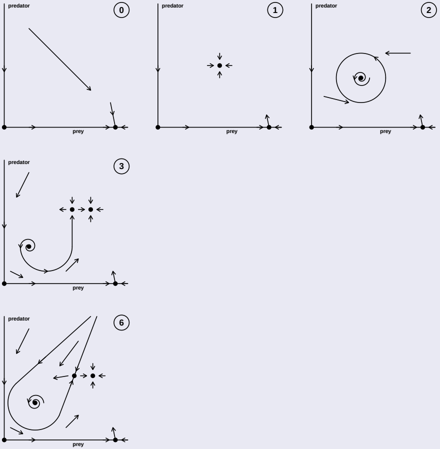

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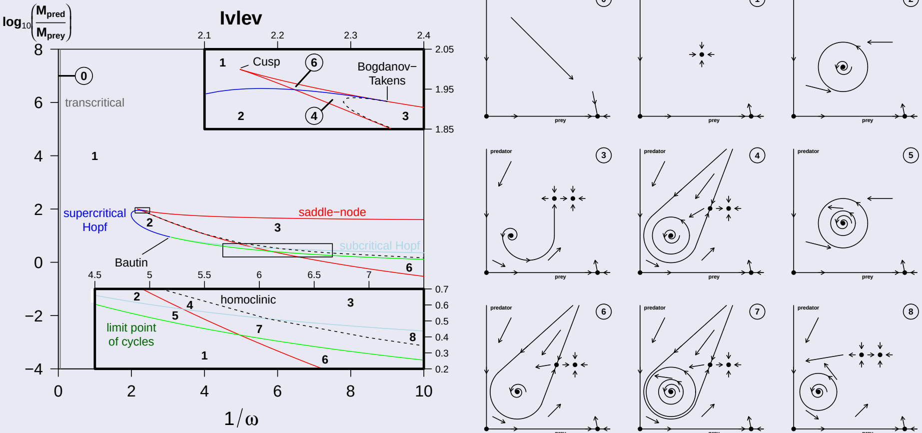

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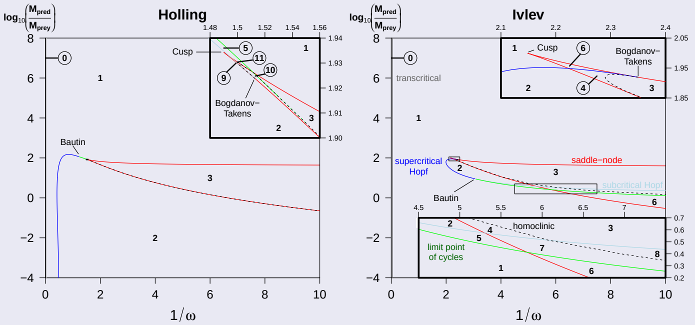
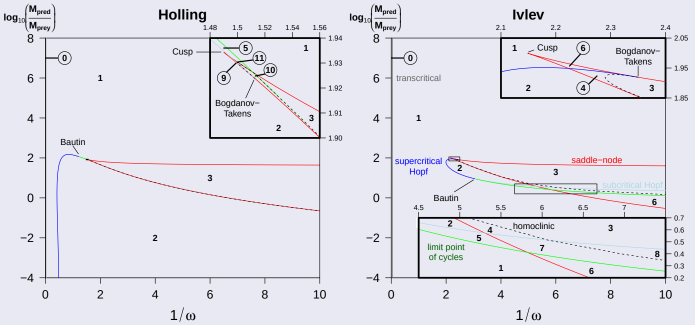


main differences

- stable equilibrium vs stable limit cycle : 26.0 % – 49.4 %

(modified from Aldebert et al., in press a, in prep. b)



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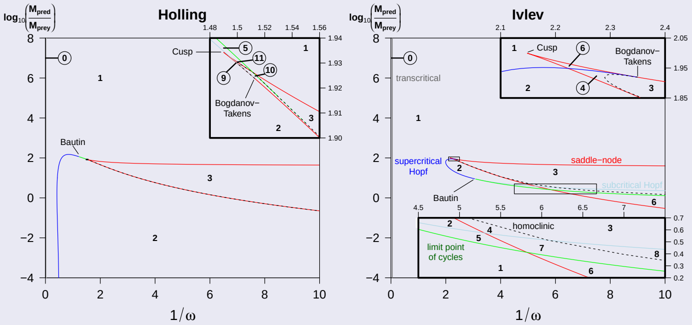
- multiple attractors (up to 3) with Ivlev : 0.1 % – 14.3 % NEW

(modified from Aldebert et al., in press a, in prep. b)

Bifurcation diagram : Holling vs Ivlev



main differences

- stable equilibrium vs stable limit cycle : 26.0 % – 49.4 %
- multiple attractors (up to 3) with Ivlev : 0.1 % – 14.3 % NEW
- continuous switch : degenerated Bogdanov-Takens bifurcation (codim 3)

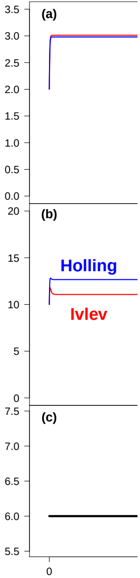
(modified from Aldebert et al., in press a, in prep. b)

Resilience in changing environmental conditions

predator

prey

prey carrying capacity



(Aldebert et al., in press a)

≈ initial prediction

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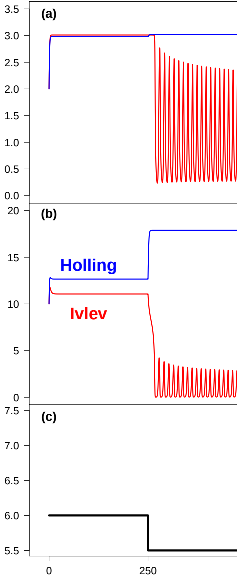

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$\approx$ initial prediction

$\neq$ response perturbation

Resilience in changing environmental conditions

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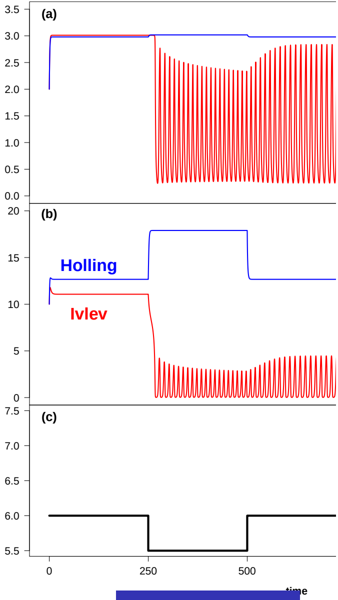


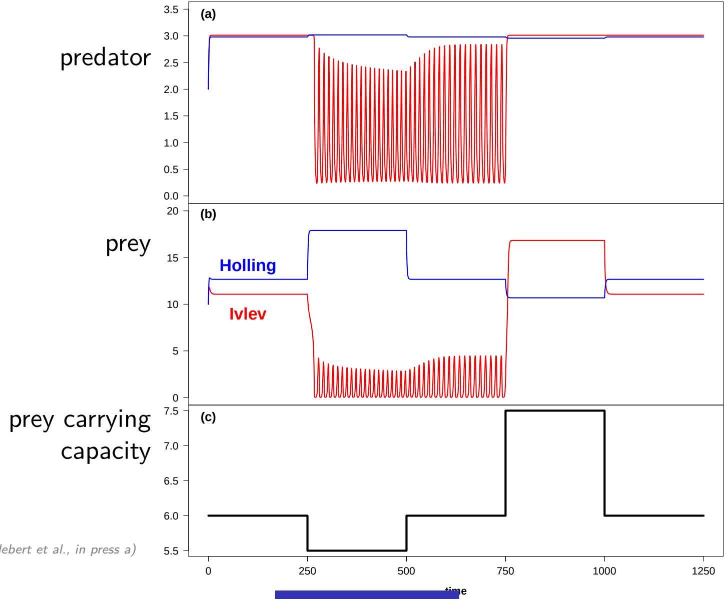
(Aldebert et al., in press a)

$\approx$ initial prediction

$\neq$ response perturbation

$\neq$ resilience,

Resilience in changing environmental conditions



(Aldebert et al., in press a)

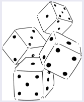
≈ initial prediction

≠ response perturbation

≠ resilience, hysteresis

Structural sensitivity in food webs

millions of theoretical networks (20-60 species, connectance : 0.1-0.3)



- randomly built using “niche model” $\Rightarrow$ empirically consistent structural properties *(Williams & Martinez, 2000, 2004 ; Cattin et al., 2004 ; Allesina et al., 2008)*
- structure $\Rightarrow$ build and parameterize a dynamical system

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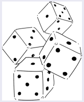

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- structure ⇒ build and parameterize a dynamical system

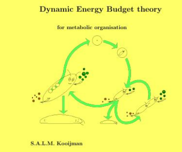
		persistence	equilib. / oscillations
trophic	# species	**0.76**	NS
complexity	connectance	0.37	0.36
	formulation	-0.17	**0.82**
functional response	maximum slope	0.12	-0.22
	maximum rate	0.07	0.07

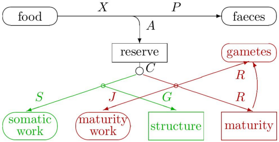
TABLE : correlation coefficients

(≈ 6.10^7 food webs were simulated to obtain this table)
computational effort : 3 years.processors

(Aldebert et al., in press b)

Structural sensitivity and metabolism : DEB theory





- focus on the individual, based on mechanistic assumptions on metabolism
- same framework for most species, metabolic classification of species

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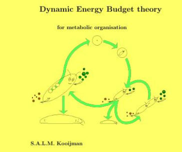

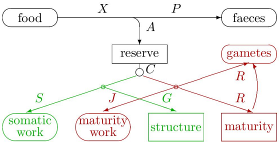

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structural sensitivity

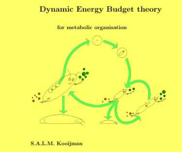
- chemostat data ⇒ ± detailled models with a coherent theoretical framework

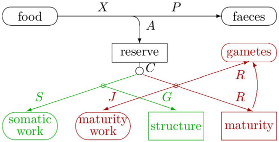
  (Canale et al., 1973, Dent et al., 1976, Kooi & Kooijman, 1994b)

- multiple stable states in DEB model (reserve and maintenance)

(Aldebert et al., in prep. a)

Structural sensitivity and metabolism : DEB theory





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  (Canale et al., 1973, Dent et al., 1976, Kooi & Kooijman, 1994b)
- multiple stable states in DEB model (reserve and maintenance)
- influence of **metabolism > functional response**
- change of functional response : no new bifurcations (and dynamics) if **minimum of biological realism** (maintenance/mortality, explicit resource)

(Aldebert et al., in prep. a)

Concluding remarks and perspectives

Conclusion

- predator-prey model : structural sensitivity affects the type and number of stable states $\rightarrow$ affects the **predicted resilience** of the system
- trophic complexity $\rightarrow$ food web persistence,
  functional response $\rightarrow$ food web variability
- DEB : details on metabolism $\searrow$ structural sensitivity to functional response

Concluding remarks and perspectives

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- trophic complexity $\rightarrow$ food web persistence,
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- DEB : details on metabolism $\searrow$ structural sensitivity to functional response

Perspectives (Predictive Ecology group, UZH, Zürich)

- **quantification method** with multiple stable states (ongoing work)
- structural sensitivity and resilience in food webs, other networks
- dealing with **uncertainty in predictions** due to model construction

Thank you for your attention ! ! !

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Original Research Article

Structural sensitivity and resilience in a predator–prey model with density-dependent mortality

C. Aldebert *, D. Nerini, M. Gauduchon, J.C. Poggiale

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Does structural sensitivity alter complexity–stability relationships?

C. Aldebert *, D. Nerini, M. Gauduchon, J.C. Poggiale

EXTRA-SLIDES

Switch Holling - Ivlev : $\bar{G}^{\xi} = \xi \bar{G}^{H} + (1 - \xi) \bar{G}^{I}$

(Aldebert et al., in prep b)

Switch Holling - Ivlev : $\bar{G}^{\xi} = \xi \bar{G}^{H} + (1-\xi)\bar{G}^{I}$

Bogdanov-Takens de point triple : forme normale

$\Rightarrow$ forme normale : Bob Kooi

(Baer, Kooi, Kuznetsov, Thieme, 2006)

$$\begin{cases} \dfrac{d\xi}{dt} &= \eta \\ \dfrac{d\eta}{dt} &= -\mu_1 - \mu_2\xi + \nu\eta + \beta\xi\eta - \xi^3 - \eta\xi^2 \end{cases}$$

(Aldebert et al., in prep b)

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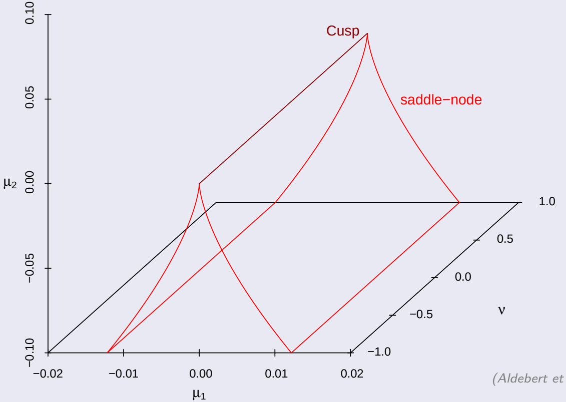

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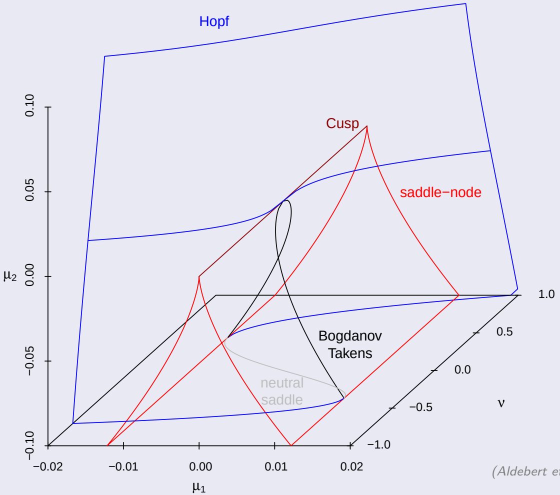

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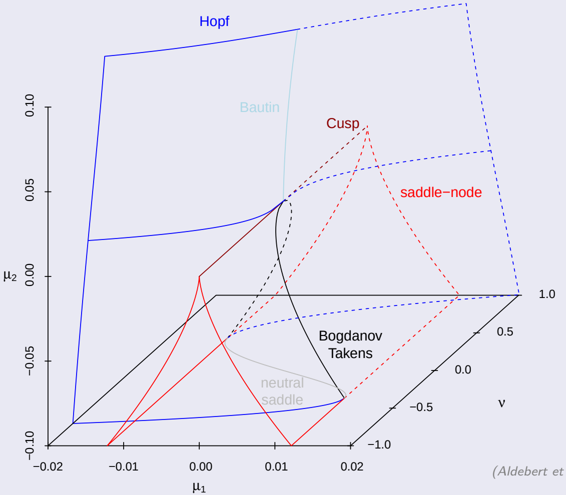

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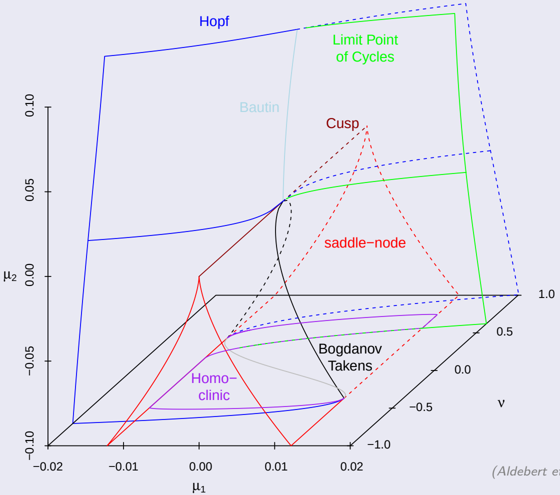

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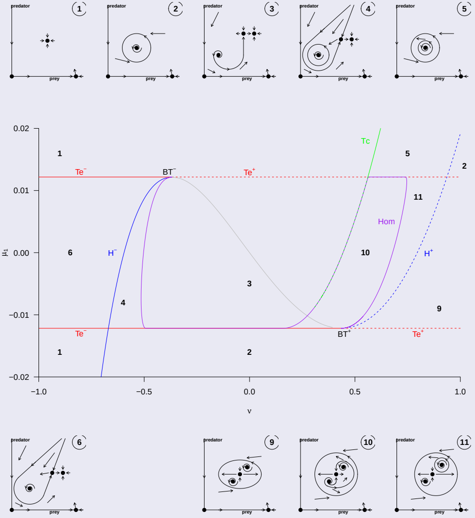

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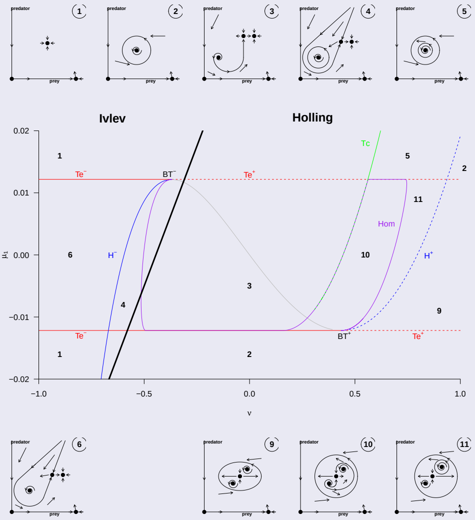
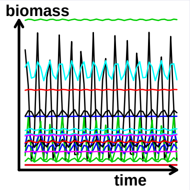


(Aldebert et al., in prep b)

Structural sensitivity vs. complexity-stability

dynamics



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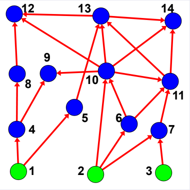
graph



+

ODEs

$$
\left\{
\begin{aligned}
\frac{dB_1}{dt} &= \left[\lambda q^{\phi} - \alpha - \beta\omega B_1\right] B_1 M_1^{-0.25} - G_{2,1}^{\phi} B_2 \\
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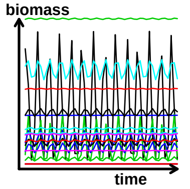
\frac{dB_6}{dt} &= \left[\lambda G_{6,5}^{\phi} - (\alpha + \beta B_6)\, M_6^{-0.25}\right] B_6 \\
&\vdots
\end{aligned}
\right.
$$

Structural sensitivity vs. complexity-stability

dynamics



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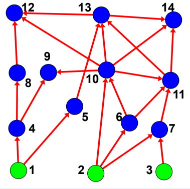
graph



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$$

complexity

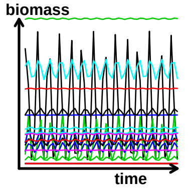
number of species and number of interactions (connectance)

formulation

the mathematical function(s) used to model a given process

Structural sensitivity vs. complexity-stability

dynamics



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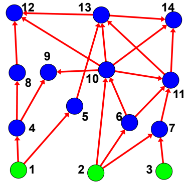

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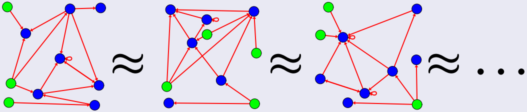
focus on food webs

species extinctions, temporal variability of species biomass

A statistical approach

same complexity level



A statistical approach

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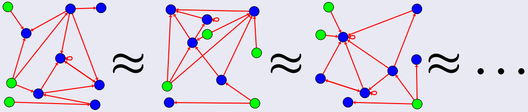
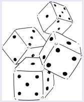


millions of “realistic” food webs



- randomly built using the niche model → structural properties that are empirically consistent *(Williams & Martinez, 2000, 2004 ; Cattin et al., 2004 ; Allesina et al., 2008)*
- use the structure to build and parameterize a dynamical system

A statistical approach

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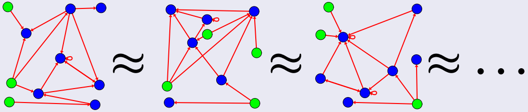

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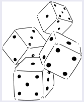

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a bio-energetic model

$$\frac{dB_i}{dt} = \underbrace{\lambda q_i^{\phi} B_i + \lambda \sum_{j \in R_i} G_{i,j}^{\phi} B_i}_{\text{gain by primary production or predation}} - \overbrace{\sum_{j \in C_i} G_{j,i}^{\phi} B_j}^{\text{losses by predation}} - \underbrace{\alpha_i B_i - \beta_i B_i^2}_{\text{mortality and competition}}$$

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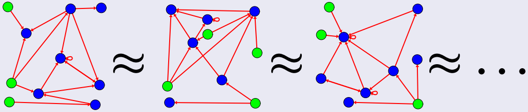

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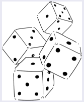

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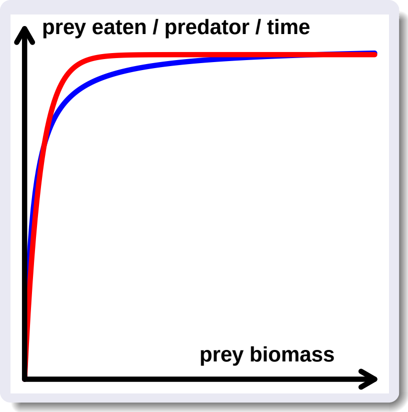
Functional response (type II)



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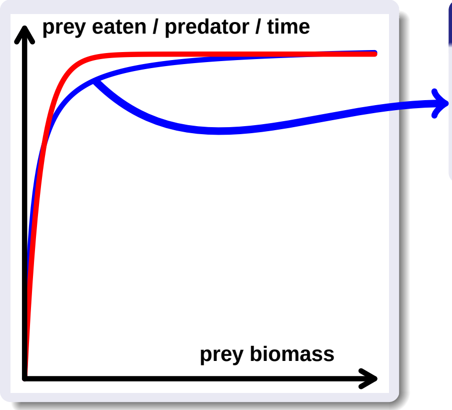

Holling (1959, 1965)

handling time

$$G_{i,j}^{H} = \frac{a_i^H f_{i,j} B_j}{1 + h_i^H a_i^H T_i}$$

$$T_i = \sum_{j \in R_i} f_{i,j} B_j$$

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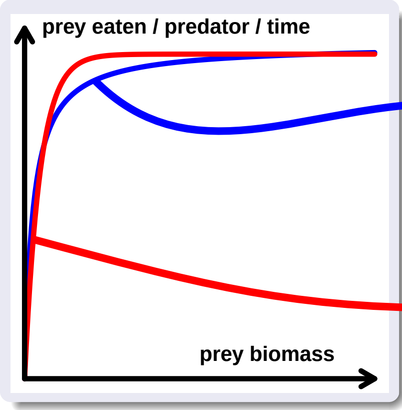


Holling (1959, 1965)

handling time

$$G_{i,j}^H = \frac{a_i^H f_{i,j} B_j}{1 + h_i^H a_i^H T_i}$$

Ivlev (1955)

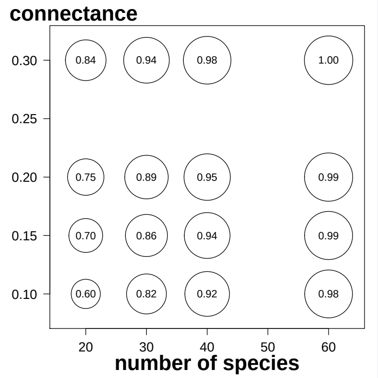
digestion

$$G_{i,j}^I = \frac{1}{h_i^I}\left(1 - e^{-h_i^I a_i^I T_i}\right)\frac{f_{i,j} B_j}{T_i}$$

$$T_i = \sum_{j \in R_i} f_{i,j} B_j$$

Fraction of food webs with extinction(s)

Holling



(modified from Aldebert et al., subm. rev. b)

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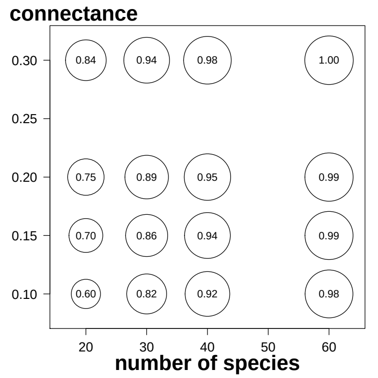
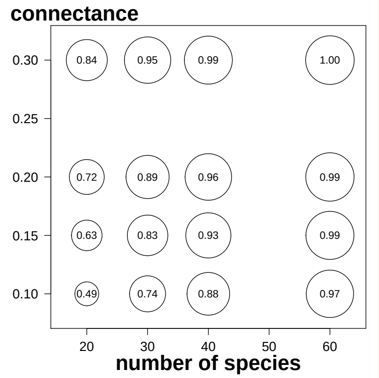


≈

Ivlev



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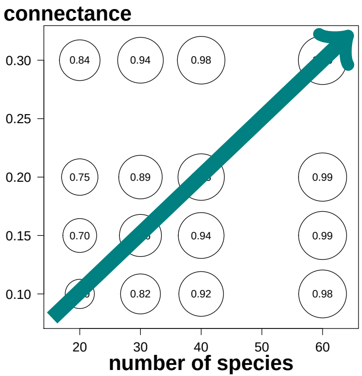

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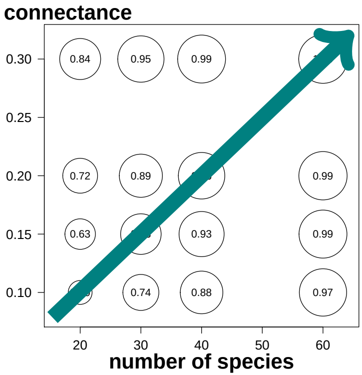
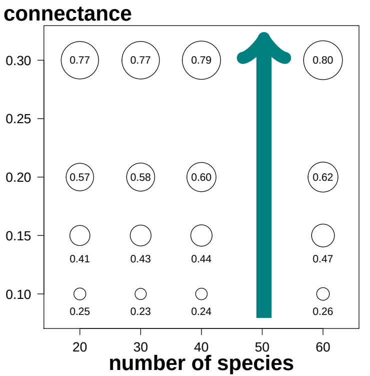


predation fluxes of similar intensity between functional responses

(modified from Aldebert et al., subm. rev. b)

Fraction of persistent food webs which reach an equilibrium

Holling



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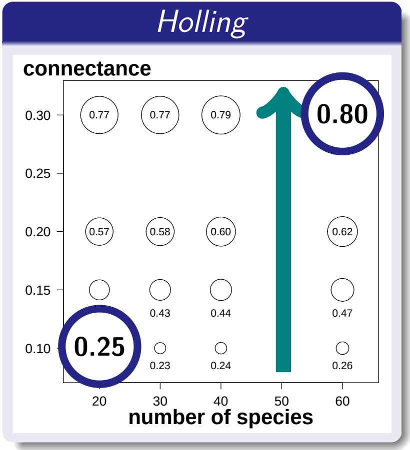
Fraction of persistent food webs which reach an equilibrium



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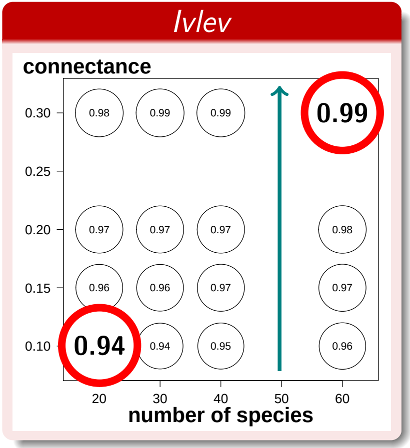

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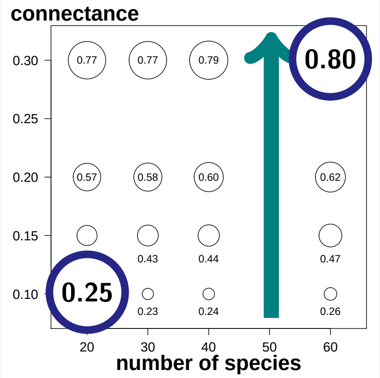

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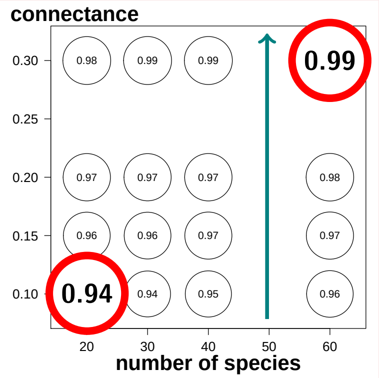

¡ ¡ ¡ formulation ≫ complexity ! ! !

(modified from Aldebert et al., subm. rev. b)

Is it a specific case ?

- functional response impact is unaffected by changes in model assumptions (primary production, cannibalism) and measure of persistence/variability
- no way to fit functional responses in order to obtain the same dynamics

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	% with extinctions	% $\rightarrow$ equilibrium
number of species	**0.76**	NS
connectance	**0.37**	**0.36**
maximum slope	0.12	-0.22
maximum rate	0.07	0.07
functional response	-0.17	**0.82**

TABLE : Correlation coefficients

($\approx 6.10^7$ food webs were simulated to obtain this table)

computational effort : 3 years.processors

Bifurcations in a predator-prey system

same model ⇒ the simplest food web

$$\begin{cases} \dot{B_{prey}}(t') = \left[\lambda q^{\xi} - \alpha - \beta\omega B_{prey}\right] B_{prey} - G^{\xi} M_{pred}^{0.25} B_{pred} \left(M_{pred}/M_{prey}\right)^{-0.25} \\ \dot{B_{pred}}(t') = \left[\lambda G^{\xi} M_{pred}^{0.25} - \alpha - \beta B_{pred}\right] B_{pred} \left(M_{pred}/M_{prey}\right)^{-0.25} \end{cases}$$

basic properties

- Rosenzweig-MacArthur's model with predator competition

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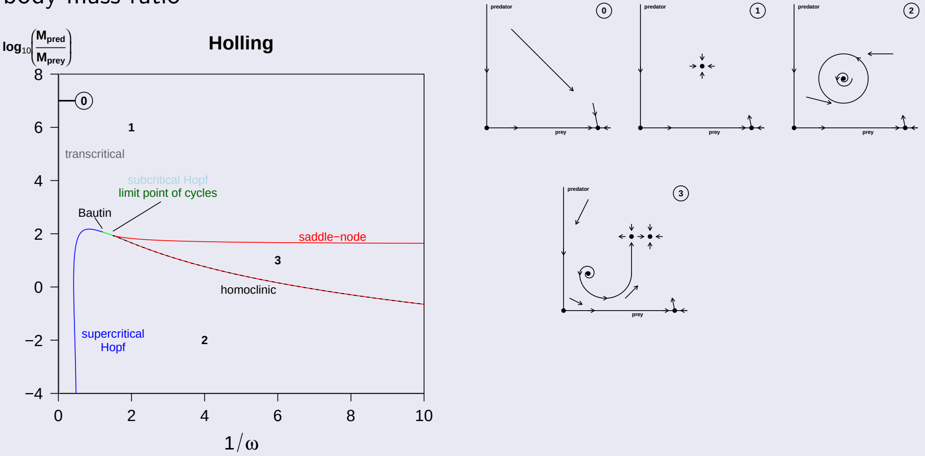
- has 2 trivial equilibria (no predator and with/without prey)
- has up to 3 positive equilibria and 2 limit cycles (12 phase portraits)
- exhibits all possible codimension 2 bifurcations in planar systems

Bifurcation diagram with Holling

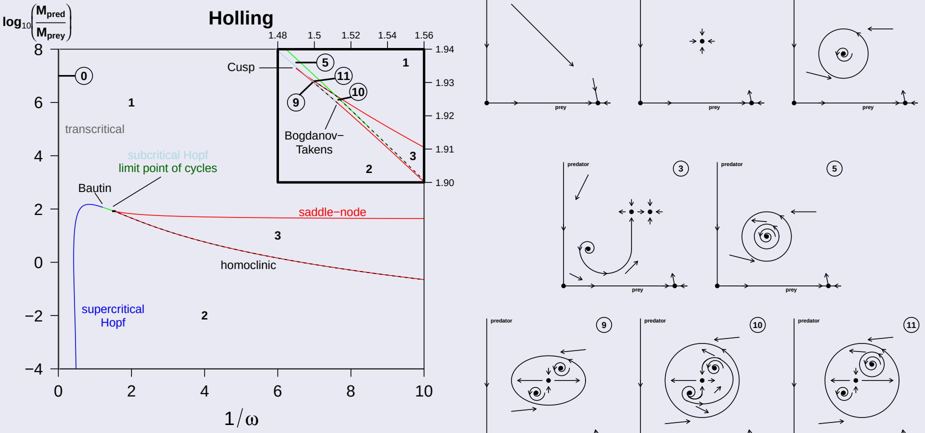
body mass ratio



⟶ prey's carrying capacity ⟶

(modified from Aldebert et al., in press)

body mass ratio



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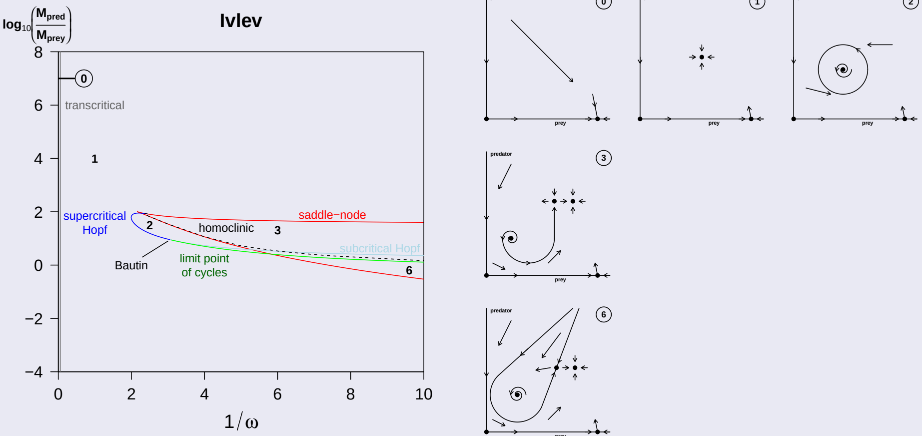

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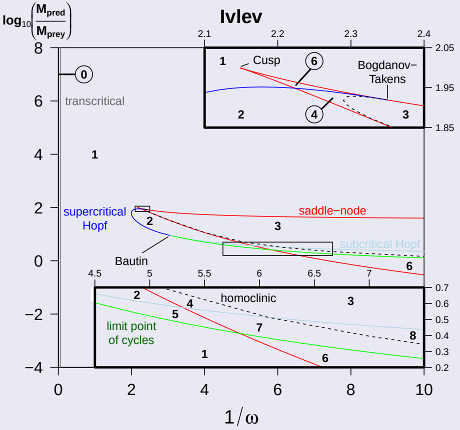

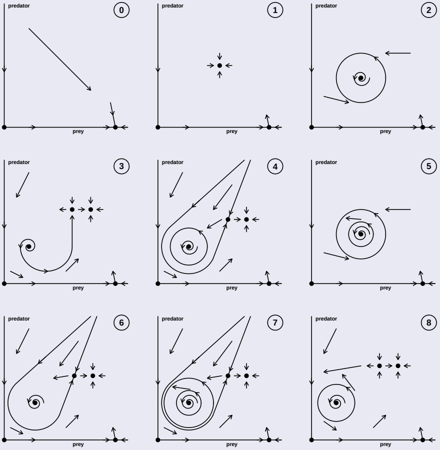

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Bifurcation diagram : Holling vs. Ivlev

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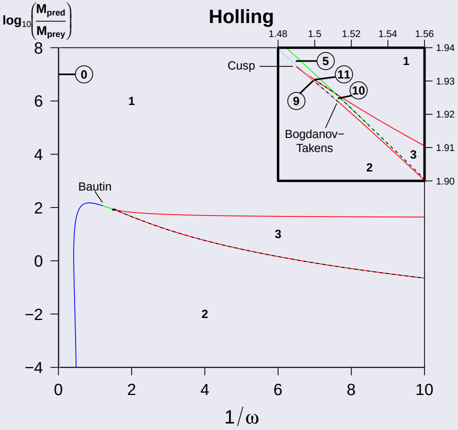

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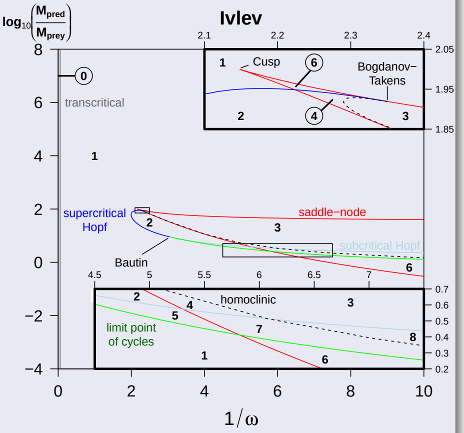

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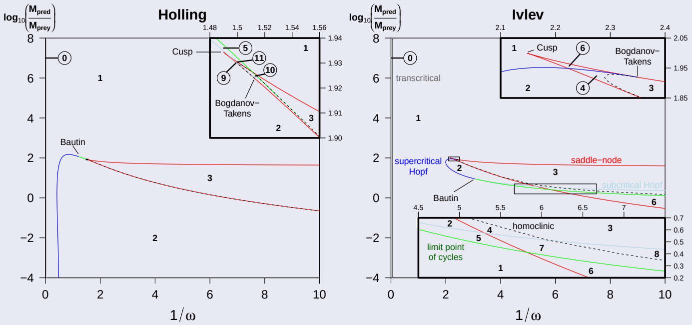

main differences

- stable equilibrium vs stable limit cycle : 26.0 % – 49.4 %
- multiple attractors (up to 3) with Ivlev : 0.1 % – 14.3 %

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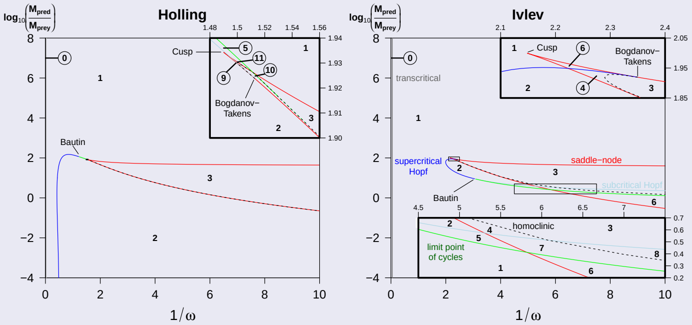

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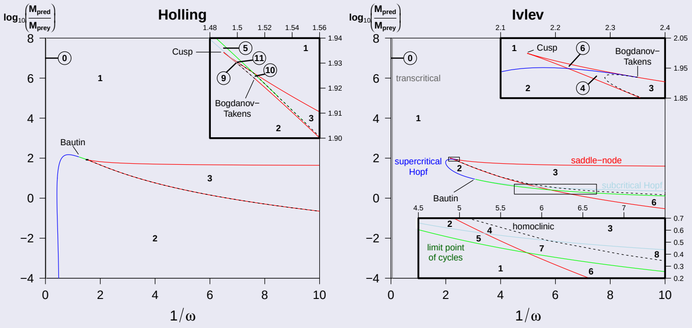

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(modified from Aldebert et al., in press, in prep.)

Generalized modelling : predator-prey system

general idea

- consider a family of models
- derive the Jacobian matrix

(modified from Aldebert et al., in press)

Generalized modelling : predator-prey system

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- re-write it with generalized parameters with an ecological meaning (e.g. non-linearity of prey's intrinsic mortality)
- these parameters describe the local behavior near an equilibrium

(modified from Aldebert et al., in press)

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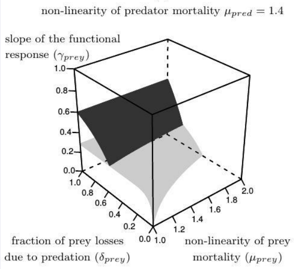

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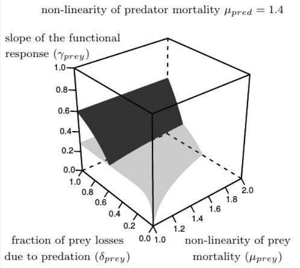
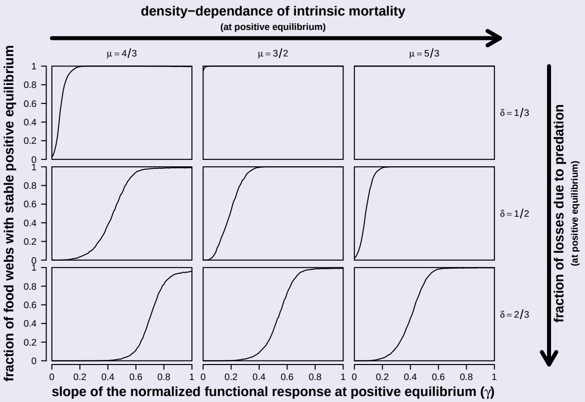


5 parameters, stabilizing factors

- high density-dependent intrinsic mortality, low losses through predation
- high slope of the functional response near equilibrium

(modified from Aldebert et al., in press)

Generalized modelling : food webs

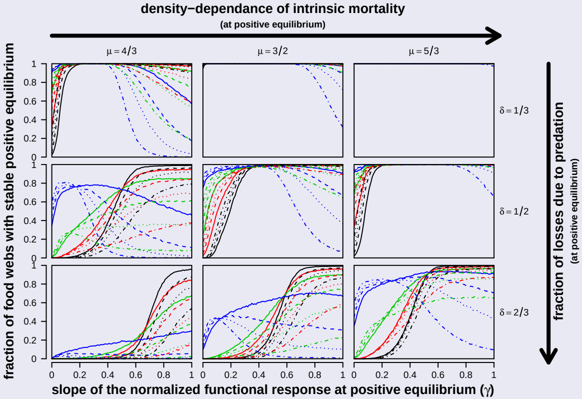


number of species : 20

connectance : 0.10

(modified from Aldebert et al., subm. rev. b)

Generalized modelling : food webs



number of species :
20, 30, 40, 60
(line type)

connectance :
0.10, 0.15, 0.20, 0.30
(line color)

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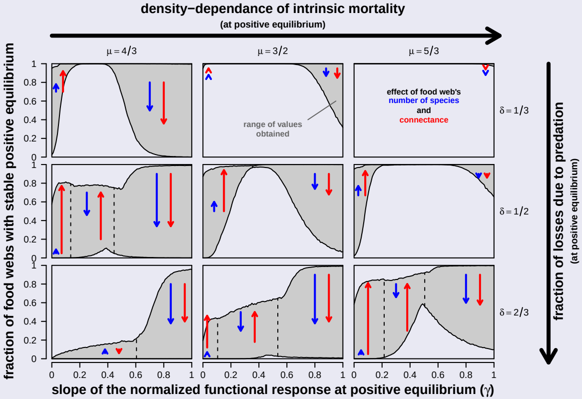

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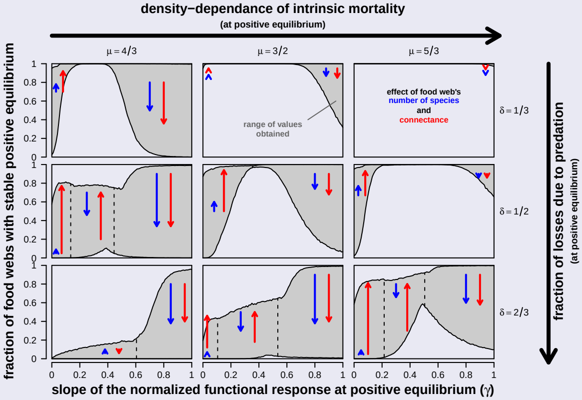

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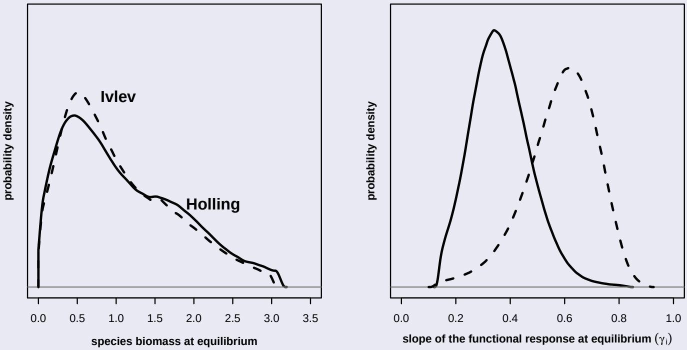
- stabilizing effect of a higher slope of the functional response
- robust to changes in model assumptions (primary production, cannibalism)

(modified from Aldebert et al., subm. rev. b)

Generalized parameters as indicators in food webs



food webs at positive equilibrium

- same species biomass and generalized parameters distributions
- except for the slope of the functional response (higher with Ivlev)

(modified from Aldebert et al., subm. rev. b)

Structural sensitivity : ongoing works

more physiological details : DEB models

- a family of bi-trophic food chain models (explicit resource) in chemostat

(Aldebert et al., in prep)

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- "low" sensitivity to the functional response (no qualitative changes)
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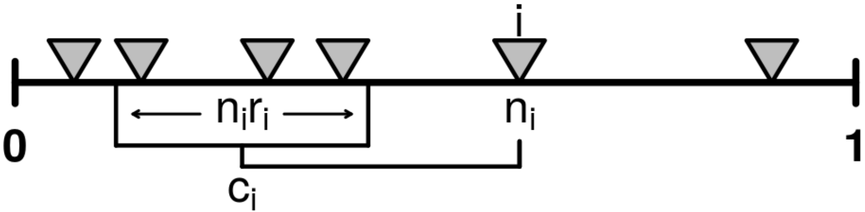
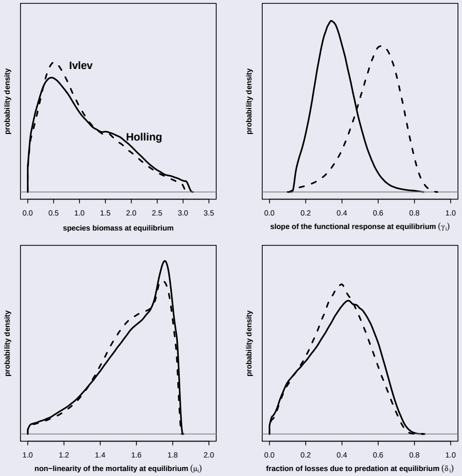
The niche model *(Williams & Martinez, 2000, 2004)*



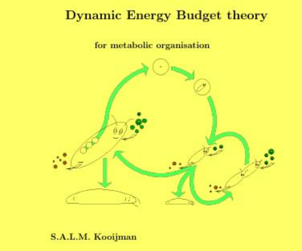
based on the principle of ecological niche *(Hutchinson, 1957)*

- the segment $[0, 1]$ summarizes the ∞-dimensional niche space
- the niche indice n_i summarizes species i's ecological niche
- the relative width of species i's feeding range r_i depends on connectance
- c_i is the center of species i's feeding range
- species i feeds on all species who belong to its feeding range $\left[c_i \pm \frac{n_i r_i}{2}\right]$
- species with an empty feeding range are defined as primary producers
- more complex models (e.g. with $\pm$ discontinuous feeding range) are based on the niche model

Generalized modelling : food webs



Dynamic Energy Budgets theory



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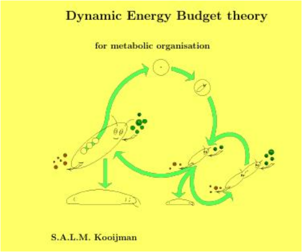

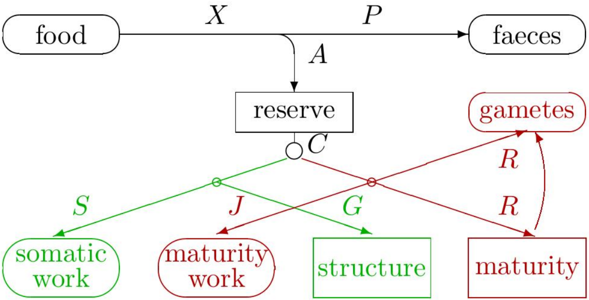

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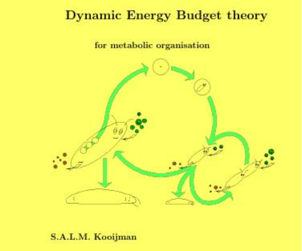

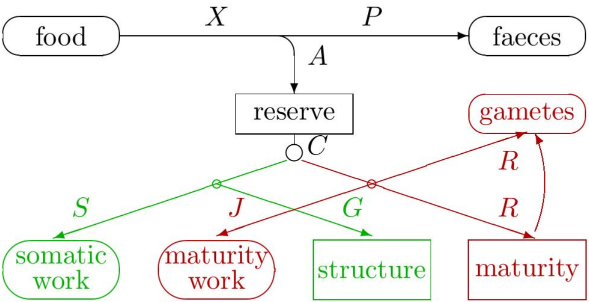

- focus on the individual, based on mechanistic assumptions on metabolism

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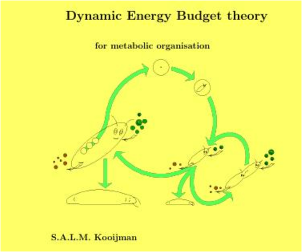

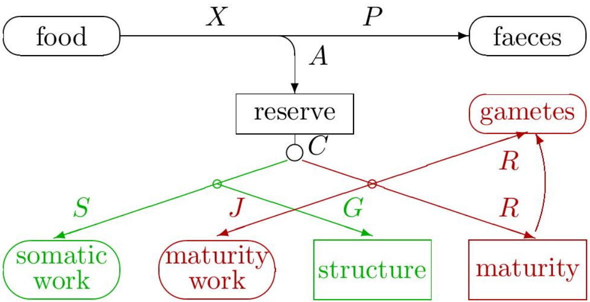

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- same framework for most species, metabolic classification of species

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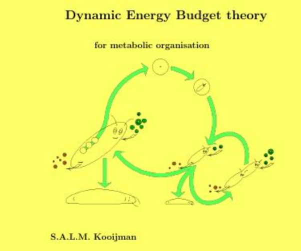

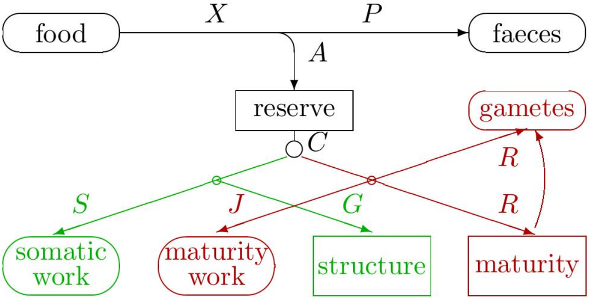

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- theory allows to build more or less detailled models within a coherent theoretical framework

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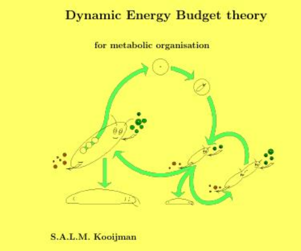
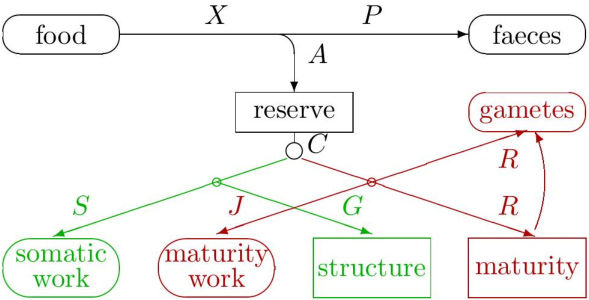




- focus on the individual, based on mechanistic assumptions on metabolism
- same framework for most species, metabolic classification of species
- theory allows to build more or less detailled models within a coherent theoretical framework
- unicellular organisms : upscaling to population dynamics is easy

DEB model for a bitrophic food chain in chemostat

(data from Dent *et al.*, 1976 ; model from Kooi & Kooijman, 1994) (fig 9.15, p 358)

$X_0(0)$	0.433			mg ml^{-1}
$X_1(0)$	0.361	$X_2(0)$	0.084	mm^3 ml^{-1}
$e_1(0)$	1	$e_2(0)$	1	-
K_1	0.40	K_2	0.18	$\frac{\mu g}{ml}$, $\frac{mm^3}{ml}$
g_1	0.86	g_2	4.43	-
$\dot{k}_M^1$	0.008	$\dot{k}_M^2$	0.16	h^{-1}
$\dot{k}_E^1$	0.67	$\dot{k}_E^2$	2.05	h^{-1}
j_{XAm}^1	0.65	j_{XAm}^2	0.26	$\frac{mg}{mm^3\,h}$, h^{-1}

$$\frac{d}{dt}e_1 = \dot{k}_E^1(f_1 - e_1); \quad f_1 = \frac{X_0}{K_1 + X_0}$$

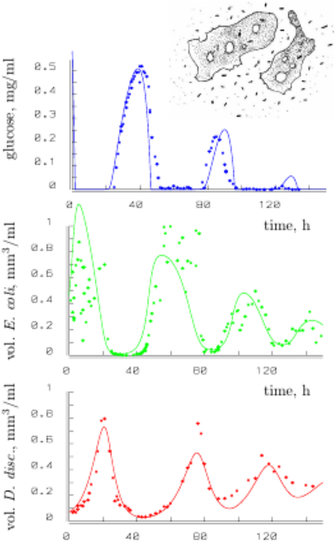
$$\frac{d}{dt}e_2 = \dot{k}_E^2(f_2 - e_2); \quad f_2 = \frac{X_1}{K_2 + X_1}$$

$$\frac{d}{dt}X_0 = \dot{h}(X_r - X_0) - f_1 j_{XAm}^1 X_1$$

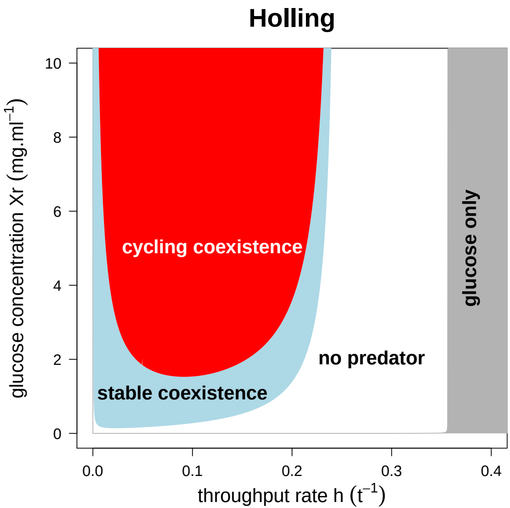
$$\frac{d}{dt}X_1 = \left(\frac{\dot{k}_E^1 e_1 - \dot{k}_M^1 g_1}{e_1 + g_1} - \dot{h}\right) X_1 - f_2 j_{XAm}^2 X_2$$

$$\frac{d}{dt}X_2 = \left(\frac{\dot{k}_E^2 e_2 - \dot{k}_M^2 g_2}{e_2 + g_2} - \dot{h}\right) X_2$$

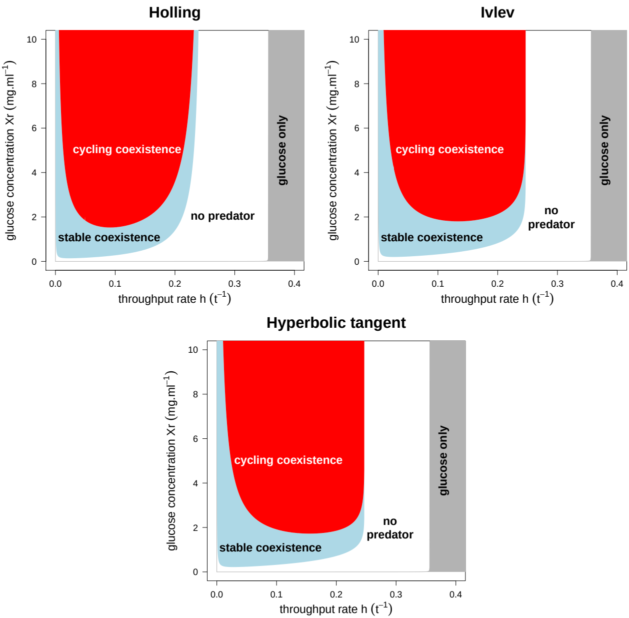
V1-morph, $\kappa \to 1$, predator feed on prey's structure, fixed environment



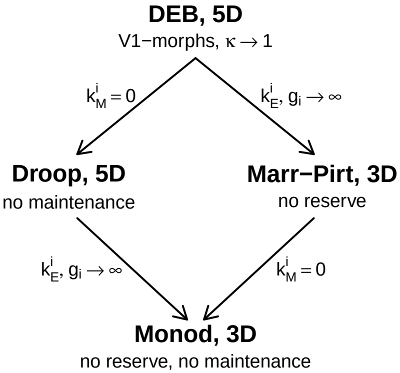
Structural sensitivity in this DEB model



Low structural sensitivity in this DEB model



A family tree of DEB models



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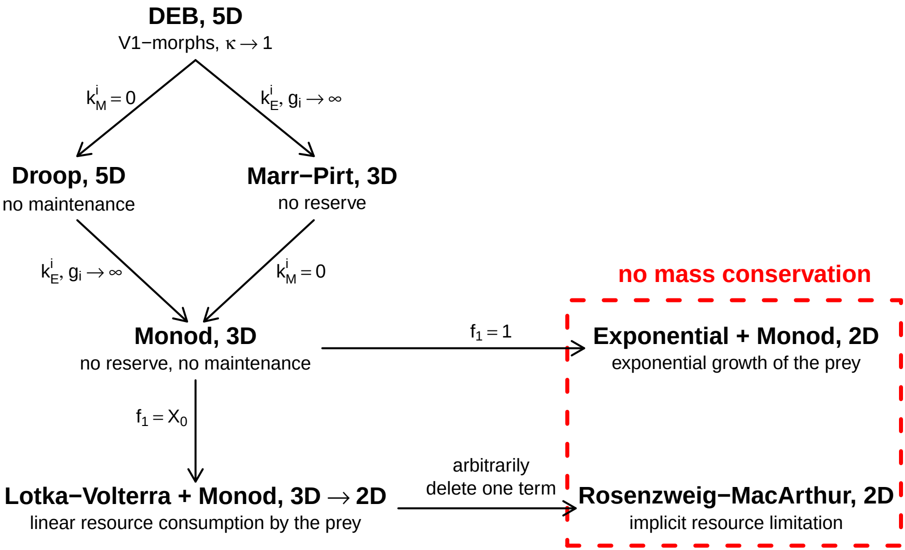

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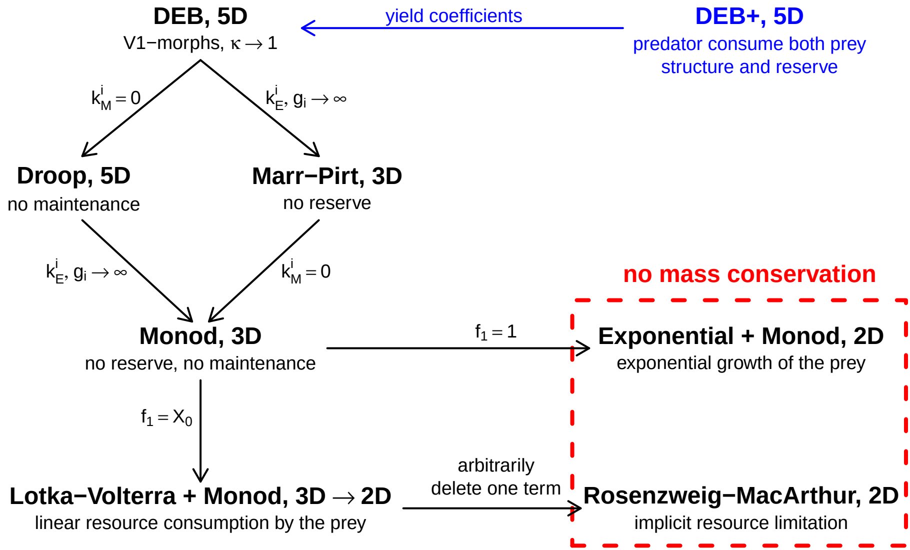

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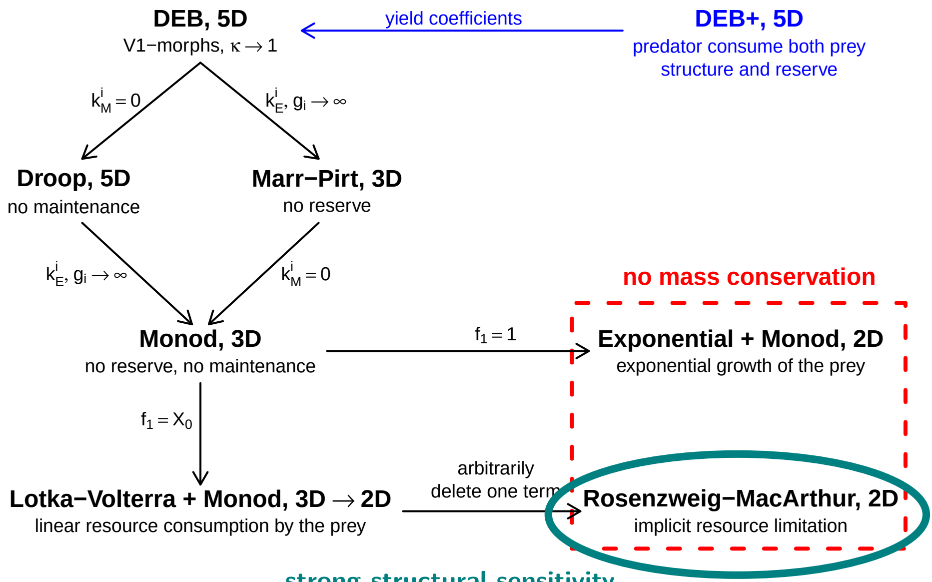

strong structural sensitivity

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