



Physiologically structured population models: **Formulation, analysis** and ecological insights

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in collaboration with

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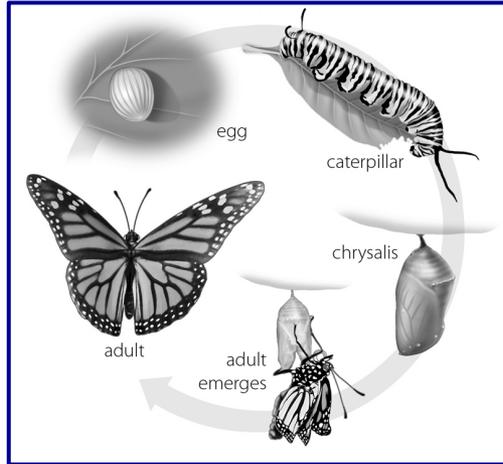
Ecology and Environmental Sciences
Umeå University, Sweden



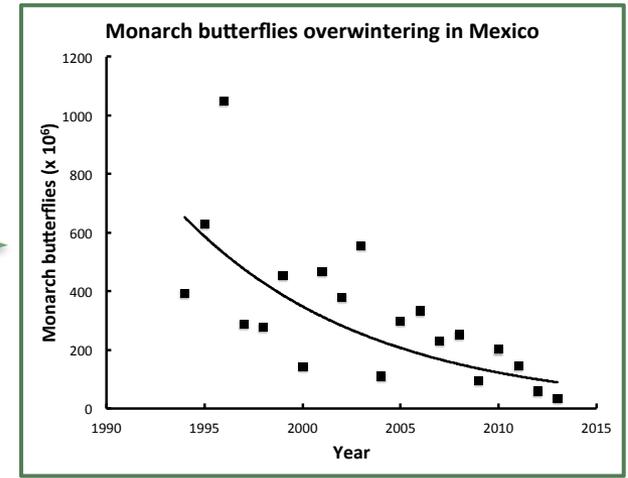


A central issue in ecology and evolution

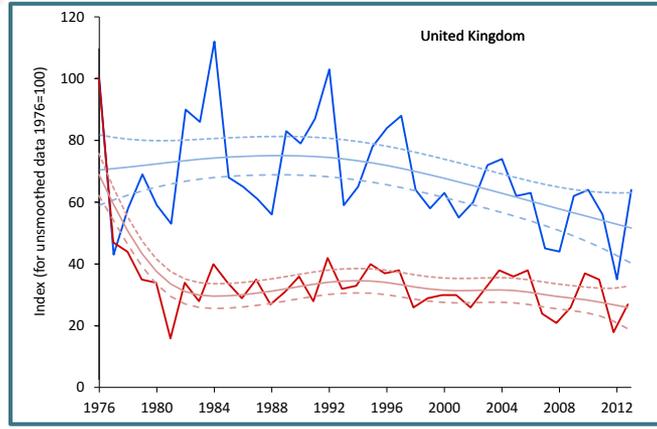
Life history



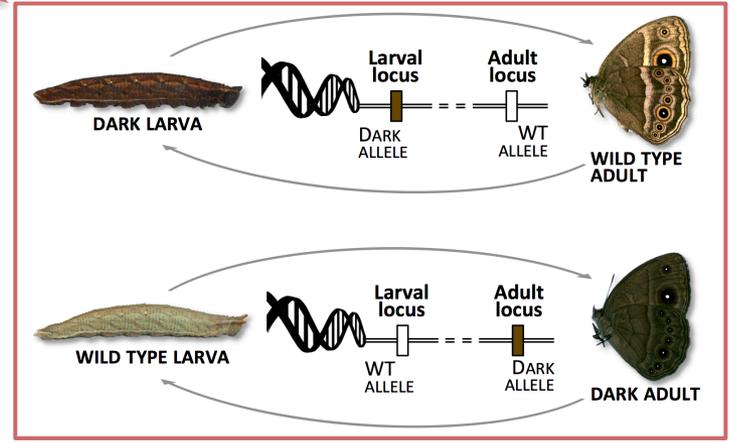
Population growth & demography



Population & Community dynamics



Life history evolution





The conceptual issue: Development like other complicating factors?

NO! Like reproduction and mortality, development is a constituent component of population dynamics

Unlike *modulating factors* such as:

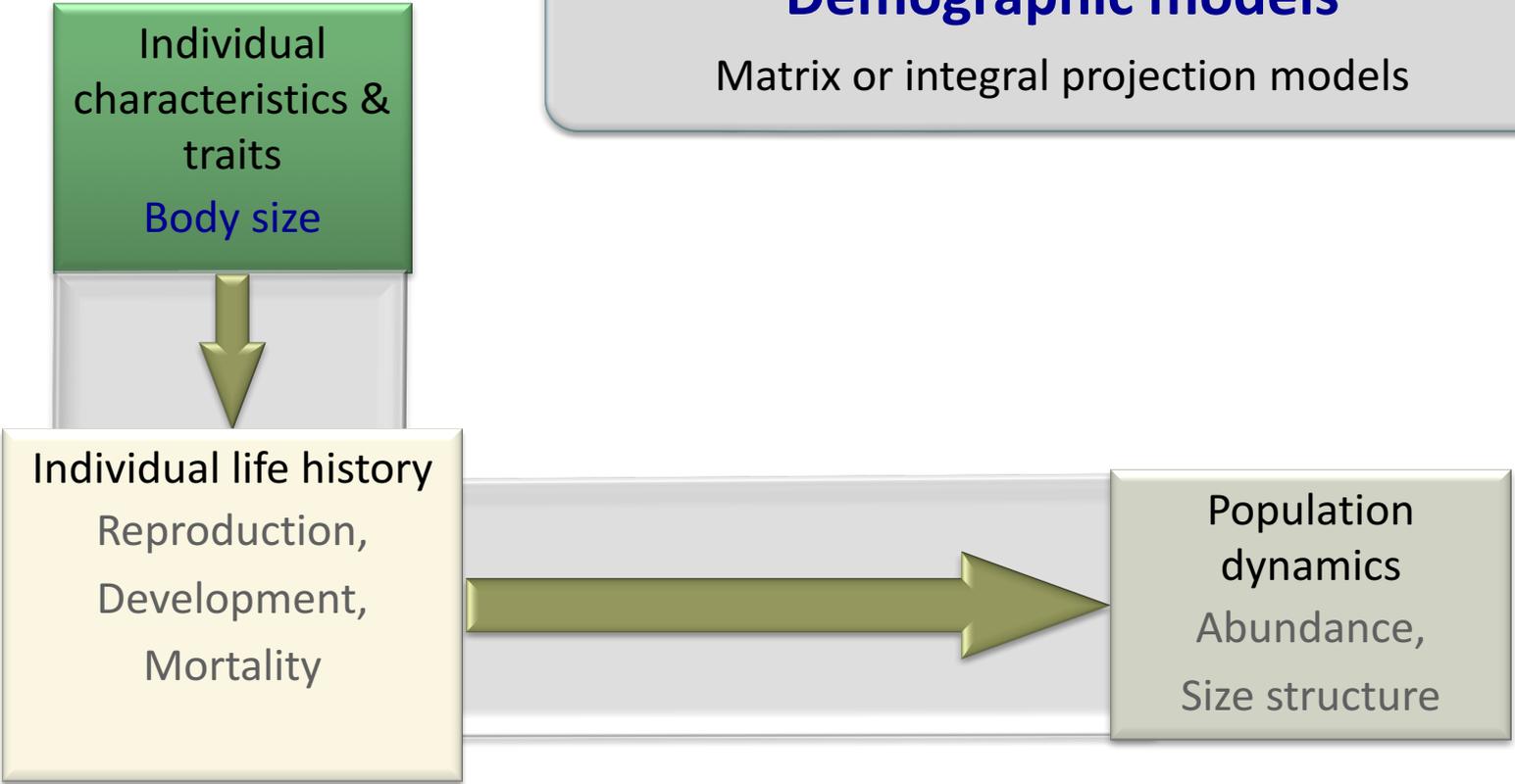
- **Spatial heterogeneity**
 - Influence excluded through homogeneous mixing (*chemostats*)
- **Intraspecific genetic variation**
 - Influence excluded by using clonal or inbred individuals (*parthenogenetic species, iso-female lines*)

Development is next to mortality the most certain population dynamics process, reproduction is only secondary



Approaches to study impacts of life history

Demographic models
Matrix or integral projection models





Commonly used approaches for analysis

- Matrix models: discrete time, discrete individual states (*i*-states)

$$\begin{pmatrix} x_1(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} a_{11} & \dots & a_{1n} \\ \vdots & \ddots & \vdots \\ a_{n1} & \dots & a_{nn} \end{pmatrix} \begin{pmatrix} x_1(t) \\ \vdots \\ x_n(t) \end{pmatrix}$$

H. Caswell, 2001. Matrix Population Models. Sinauer Associates

- Integral projection models: discrete time, continuous *i*-states

$$x(l, t+1) = \int_{\Omega} \left(\underbrace{D(l, \ell)}_{\text{inheritance}} \overbrace{R(\ell)}^{\text{fecundity}} + \underbrace{G(l, \ell)}_{\text{growth}} \overbrace{S(\ell)}^{\text{survival}} \right) x(\ell, t) d\ell$$

Ellner, Child & Rees, 2016. Data-driven Modelling of Structured Populations: A Practical Guide to the Integral Projection Model. Springer

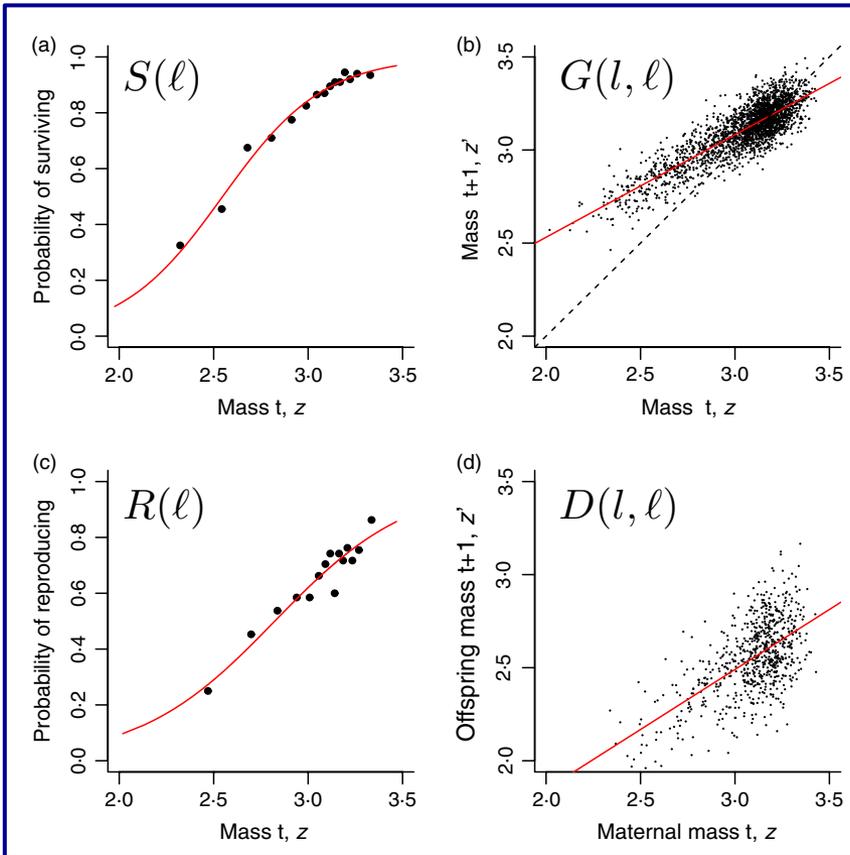
- Characteristics:

- Data-driven, tight link with life history observations
- Non-mechanistic, no functional individual life history description

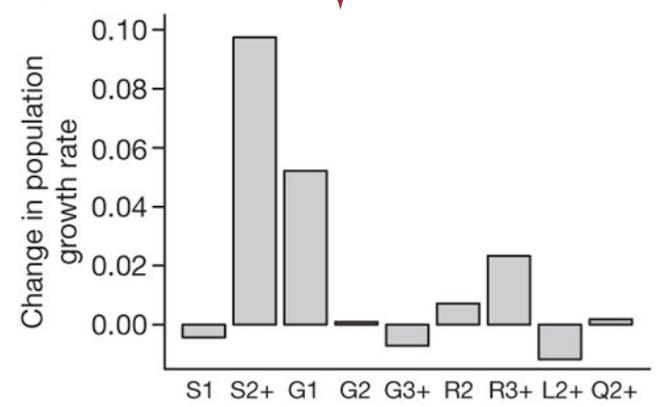
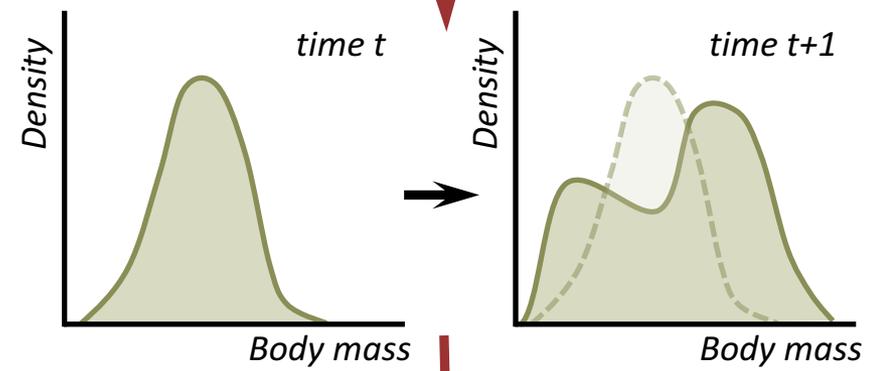


A data-driven approach: IPMs

Life history



$$x(l, t + 1) = \int_{\Omega} \left(\underbrace{D(l, \ell)R(\ell)}_{\text{reproduction}} + \underbrace{G(l, \ell)}_{\text{growth}} \underbrace{S(\ell)}_{\text{survival}} \right) x(l, t) d\ell$$

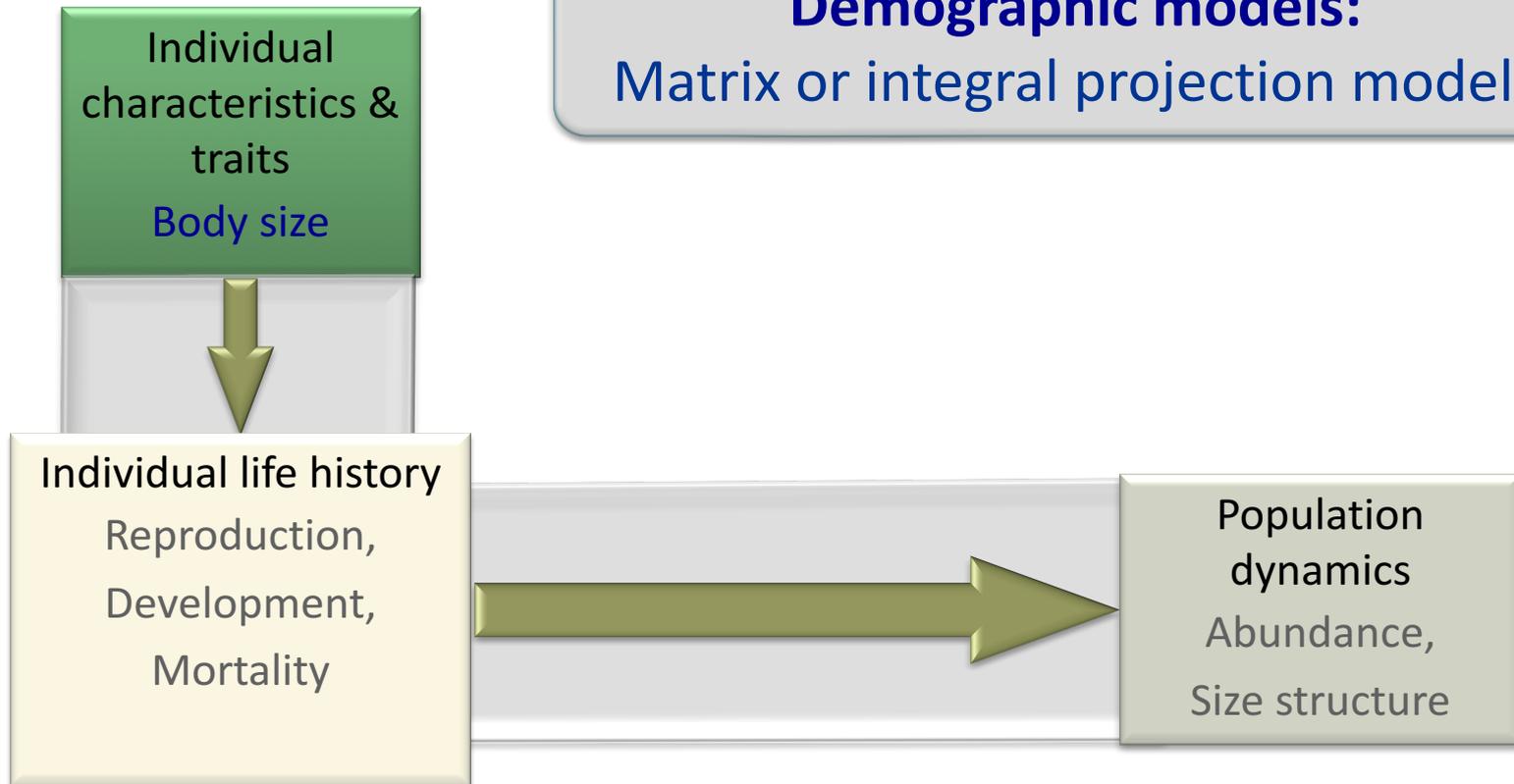


*Non-mechanistic representation of life history based on data representative of **current** conditions*



Structured population models

Demographic models:
Matrix or integral projection models



- Population rather than community dynamics (**population growth rate**)
- Fixed development rates (age, stage), independent of food
- Energetics ignored (maintenance costs, mass/energy conservation)



Life history's most prominent feature: Growth in body size (a doubling at least)

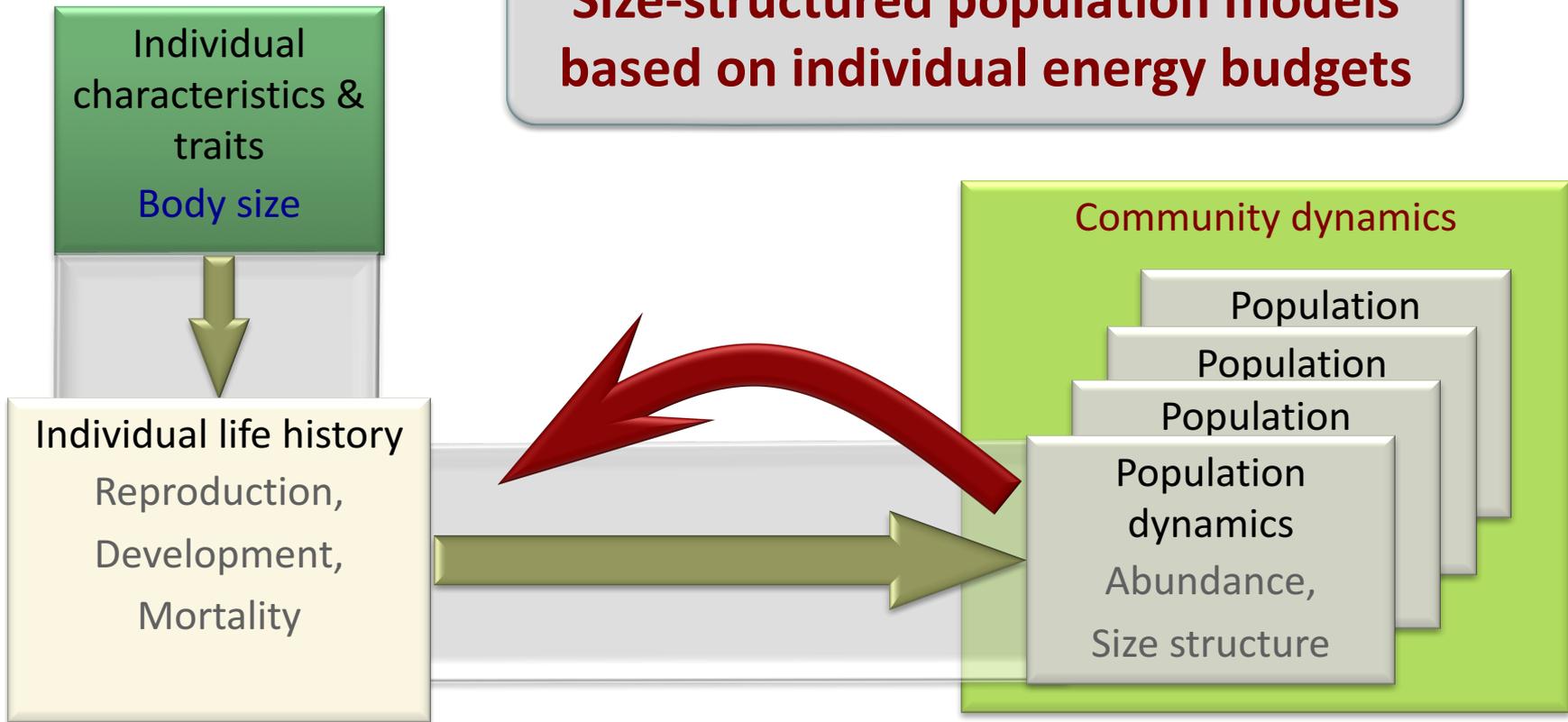


Intra-specific variation in body size!



Structured population models

Size-structured population models based on individual energy budgets

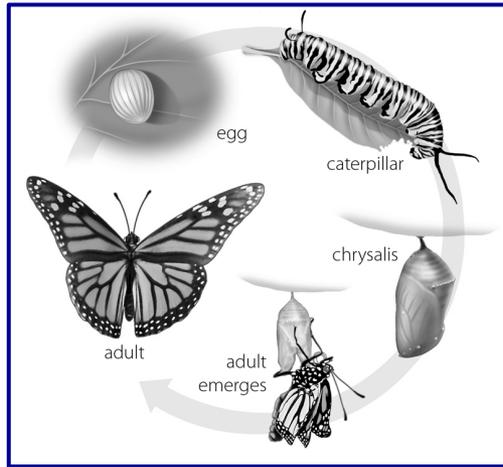


- Community dynamics (resources, consumers, predators)
- Food-dependent growth in body size
- Strict conservation of mass/energy including maintenance costs

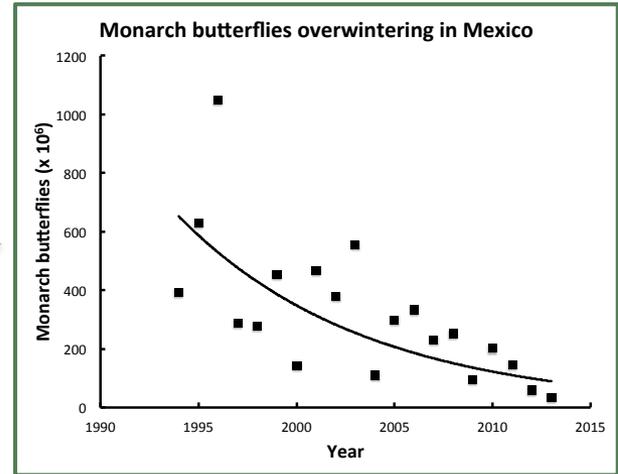


Nonlinearity: population feedback on life history

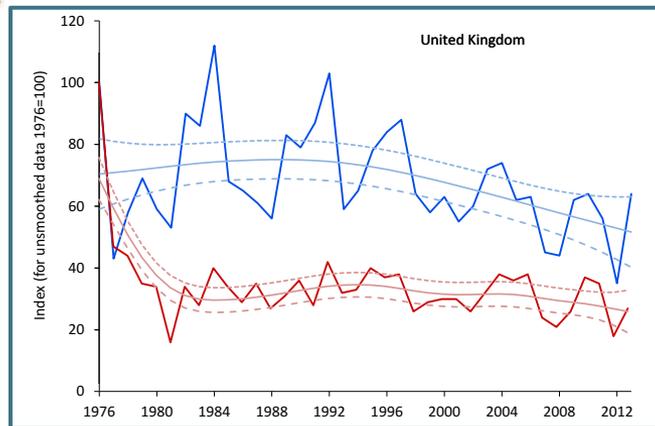
Life history



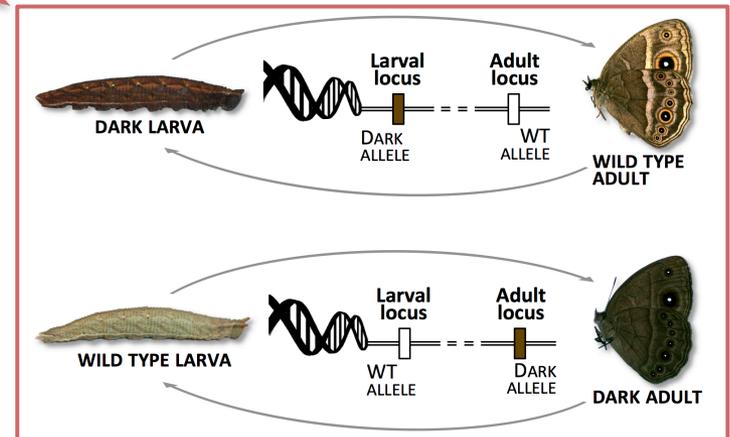
Population growth & demography



Population & Community dynamics

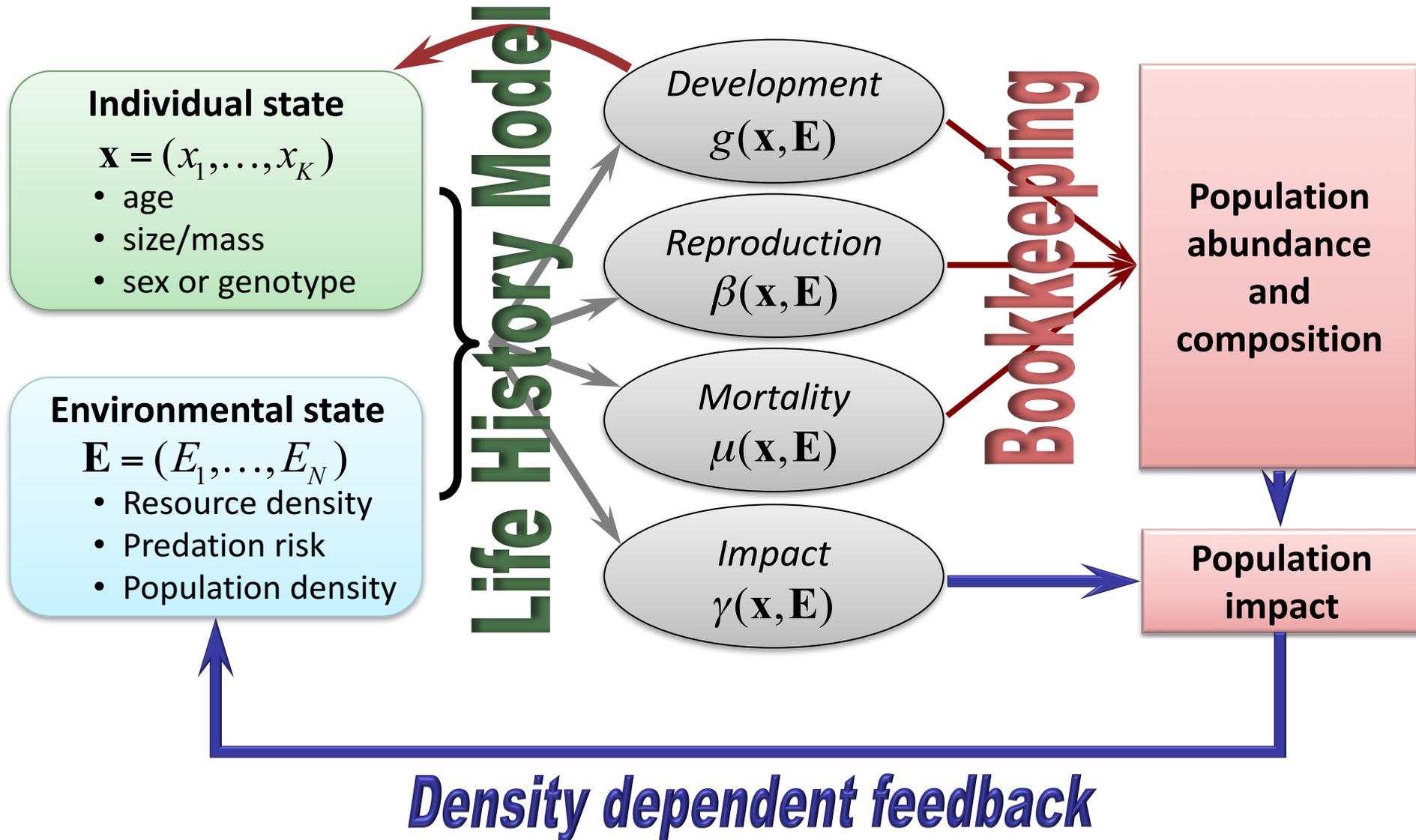


Life history evolution





Physiologically Structured Population Models





Types of population feedback on life history

Individual

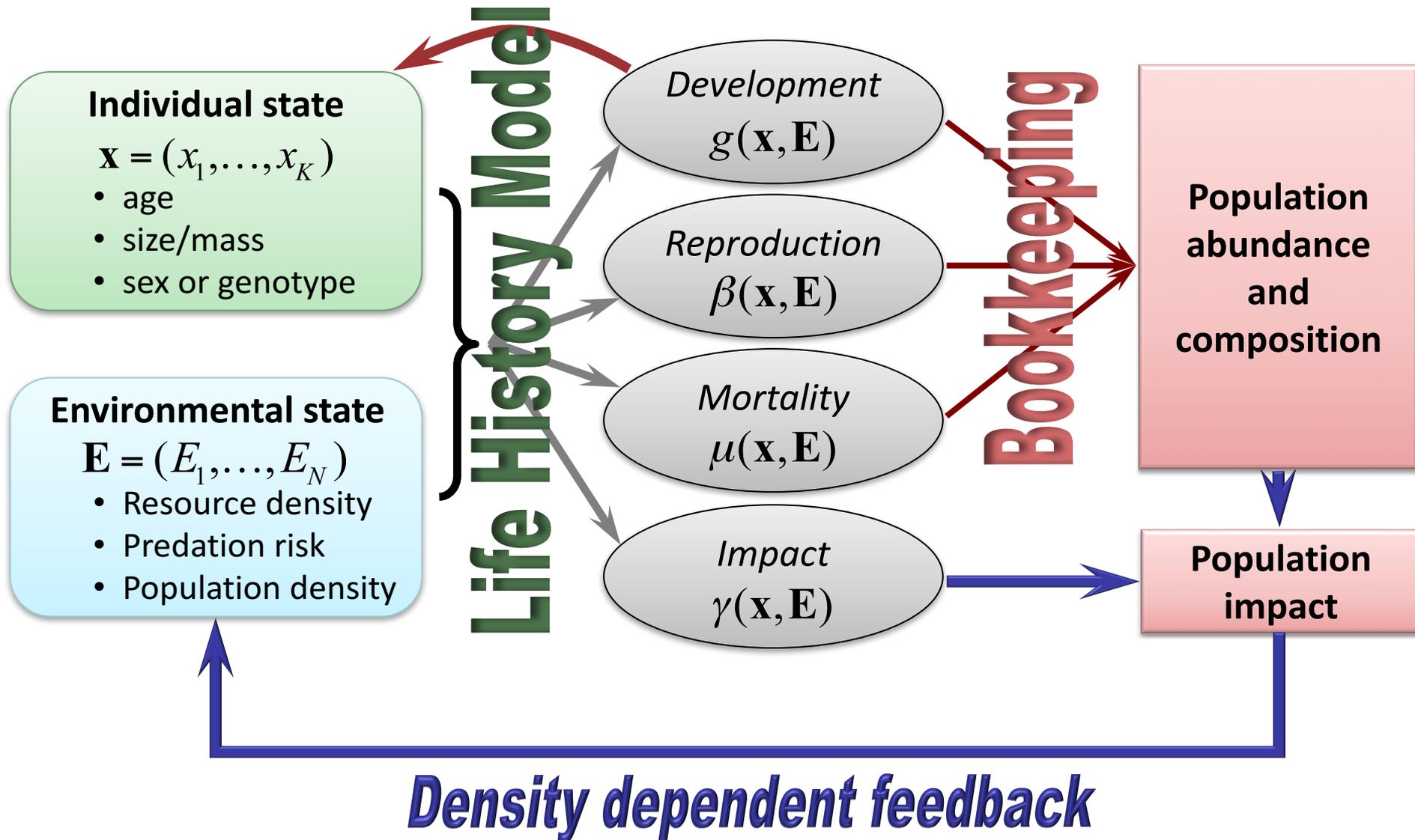
- **Dynamic traits (*i*-state variables)**
 - Age, body size, energy reserves
- **Static traits (*i*-state variables)**
 - Sex, frailty, genotype

Environment

- **Number of conspecifics (direct density-dependence)**
 - Interference competition, e.g. for mates or nesting sites
 - Phenomenological, non-mechanistic
- **Resource density (indirect)**
 - Exploitative foraging on shared resource
- **Predation risk (indirect)**
 - Top-down control on prey population through shared predator

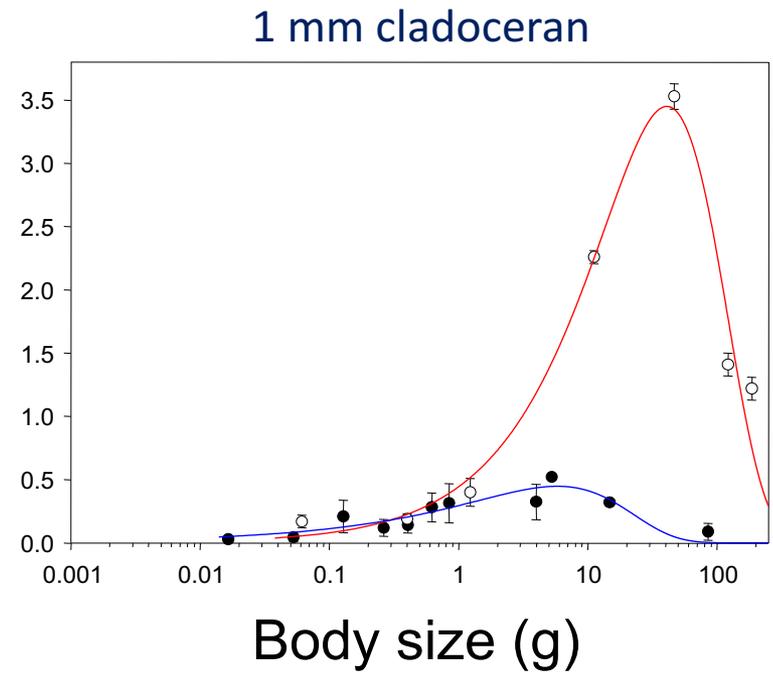
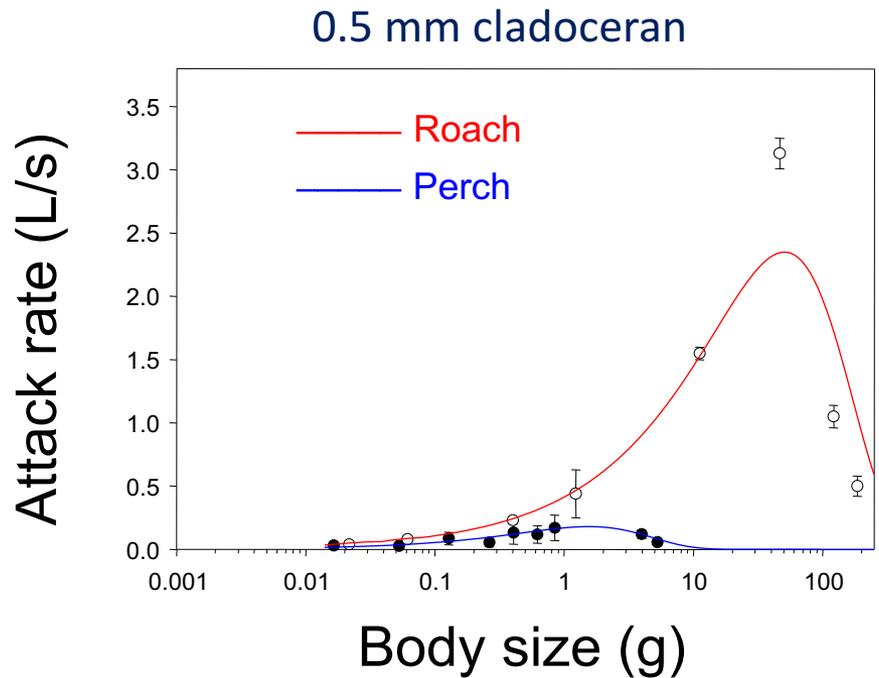


Physiologically Structured Population Models





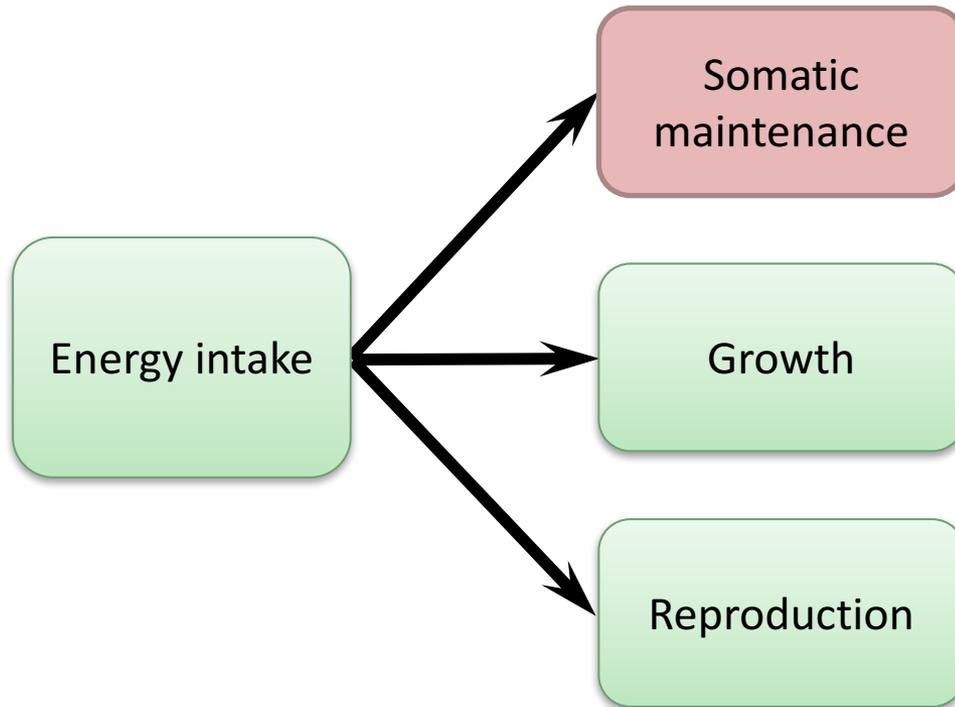
Model ingredients and parameterization



On the basis of independent, individual-level data and experiments



Dynamic energy budget models: Energy/mass conservation principle



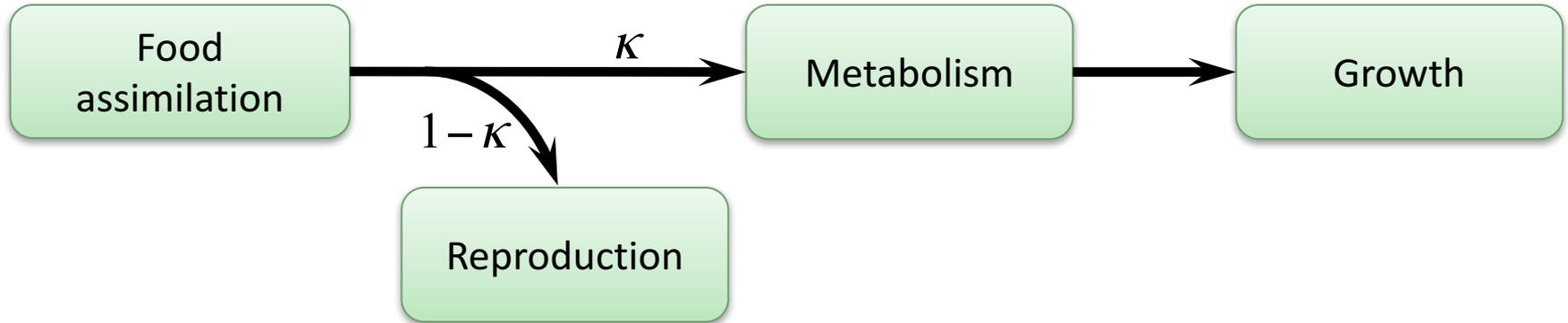
- “Kappa-rule” models (Kooijman, 1993, 2002, 2009)
Reproduction proportional to ingestion
- Net-production models
Maintenance covered first

$$\text{Energy intake (assimilation from food)} = \text{Energy expenditure (maintenance, growth, reproduction)}$$

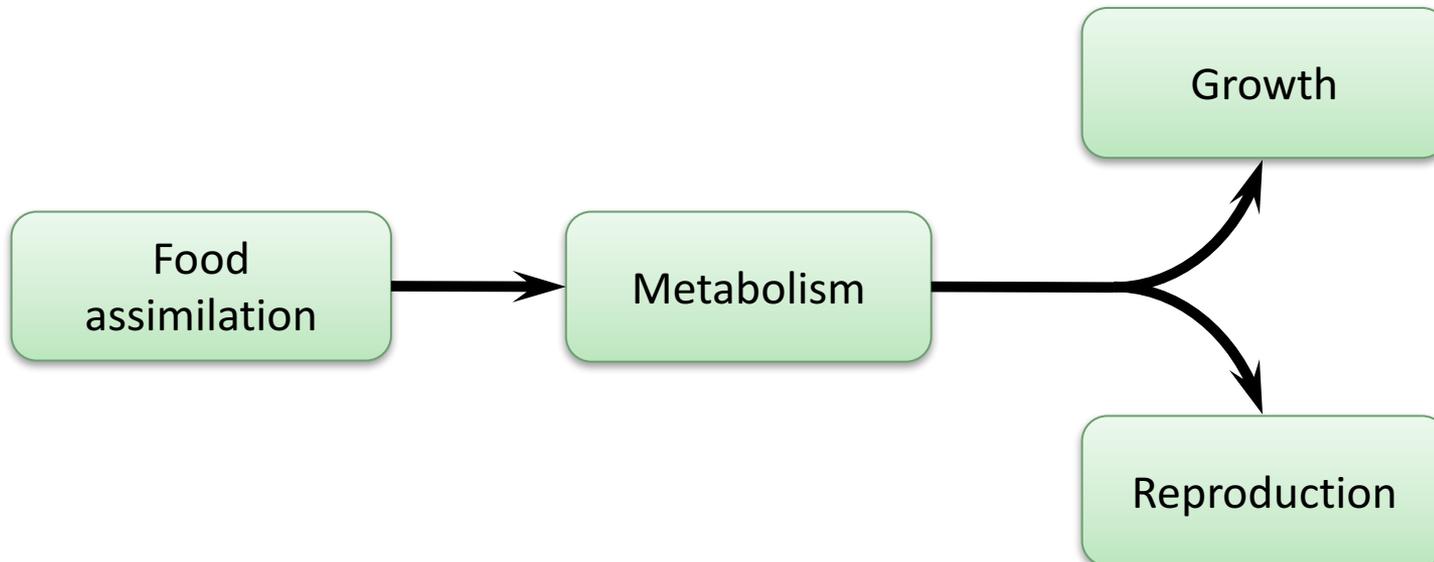


Dynamic energy budget model

“Kappa-rule” model or net-assimilation model

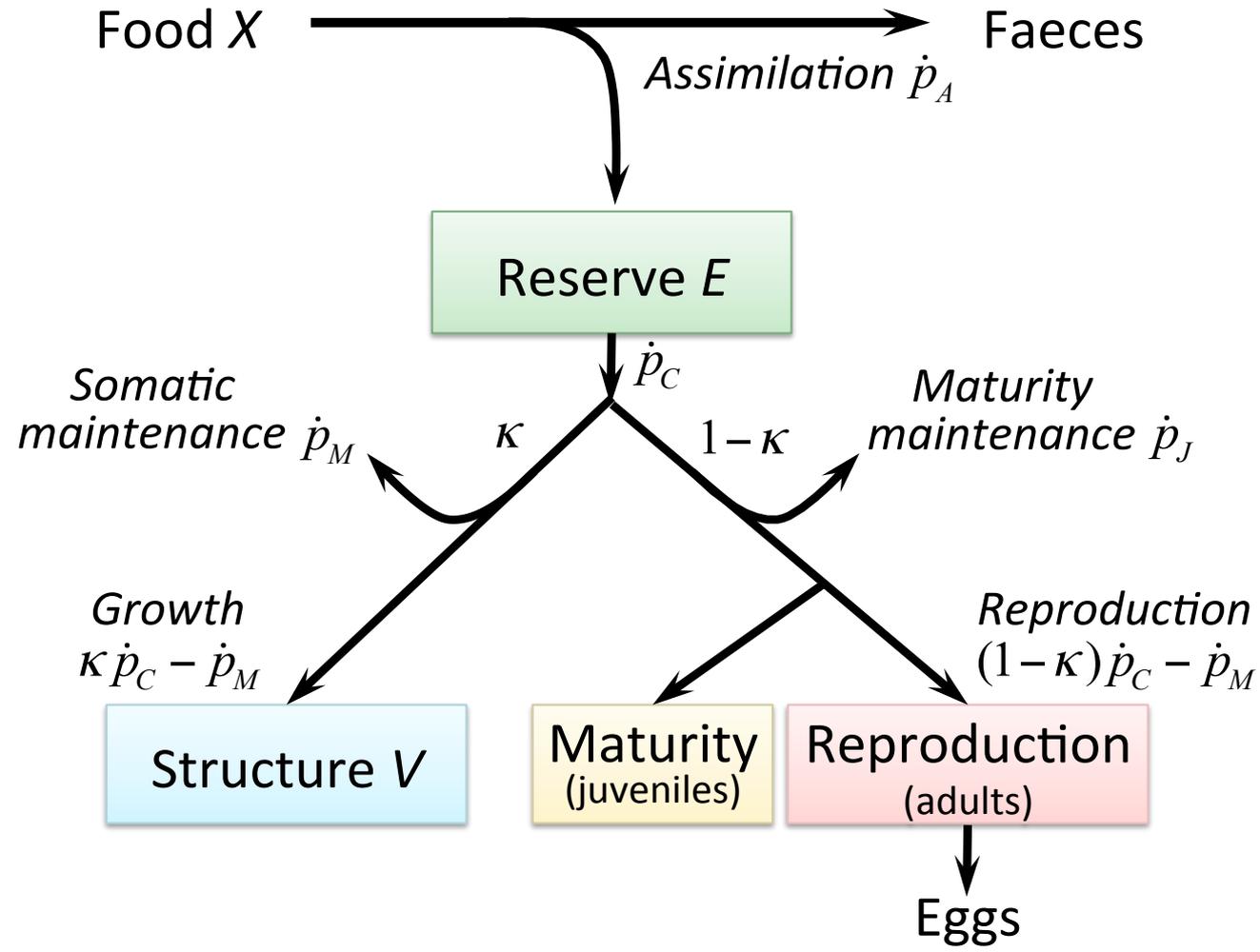


Net-production model





Kooijman's Dynamic Energy Budget theory



Estimating DEB parameters from individual data

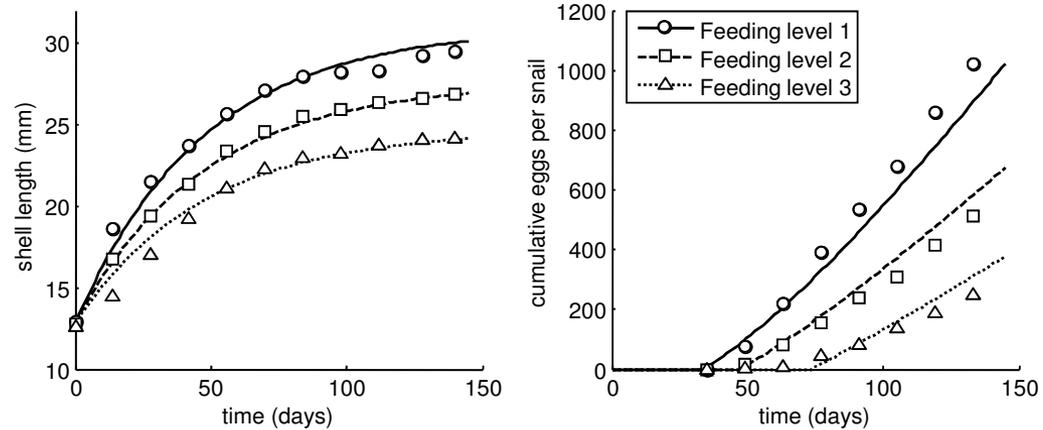


Figure 3.2: Fits of the DEBkiss model to growth and reproduction data for the pond snail in three feeding regimes (data from [83]).

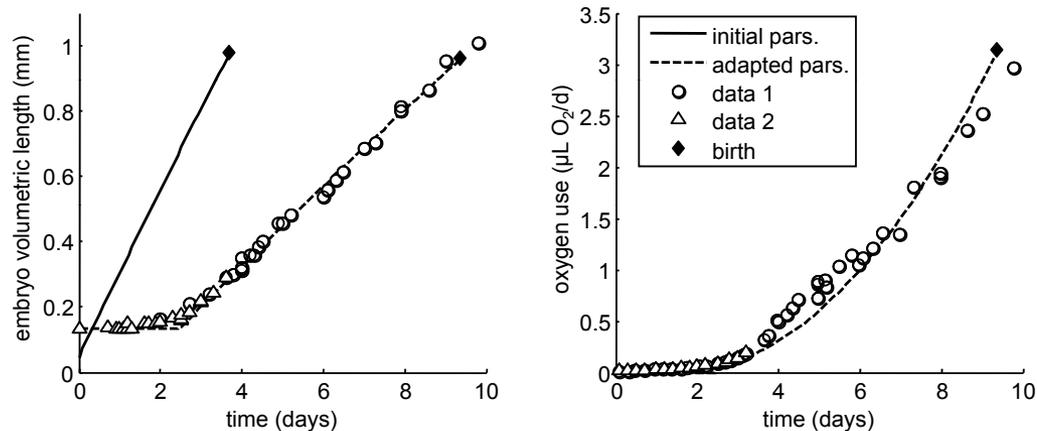


Figure 3.4: Data for snail embryo size and oxygen use over time [24]. Solid line represent model predictions with the parameters from last column of Table 3.1; broken lines are quick-fixes (not fitted) to get a closer correspondence to the data (see text Section 3.3).



A generic size-structured model

- Individuals are born with size (*mass*) s_b
- Growth rate in body size: $g(s, R)$
- Reproduction rate: $\beta(s, R)$
- Resource intake rate: $\gamma(s, R)$
- Mortality rate: $\mu(s, R)$

$$\frac{\partial c(t, s)}{\partial t} + \frac{\partial g(s, R) c(t, s)}{\partial s} = -\mu(s, R) c(t, s)$$

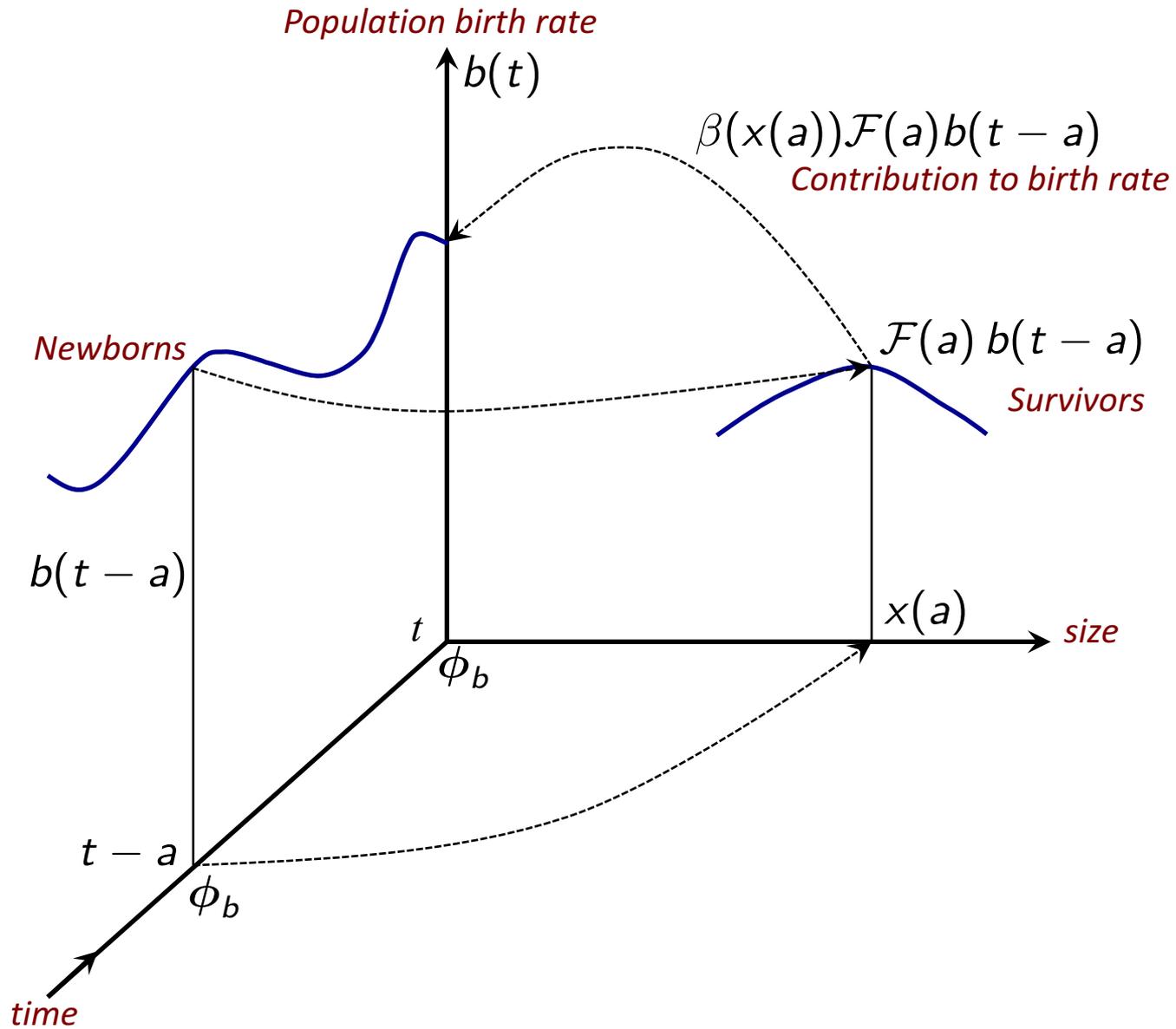
$$g(s_b, R) c(t, s_b) = \int_{s_b}^{s_m} \beta(s, R) c(t, s) ds$$

$$\frac{dR}{dt} = G(R) - \int_{s_b}^{s_m} \gamma(s, R) c(t, s) ds$$

- “Sinko & Streifer model”
(*Ecology*, 1967)
- VonFoerster (1959)
- Frederickson et al. (1967)
- Bell & Anderson (1967)
- Metz & Diekmann (1986)
*Springer Lecture Notes
in Biomathematics 68*



Integro-delay-differential equation formulation





The general structured model

$$b(t) = \int_0^\infty \overbrace{\beta(\Xi(a, E_t), E(t))}^{\text{Fecundity}} \underbrace{\mathcal{F}(a, E_t)}_{\text{Survival}} b(t-a) da$$

$$I(t) = \int_0^\infty \overbrace{\gamma(\Xi(a, E_t), E(t))}^{\text{Impact}} \underbrace{\mathcal{F}(a, E_t)}_{\text{Survival}} b(t-a) da$$

$$E(t) = \begin{pmatrix} X(t) \\ Y(t) \end{pmatrix}$$

$$X(t) = G_X(X(t), Y(t), I(t)), \quad \frac{dY}{dt} = G_Y(X(t), Y(t), I(t))$$

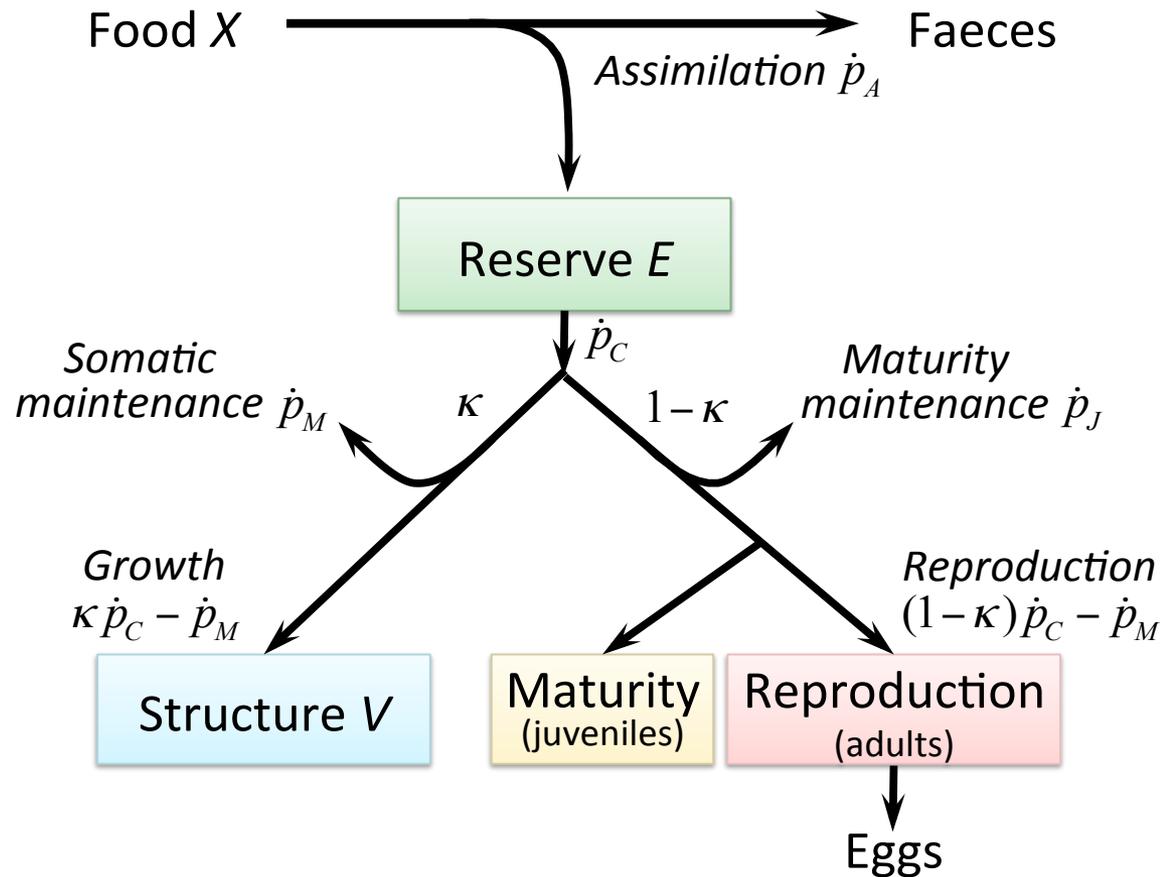
Needed: $\Xi(a, E_t)$, the solution of

$$\frac{d\xi}{d\tau} = g(\xi(\tau), E(t-a+\tau)), \quad 0 < \tau < a, \quad \xi(0) \in \Omega_b$$



Functional life history representations

Kooijman's Dynamic Energy Budget model



How can we compute model equilibria given a mildly complex life history model?



Steady state analysis

NUMERICAL CONTINUATION OF EQUILIBRIA OF PHYSIOLOGICALLY STRUCTURED POPULATION MODELS. I. THEORY

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**Theoretical
Population
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Steady-state analysis of structured population models

O. Diekmann,^a M. Gyllenberg,^{b,*} and J.A.J. Metz^{c,d}



Equilibrium analysis

- Individuals are assumed to live in an environment characterized by a (finite) set of *environment variables*:

$$E = (E_1, \dots, E_m) \in \mathbb{R}^m$$

Environment variables can include independent quantities like resource density and density of predators, but also density-dependent measures like total number of individuals or biomass in the population

- Individuals are characterized by their *individual* or *i-state*, which is a (finite) set of physiological characteristics (traits such as age, size, sex, energy reserves):

$$x = (x_1, \dots, x_k) \in \Omega \subset \mathbb{R}^k$$

- Individual and environmental state variables determine the individual life history (development, impact, reproduction, mortality)



The generic model for individual life history

- Development follows a deterministic process that is continuous in time:

$$\frac{dx}{da} = g(x, E)$$

- Individuals have an impact $\gamma(x, E)$ on their environment
- Reproduction is a function $\beta(x, E)$ of individual and environment state
- Mortality is a function $\mu(x, E)$ of individual state and environment state
- Individuals are born with an *i-state* ϕ_b that is one of a finite set of possible states at birth:

$$\phi_b \in \{\phi_1, \dots, \phi_m\}$$

with each potential state at birth ϕ_j a valid *i-state*:

$$\phi_j = (\phi_{j1}, \dots, \phi_{jk}) \in \Omega \subset \mathbb{R}^k$$



Environment dynamics

- Environment variables may in isolation follow autonomous dynamics:

$$\frac{dE}{dt} = G(E)$$

or may be functions of the population (to model direct density dependence):

$$E(t) = \int_{\Omega} \gamma(x, E) n(t, x) dx$$



Computing an equilibrium of a structured model

- In equilibrium of the structured population the expected lifetime reproduction equals 1:

$$\underbrace{\int_0^{\infty} \beta(x(a, \tilde{E}), \tilde{E}) \mathcal{F}(a, \tilde{E}) da}_{\text{Expected lifetime reproduction}} = 1$$

- In addition, the dynamics of the environment should be balanced by the impact of the population:

$$\tilde{b} \underbrace{\int_0^{\infty} \gamma(x(a, \tilde{E}), \tilde{E}) \mathcal{F}(a, \tilde{E}) da}_{\text{Lifetime impact on environment}} = G(\tilde{E})$$

or

$$\tilde{b} \underbrace{\int_0^{\infty} \gamma(x(a, \tilde{E}), \tilde{E}) \mathcal{F}(a, \tilde{E}) da}_{\text{Lifetime impact on environment}} = \tilde{E}$$

How to compute these integrals?



Computing an equilibrium of a structured model

- Probability of survival up to age a :

$$\mathcal{F}(a, \tilde{E}) = \exp \left(- \int_0^a \mu \left(x(\alpha, \tilde{E}) \right) d\alpha \right)$$

- Cumulative number of offspring up to age a :

$$H(a, \tilde{E}) = \int_0^a \beta(x(\alpha, \tilde{E}), \tilde{E}) \mathcal{F}(\alpha, \tilde{E}) d\alpha$$

- Cumulative impact up to age a :

$$I(a, \tilde{E}) = \int_0^a \gamma(x(\alpha, \tilde{E}), \tilde{E}) \mathcal{F}(\alpha, \tilde{E}) d\alpha$$



Equilibrium conditions

$$H(\infty, \tilde{E}) = \int_0^{\infty} \beta(x(\alpha, \tilde{E}), \tilde{E}) \mathcal{F}(\alpha, \tilde{E}) d\alpha = 1$$

$$\tilde{b} I(\infty, \tilde{E}) = \tilde{b} \int_0^{\infty} \gamma(x(\alpha, \tilde{E}), \tilde{E}) \mathcal{F}(\alpha, \tilde{E}) d\alpha = G(\tilde{E})$$



The computational approach

- Differentiating the probability of survival up to age $\mathcal{F}(a, \tilde{E})$ leads to:

$$\frac{d\mathcal{F}}{da} = -\mu(x(a, \tilde{E}), \tilde{E})\mathcal{F}(a, \tilde{E}), \quad \mathcal{F}(0, \tilde{E}) = 1$$

- Differentiating $H(a, \tilde{E})$ with respect to a yields:

$$\frac{dH}{da} = \beta(x(a, \tilde{E}), \tilde{E})\mathcal{F}(a, \tilde{E}), \quad H(0, \tilde{E}) = 0$$

- Differentiating $I(a, \tilde{E})$ with respect to a yields:

$$\frac{dI}{da} = \gamma(x(a, \tilde{E}), \tilde{E})\mathcal{F}(a, \tilde{E}), \quad I(0, \tilde{E}) = 0$$



Putting it all together

- The equilibrium of a non-linear structured population model is determined by:

$$H(\infty, \tilde{E}) = 1$$

$$\tilde{b} I(\infty, \tilde{E}) = G(\tilde{E})$$

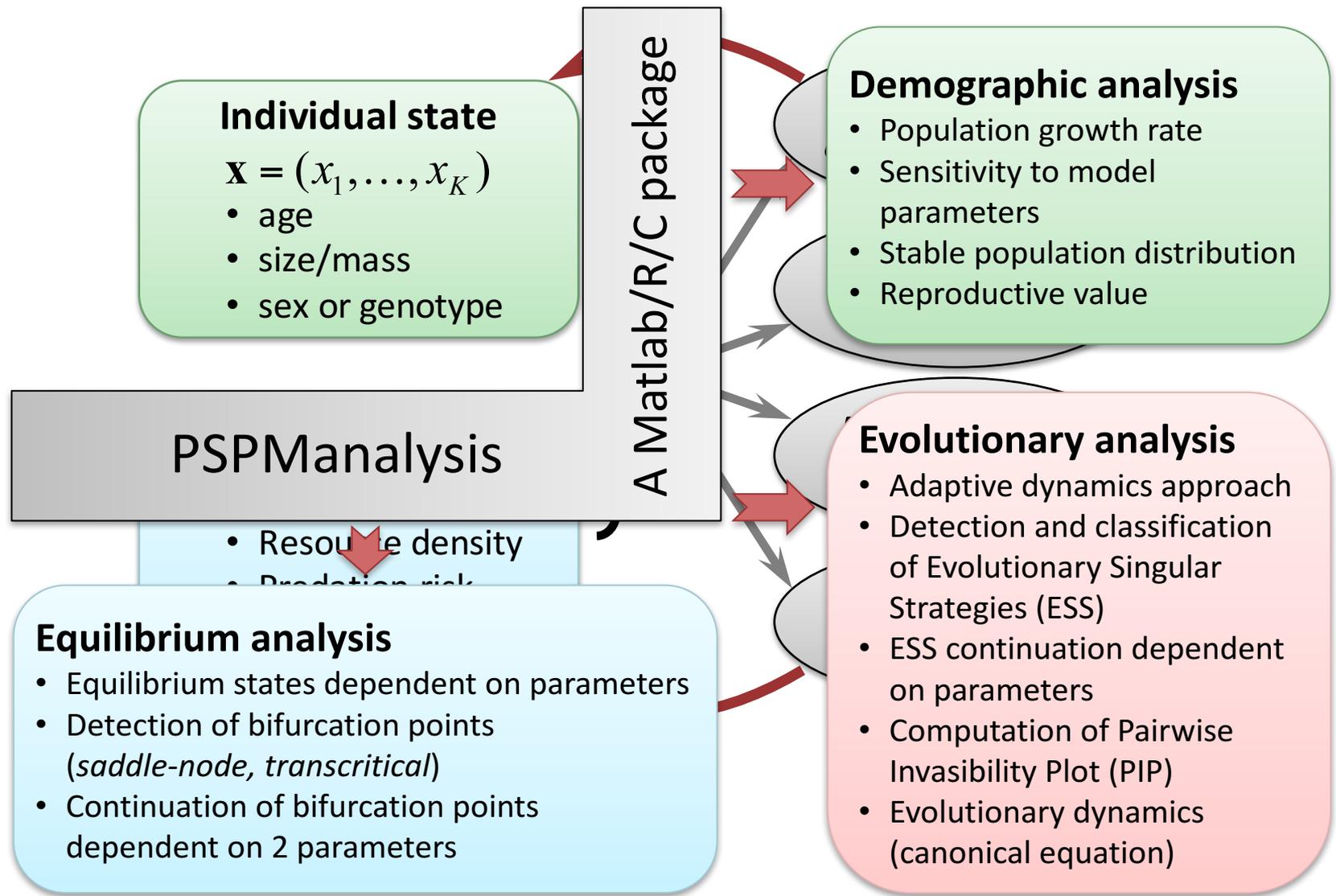
which has to be solved (*numerically and iteratively*) for the unknowns \tilde{E} and \tilde{b} .

- The values of $H(\infty, \tilde{E})$ and $I(\infty, \tilde{E})$ are evaluated by integration of the ODEs:

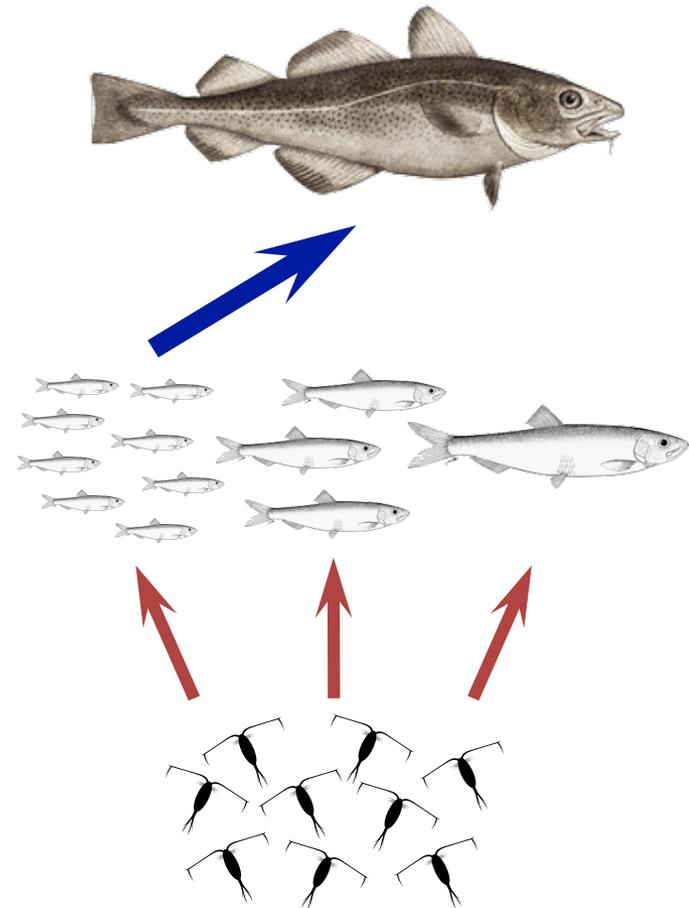
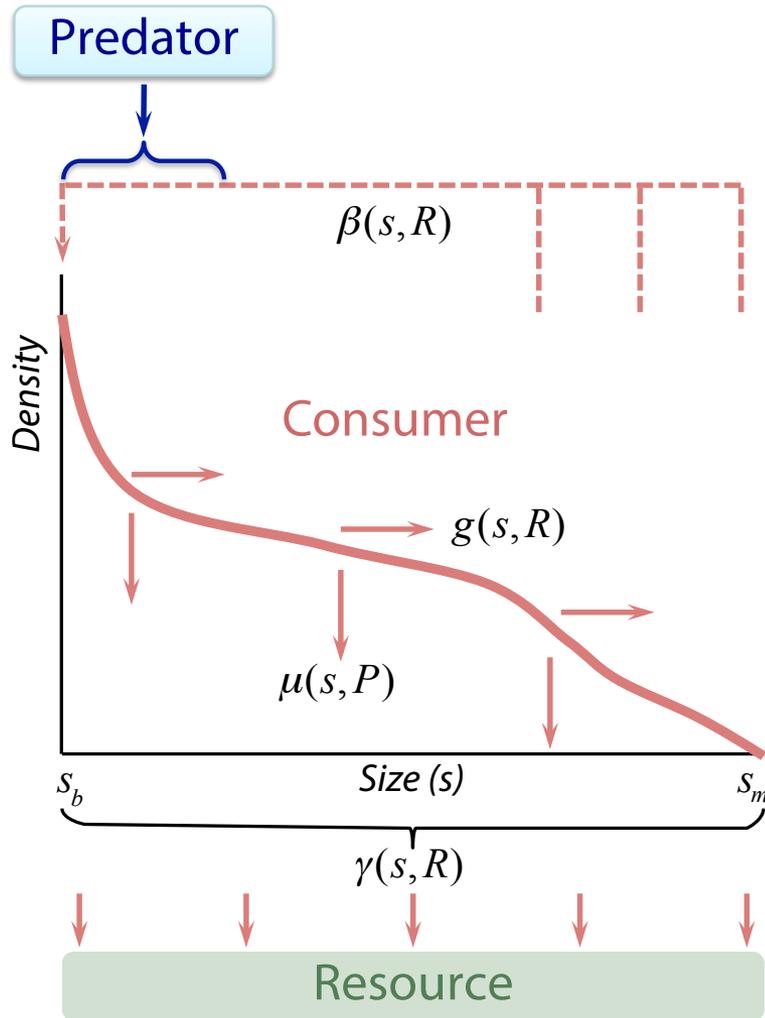
$$\left\{ \begin{array}{ll} \frac{dx}{da} = g(x(a, \tilde{E}), \tilde{E}), & x(0, \tilde{E}) = \phi_b \\ \frac{d\mathcal{F}}{da} = -\mu(x(a, \tilde{E}), \tilde{E}) \mathcal{F}(a, \tilde{E}), & \mathcal{F}(0, \tilde{E}) = 1 \\ \frac{dH}{da} = \beta(x(a, \tilde{E}), \tilde{E}) \mathcal{F}(a, \tilde{E}), & H(0, \tilde{E}) = 0 \\ \frac{dI}{da} = \gamma(x(a, \tilde{E}), \tilde{E}) \mathcal{F}(a, \tilde{E}), & I(0, \tilde{E}) = 0 \end{array} \right.$$



Physiologically Structured Population Models: Analysis



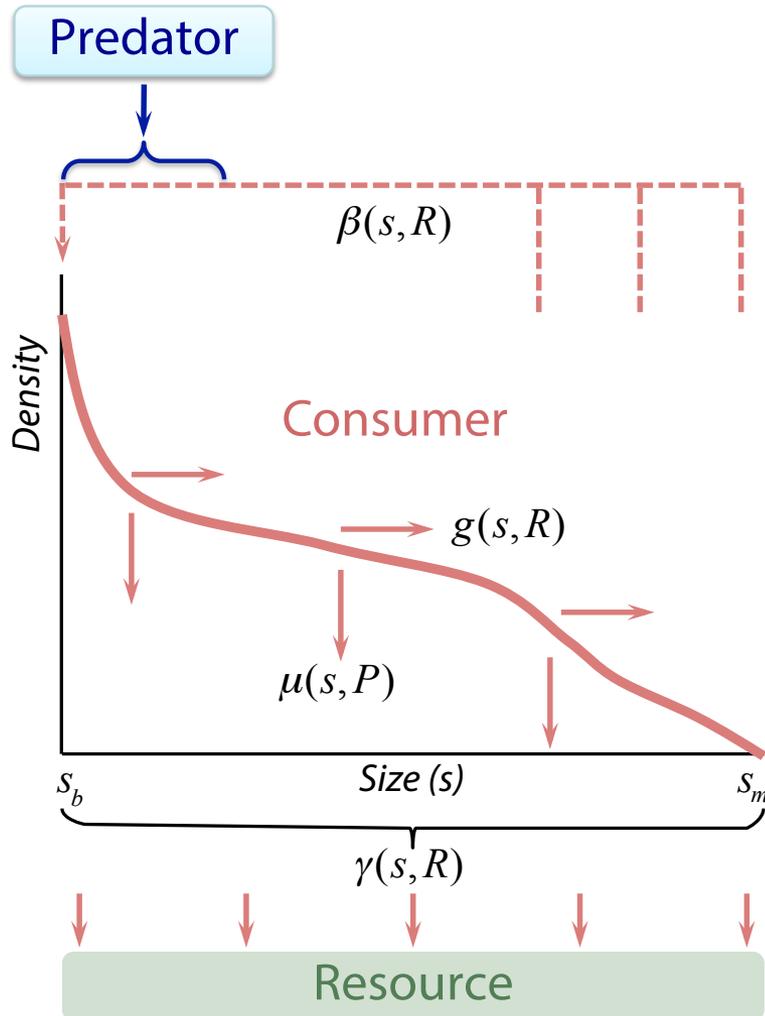
A size-structured, tritrophic example



- *Ingestion scales allometrically with size*
- *Adults continue growing, while reproducing*
- *Food-dependent growth and reproduction*
- *Maturation when reaching size threshold*



A size-structured, tritrophic example



Predator per capita growth rate:

$$\frac{B}{1 + aT_h B} - \delta$$

Consumer growth rate in size:

$$\rightarrow g(s, R) = \nu \left(s_m \frac{R}{R_h + R} - s \right)$$

Consumer fecundity:

$$\beta(s, R) = r_m \frac{R}{R_h + R} s^2 \quad \text{if } s \geq s_j$$

Consumer mortality:

$$\mu(s, P) = \begin{cases} \mu_b + \frac{aP}{1 + aT_h B} & \text{if } s < s_V \\ \mu_b & \text{otherwise} \end{cases}$$

Consumer foraging:

$$\gamma(s, R) = I_m \frac{R}{R_h + R} s^2$$

Resource turnover:

$$\rho (R_{max} - R)$$



A size-structured, tritrophic example

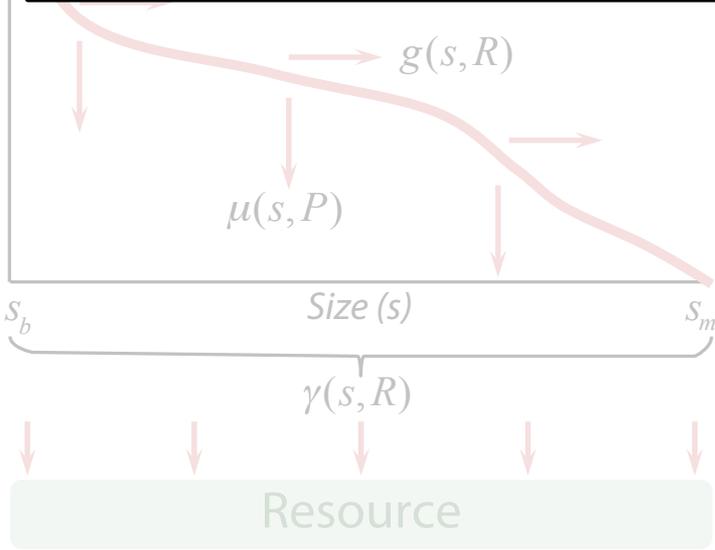
Predator per capita growth rate:

```

void Development(int lifestage[POPULATION_NR],
                double *istate[POPULATION_NR],
                double *birthstate[POPULATION_NR],
                int BirthStateNr, double E[],
                double development[POPULATION_NR][I_STATE_DIM])
{
    // Implement the development function below
    development[0][0] = NU*(SM*R/(R + RH) - S);

    return;
}
    
```

Density



$\geq s_j$

Consumer mortality:

$$\mu(s, P) = \begin{cases} \mu_b + \frac{aP}{1 + aT_h B} & \text{if } s < s_V \\ \mu_b & \text{otherwise} \end{cases}$$

Consumer foraging:

$$\gamma(s, R) = I_m \frac{R}{R_h + R} s^2$$

Resource turnover:

$$\rho (R_{max} - R)$$



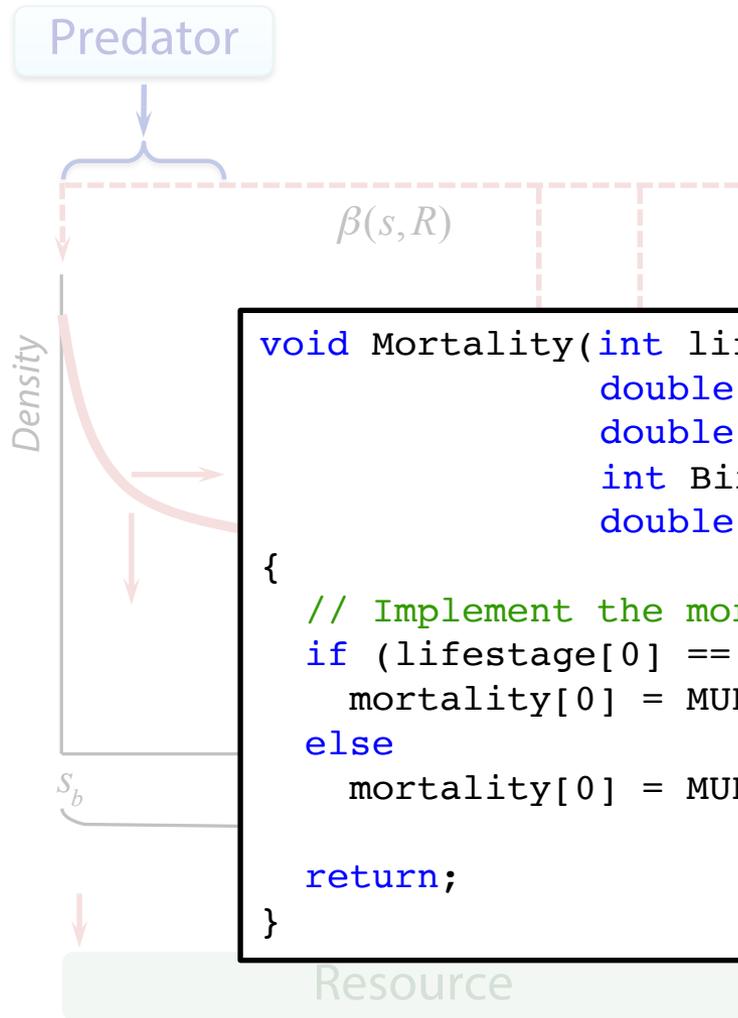
A size-structured, tritrophic example

Predator per capita growth rate:

$$\frac{B}{1 + aT_h B} - \delta$$

Consumer growth rate in size:

$$g(s, R) = \nu \left(s_m \frac{R}{R_h + R} - s \right)$$



```

void Mortality(int lifestage[POPULATION_NR],
               double *istate[POPULATION_NR],
               double *birthstate[POPULATION_NR],
               int BirthStateNr, double E[],
               double mortality[POPULATION_NR])
{
  // Implement the mortality function below
  if (lifestage[0] == 0)
    mortality[0] = MUB + A*P/(1+A*TH*B);
  else
    mortality[0] = MUB;

  return;
}

```

if $s \geq s_j$

$\frac{1}{T_h B}$ if $s < s_v$

otherwise

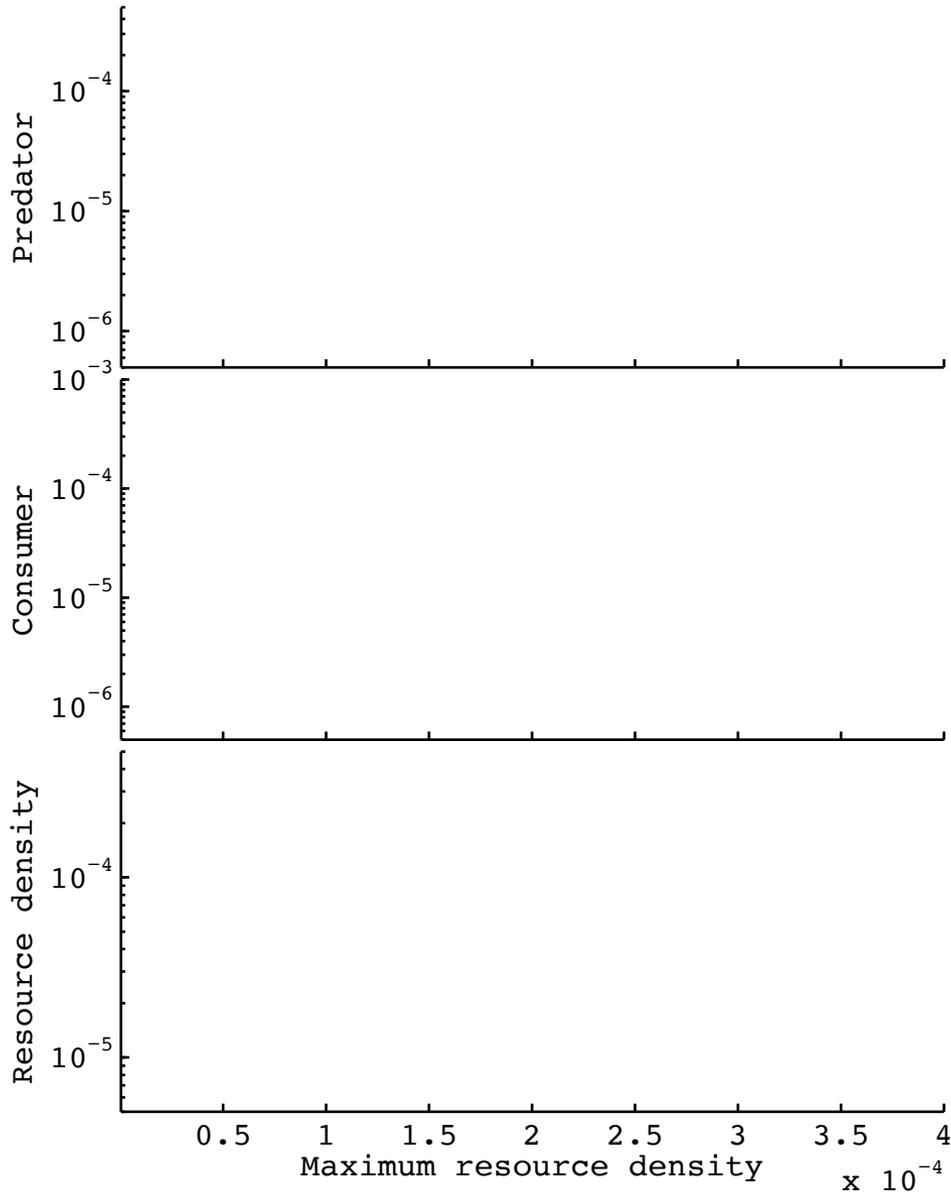
$$\rho (R_{max} - R)$$



Equilibrium analysis of non-linear, density dependent models

1. Starting from a trivial equilibrium

```
>> [data1, repl, bp1, bt1] = ...  
    PSPMequi('Test', 'EQ', [1.0E-06 1.0E-06],...);
```





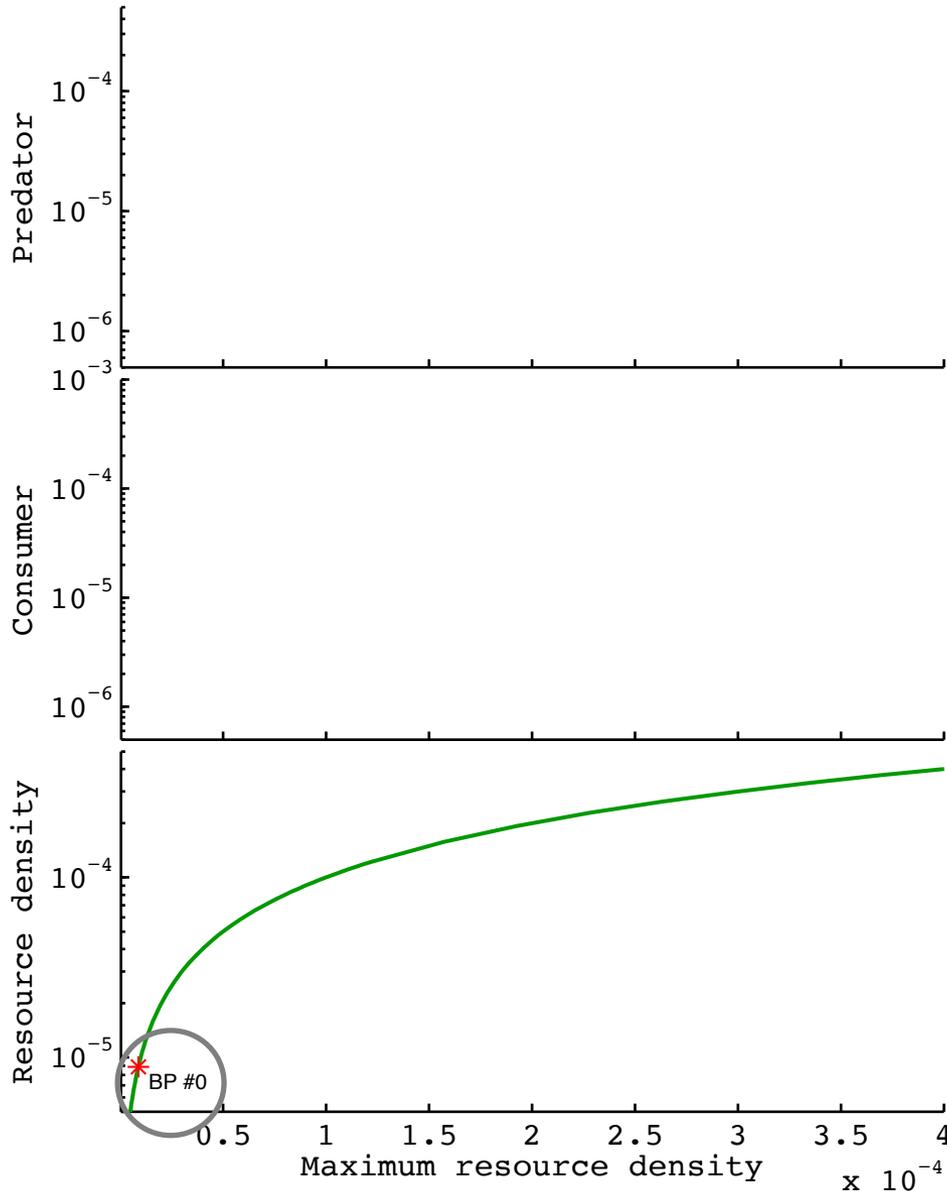
Equilibrium analysis of non-linear, density dependent models

1. Starting from a trivial equilibrium

```
>> [data1, rep1, bp1, bt1] = ...  
    PSPMequi('Test', 'EQ', [1.0E-06 1.0E-06],...);
```

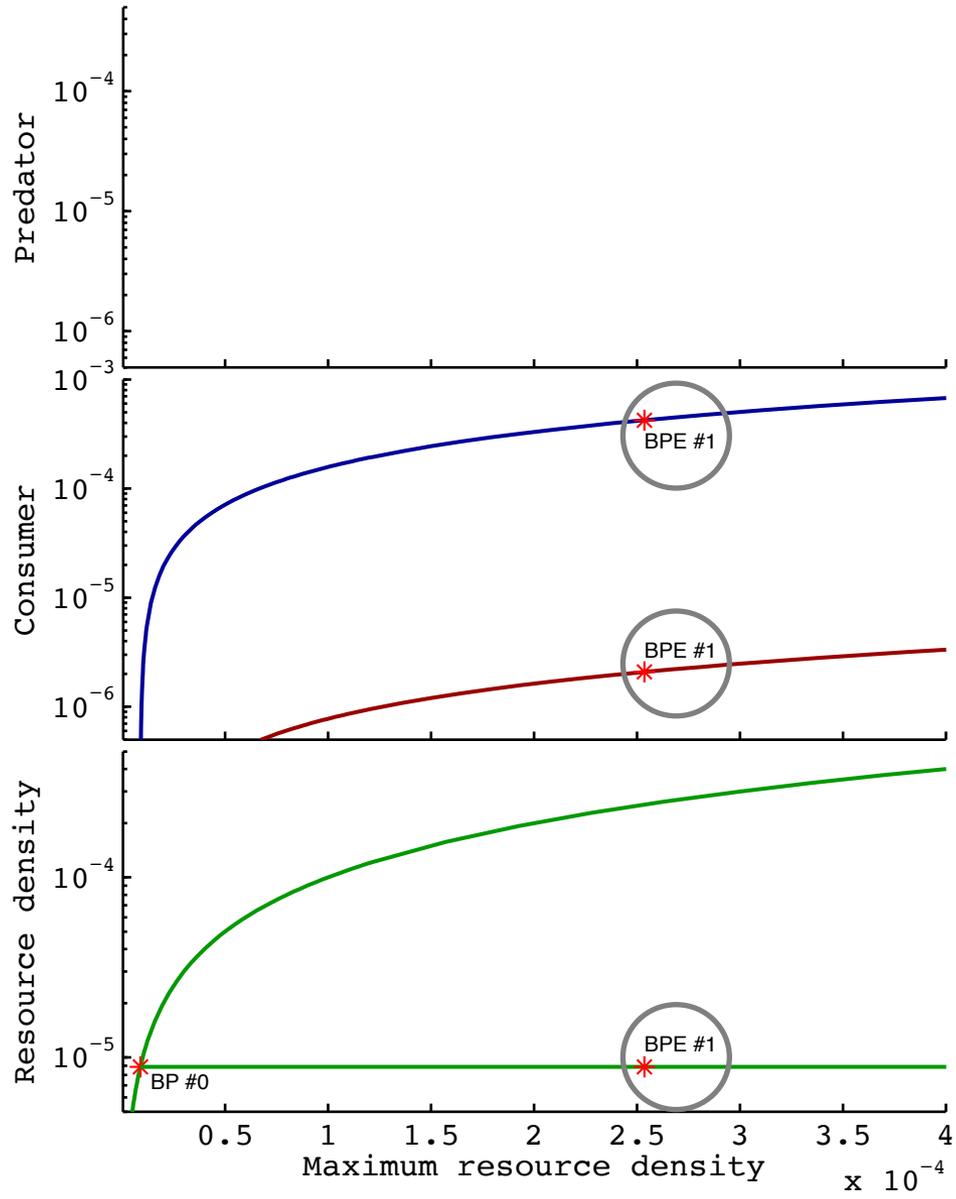
2. Starting from the detected consumer invasion point

```
>> [data2, rep2, bp2, bt2] =  
    PSPMequi('Test', 'EQ', bp1([1 2 5]),...);
```





Equilibrium analysis of non-linear, density dependent models



1. Starting from a trivial equilibrium

```
>> [data1, rep1, bp1, bt1] = ...  
    PSPMequi('Test', 'EQ', [1.0E-06 1.0E-06],...);
```

2. Starting from the detected consumer invasion point

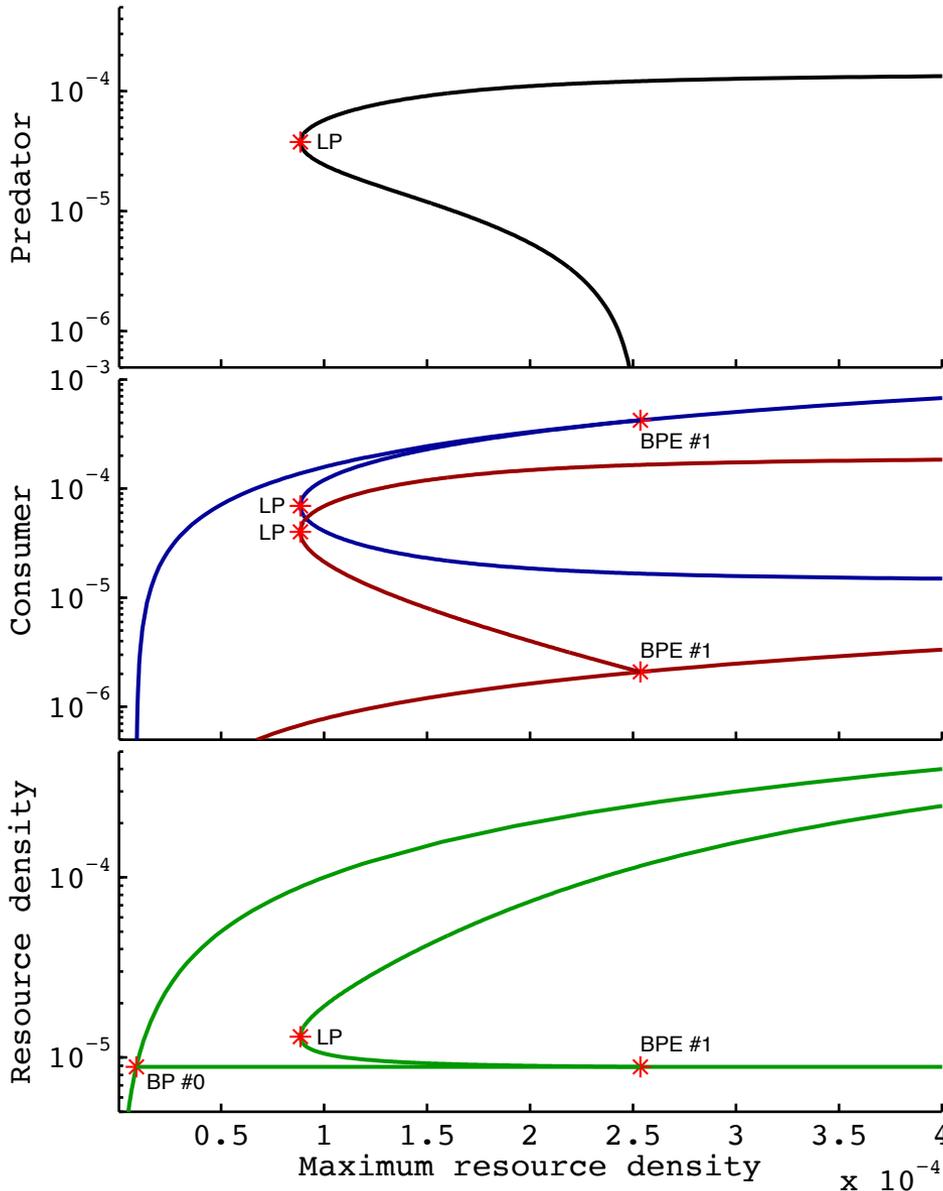
```
>> [data2, rep2, bp2, bt2] =  
    PSPMequi('Test', 'EQ', bp1([1 2 5]),...);
```

3. Starting from the detected predator invasion point

```
>> [data3, rep3, bp3, bt3] =  
    PSPMequi('Test', 'EQ', bp2([1 2 3 7 5]),...);
```



Equilibrium analysis of non-linear, density dependent models



1. Starting from a trivial equilibrium

```
>> [data1, rep1, bp1, bt1] = ...  
    PSPMequi('Test', 'EQ', [1.0E-06 1.0E-06],...);
```

2. Starting from the detected consumer invasion point

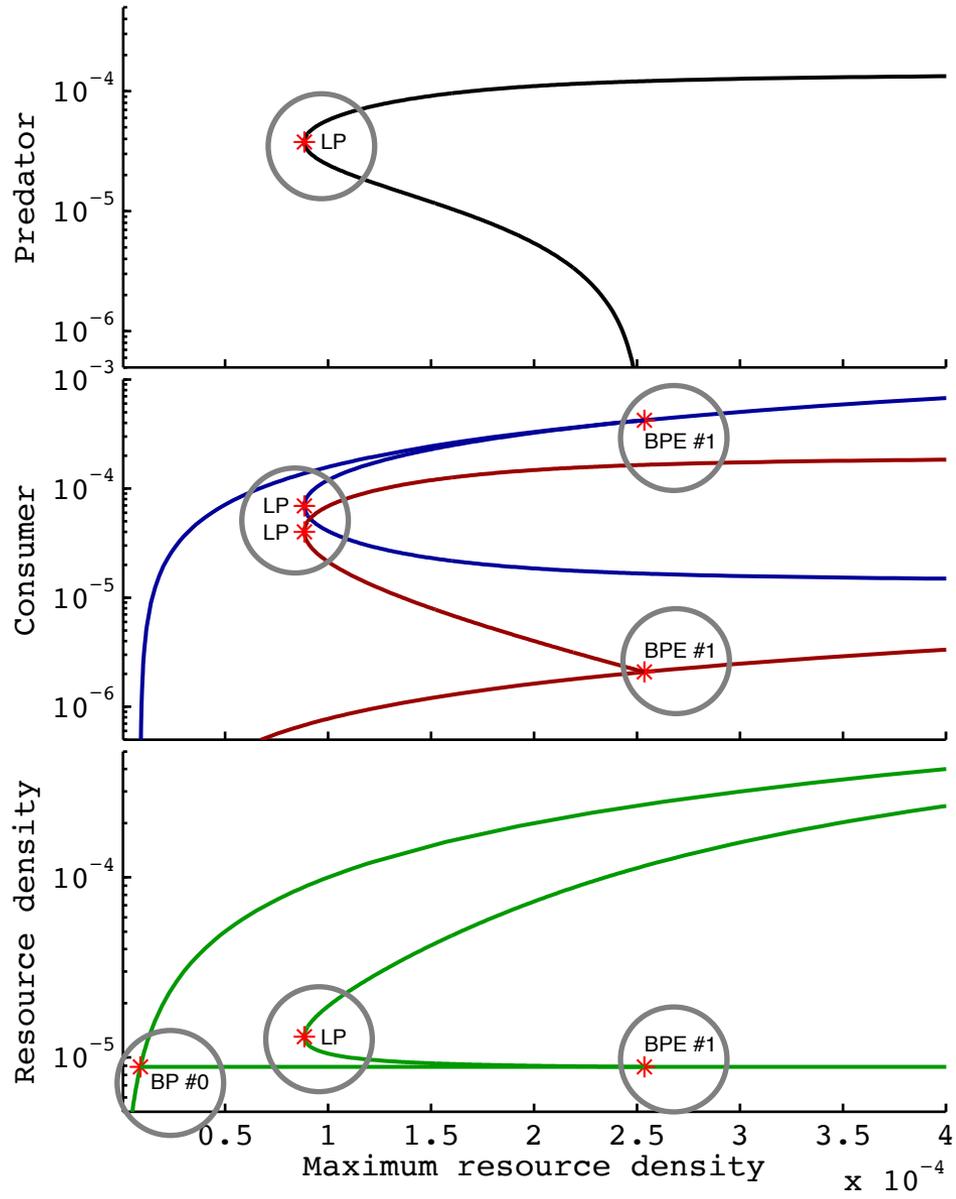
```
>> [data2, rep2, bp2, bt2] =  
    PSPMequi('Test', 'EQ', bp1([1 2 5]),...);
```

3. Starting from the detected predator invasion point

```
>> [data3, rep3, bp3, bt3] =  
    PSPMequi('Test', 'EQ', bp2([1 2 3 7 5]),...);
```



Equilibrium analysis of non-linear, density dependent models



1. Continuing consumer invasion boundary

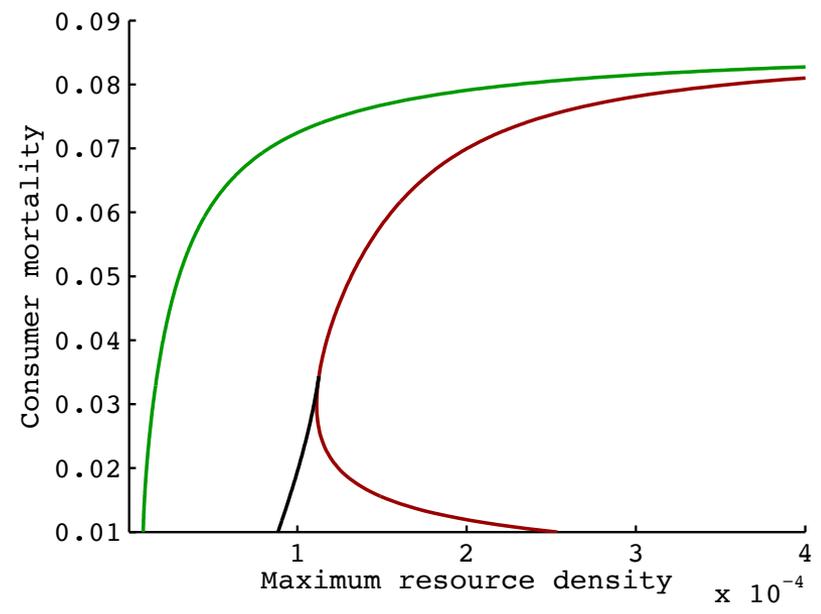
```
>> [data4, rep4] = ...  
    PSPMequi('Test', 'BP', [bp1([1 2]) 0.01], ...);
```

2. Continuing predator invasion boundary

```
>> [data5, rep5] =  
    PSPMequi('Test', 'BPE', [bp2([1 2 5]) 0.01], ...);
```

3. Continuing predator persistence boundary

```
>> [data6, rep6] =  
    PSPMequi('Test', 'LP', [bp3([1:5]) 0.01], ...);
```





Evolutionary Stable Strategy (ESS)

- Selection gradient:

$$\left. \frac{d\mathcal{R}_0}{dq} \right|_{q=q_{res}} = \left. \frac{d}{dq} \int_0^{\infty} \beta(s(a, \tilde{R}), \tilde{R}) p(a, s(\cdot, \tilde{R}), \tilde{R}) da \right|_{q=q_{res}}$$

(computed numerically, while computing ecological equilibrium as function of a life history parameter)

- Evolutionary endpoint:

$$\left. \frac{d\mathcal{R}_0}{dq} \right|_{q=q_{res}} = 0$$

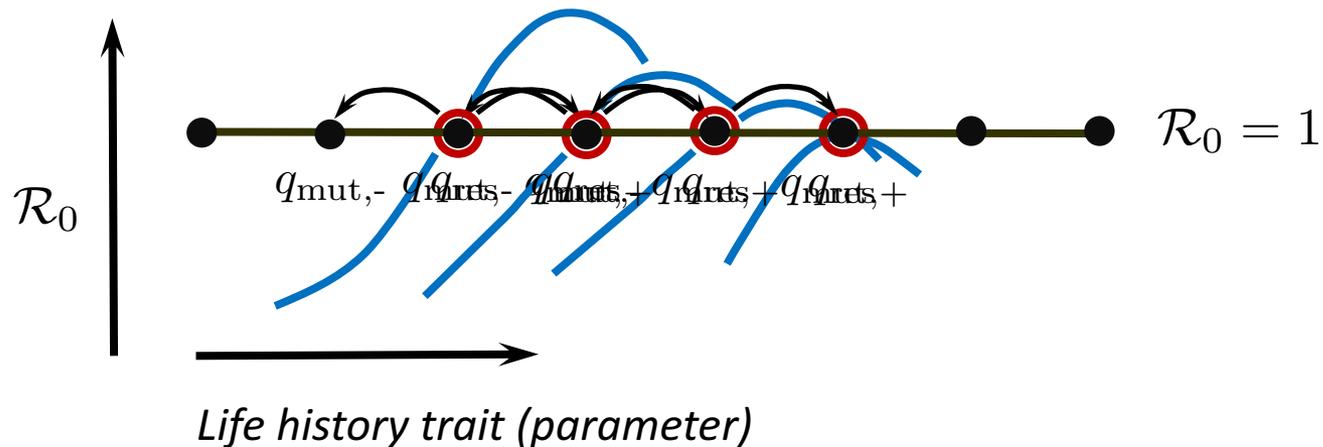
- Evolutionary dynamics: (Canonical equation of adaptive dynamics):

$$\frac{dq_{res}}{d\tau} \propto \mu(q_{res}) \frac{\sigma_0(q_{res})}{2} \tilde{b}(q_{res}) \left. \frac{d\mathcal{R}_0}{dq} \right|_{q=q_{res}}$$



Adaptive Dynamics

- Evolution in environment set by ecological dynamics
 - **Resident-mutant interaction**: Resident sets the environment, $\tilde{R}(q_{\text{res}})$, which determines the mutant's fitness
- Separation of evolutionary and ecological timescale
 - **Mutation limitation**: Convergence to (new) ecological equilibrium between mutation events
 - **Domination or demise**: Positive fitness (mutant growth) results in take-over, negative fitness leads to mutant disappearance





Consumer-resource model for ESS analysis

Life history functions:

$$\gamma(s, R) = I_{max} R s^q$$

$$g(s, R) = \kappa(s) (\sigma \gamma(s, R) - T s^p)$$

$$\beta(s, R) = \frac{(1 - \kappa(s)) (\sigma \gamma(s, R) - T s^p)}{s_b}$$

$$\kappa(s) = \begin{cases} 1 & \text{if } s \leq s_j \\ 1 - 3 \left(\frac{s - s_j}{s_m - s_j} \right)^2 + 2 \left(\frac{s - s_j}{s_m - s_j} \right)^3 & \text{otherwise} \end{cases}$$



Consumer-resource model for ESS analysis

Population-level model:

$$\frac{\partial c(t, s)}{\partial t} + \frac{\partial (g(s, R)c(t, s))}{\partial s} = -\mu c(t, s)$$

$$g(s_b, R) c(t, s_b) = \int_{s_b}^{s_m} \beta(s, R) c(t, s) ds$$

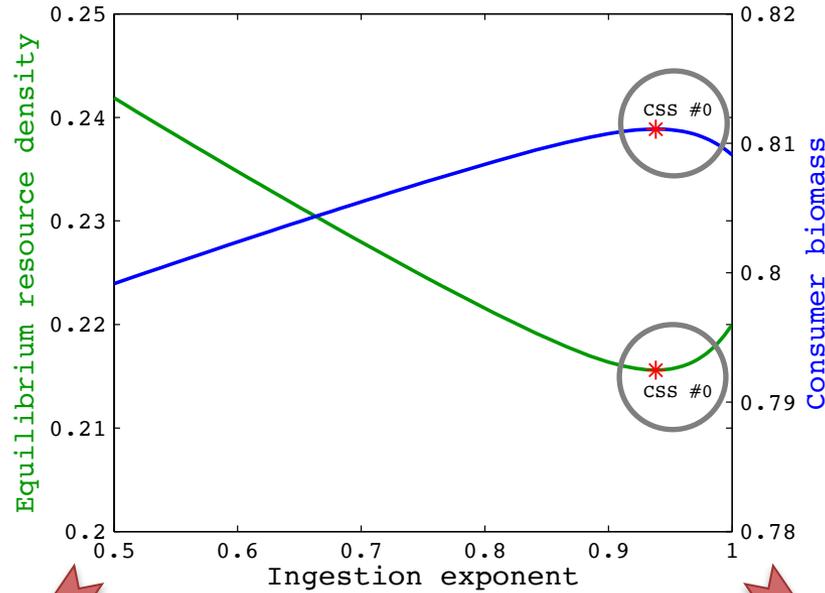
$$\frac{dR}{dt} = \delta (R_{max} - R) - \int_{s_b}^{s_m} \gamma(s, R) c(t, s) ds$$



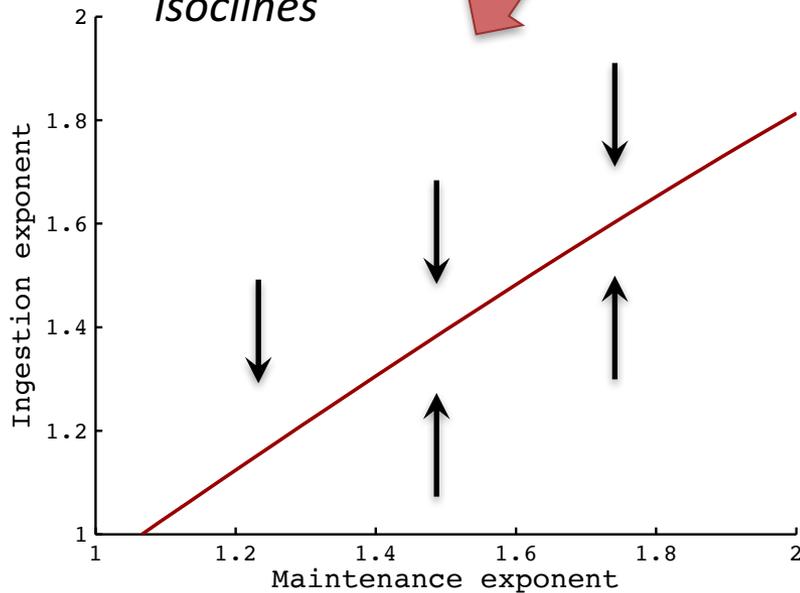
Evolutionary analysis through adaptive dynamics

Consumer ingestion:
 $\sim s^q$

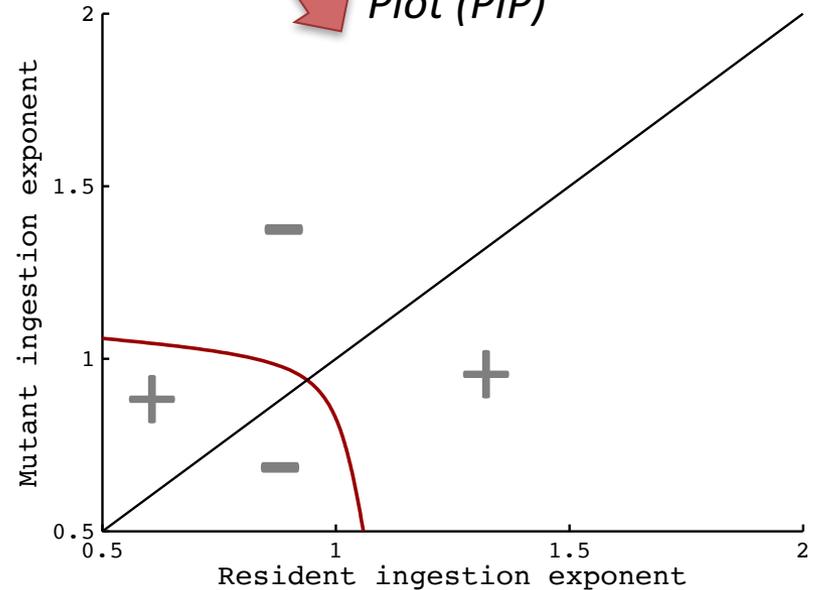
Consumer maintenance:
 $\sim s^p$



Evolutionary isoclines



Pairwise Invasibility Plot (PIP)

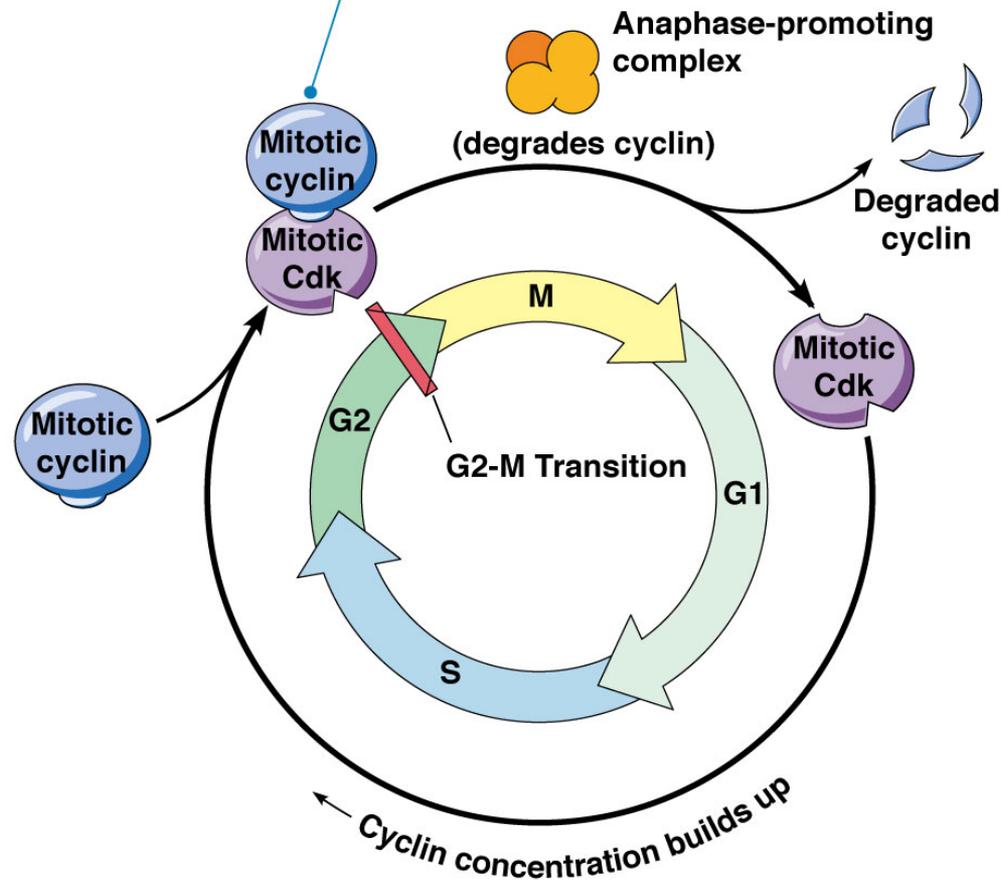




Cell cycle control: Cyclin-dependent kinases

Active mitotic Cdk-cyclin stimulates:

1. Nuclear envelope breakdown
2. Chromosome condensation
3. Mitotic spindle formation
4. Targeted protein degradation





Tyson & Novak model for cell division

$$\frac{dm}{dt} = \mu m \left(1 - \frac{m}{m^*}\right) \frac{S}{\xi + S}$$

$$\frac{d[CycB_T]}{dt} = k_1 - (k'_2 + k''_2[Cdh1]) [CycB_T]$$

$$\frac{d[Cdc20_T]}{dt} = k'_5 + k''_5 \frac{([CycB_T]m)^n}{J_5^n + ([CycB_T]m)^n} - k_6[Cdc20_T]$$

$$[Cdh1] = G(k'_3 + k''_3[Cdc20_T], k_4m[CycB], J_3, J_4)$$

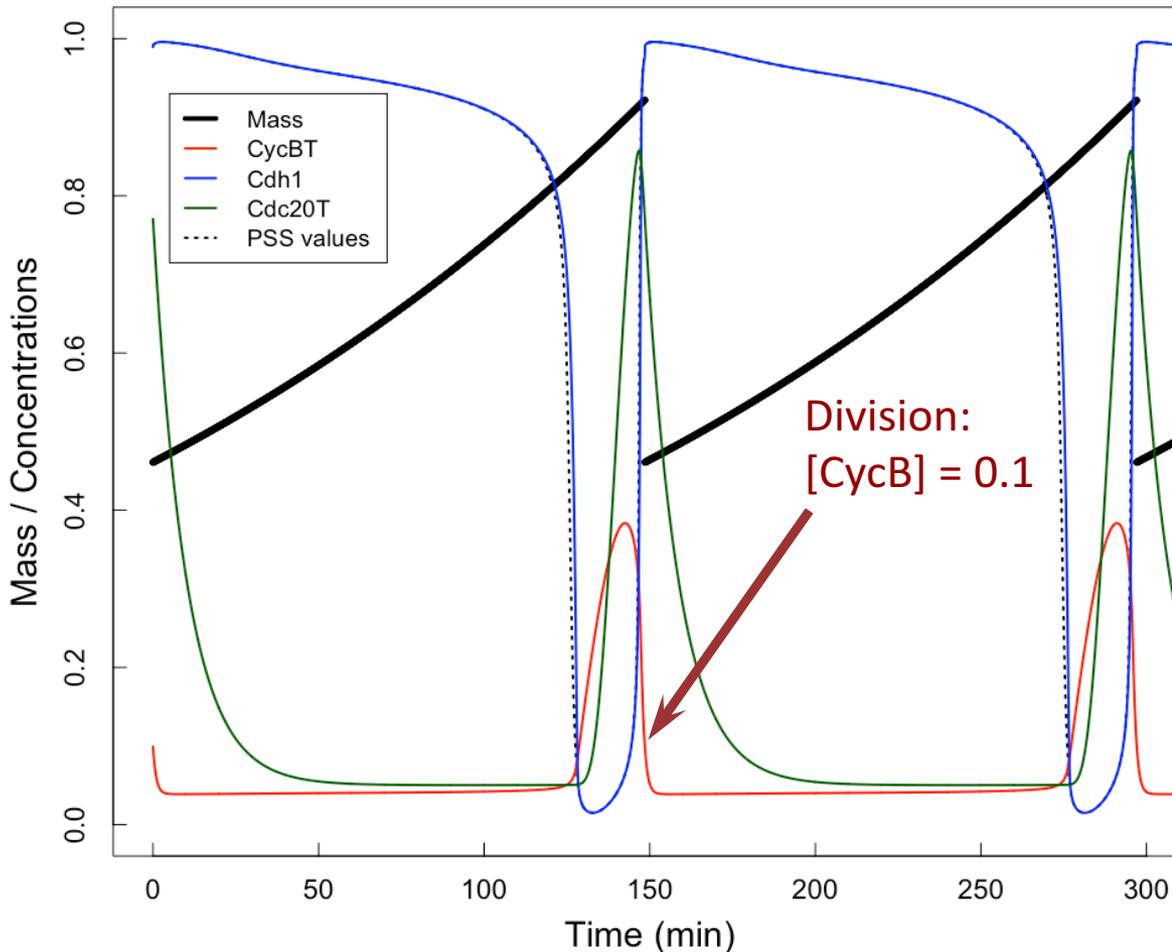
With G the is the Goldbeter-Koshland function:

$$G(v_1, v_2, J_1, J_2) = \frac{2v_1J_2}{(v_2 - v_1 + v_1J_2 + v_2J_1) + \sqrt{(v_2 - v_1 + v_1J_2 + v_2J_1)^2 - 4(v_2 - v_1)v_1J_2}}$$



Cell division

Time dynamics of mass, CycBT, Cdh1 and Cdc20T



- Cell divides when $[CycB]$ drops below 0.1
- Splits in 2 daughter cells with mass ϕm and $(1 - \phi)m$
- Both daughter have $[Cdc20T]$ equal to their mother



A structured model for an entire cell population: Equilibrium states when competing for substrate

Single cell model (core of the population model):

$$\frac{dm}{dt} = \mu m \left(1 - \frac{m}{m^*}\right) \frac{S}{\xi + S}$$

$$\frac{d[CycB_T]}{dt} = k_1 - (k'_2 + k''_2[Cdh1]) [CycB_T]$$

$$\frac{d[Cdc20_T]}{dt} = k'_5 + k''_5 \frac{([CycB_T]m)^n}{J_5^n + ([CycB_T]m)^n} - k_6[Cdc20_T]$$

$$[Cdh1] = G(k'_3 + k''_3[Cdc20_T], k_4m[CycB], J_3, J_4)$$

Competing for a limiting substrate:

$$\frac{dS}{dt} = D(S_0 - S) - \int_0^\infty \mu m \left(1 - \frac{m}{m^*}\right) Q \frac{S}{\xi + S} n(t, s) ds$$

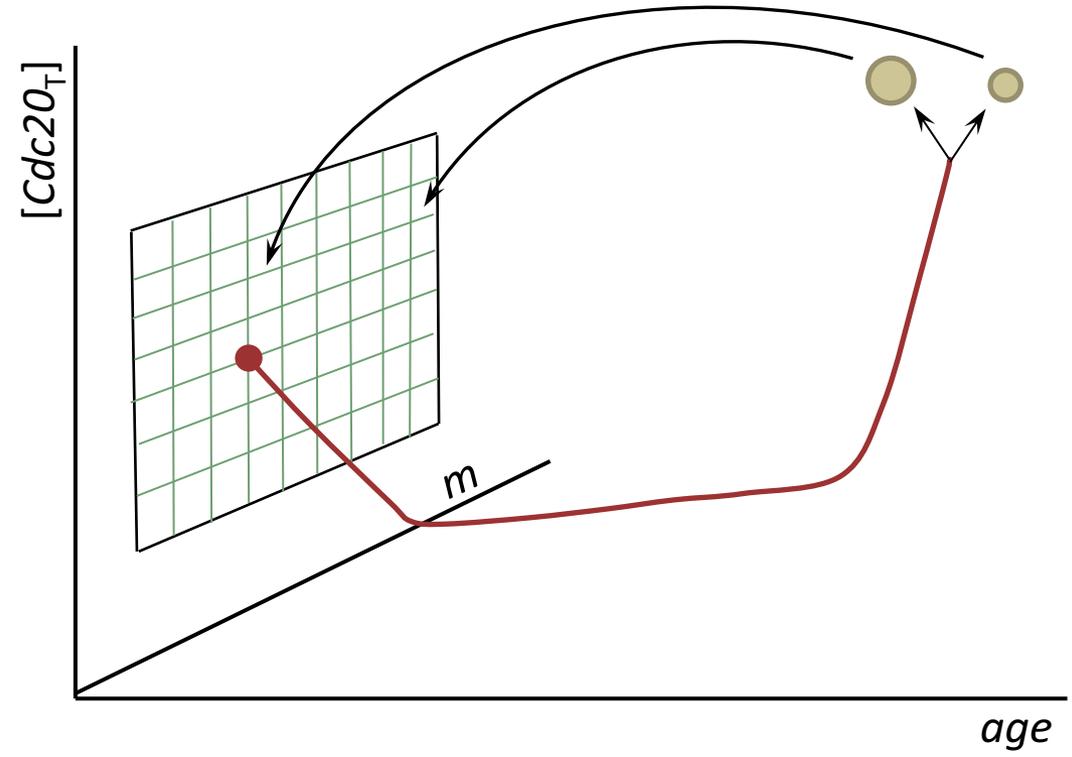


A structured model for an entire cell population: Computational approach

- Take a 40 x 40 grid of initial states at birth covering a range of masses at birth $m = 0.3, \dots, 1.0$ and $[Cdc20_T] = 0.7, \dots, 1.4$
- From each of these states of birth, compute the life history trajectory, including the contribution of daughter cells to potential states at birth

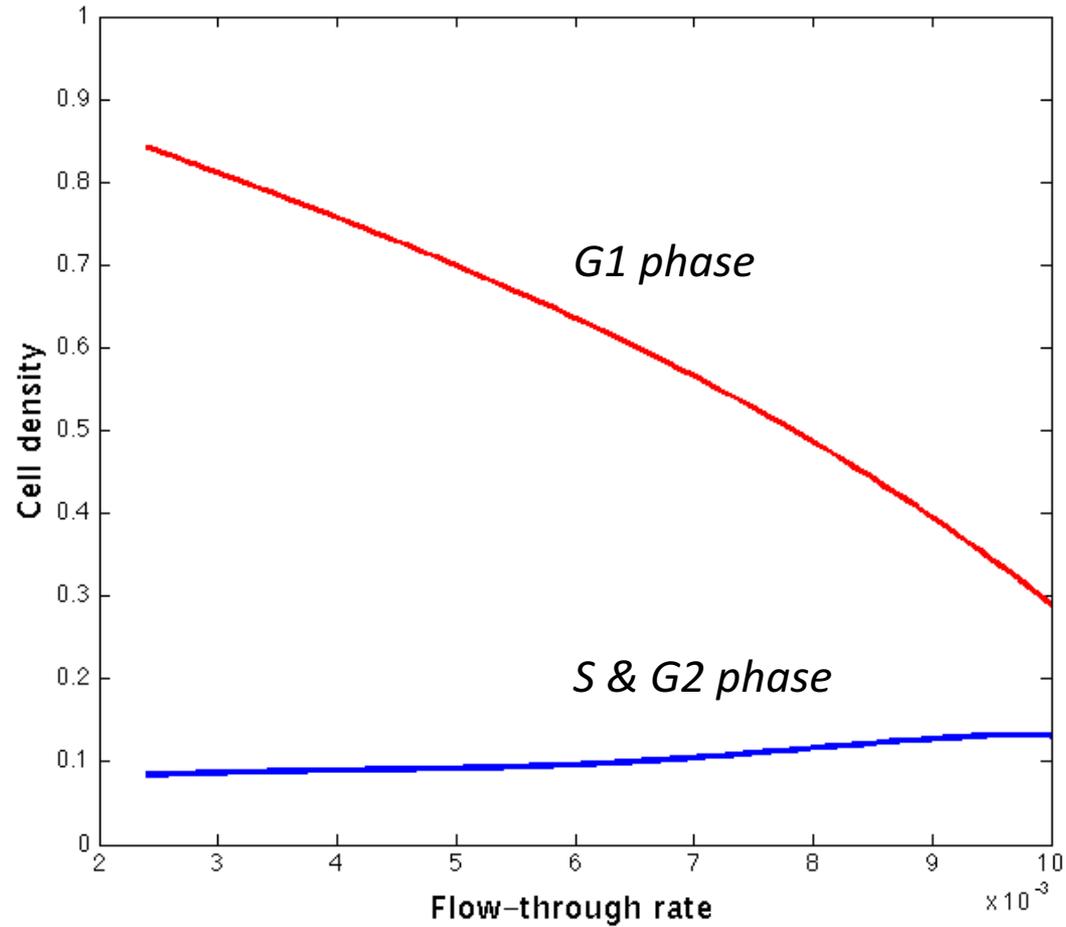
▪ Next-generation matrix A

- Dominant eigenvalue should equal 1 ($= R_0$)
- Stable distribution of states at birth
- Stable cell size distribution



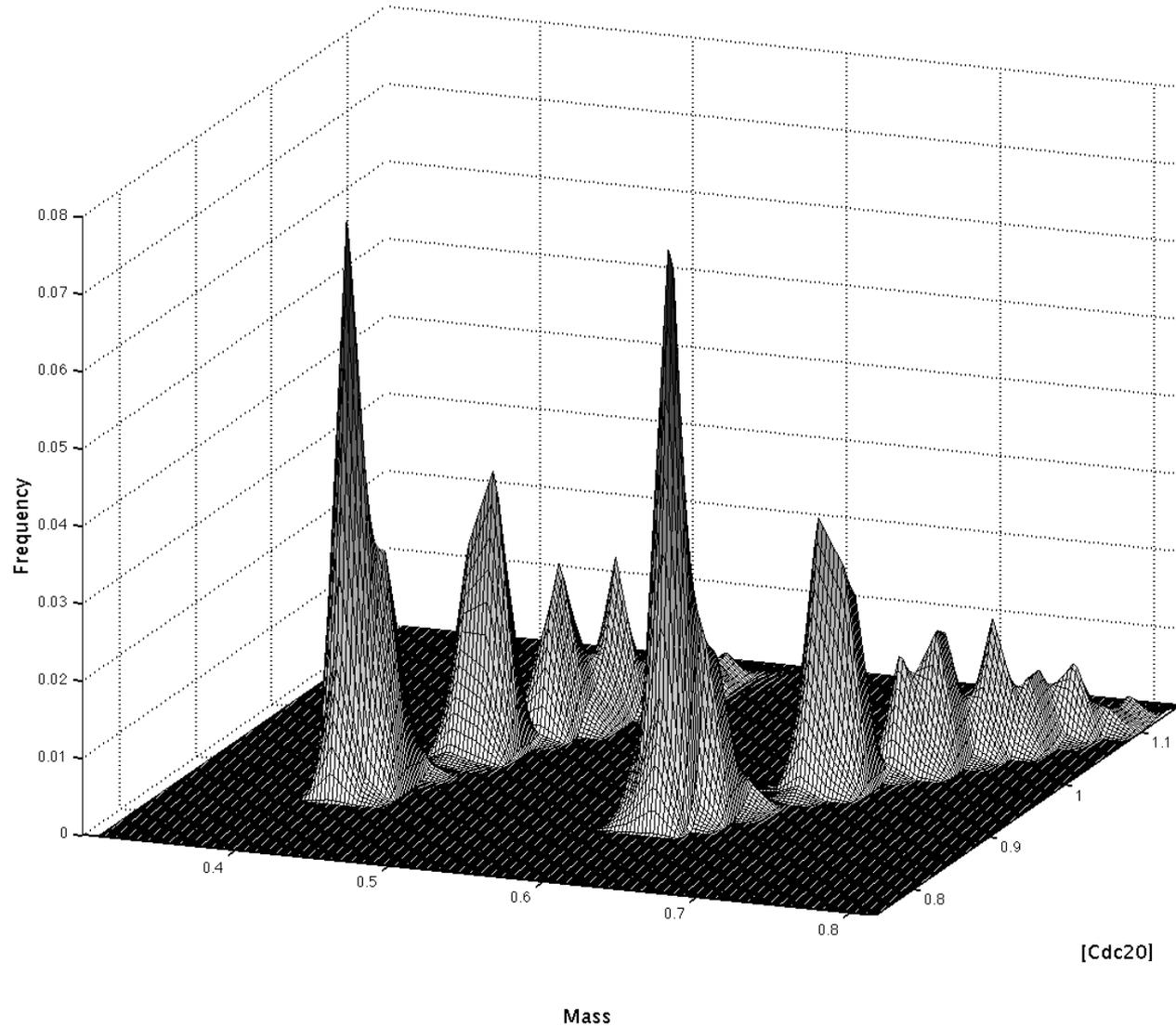


Competing for resources





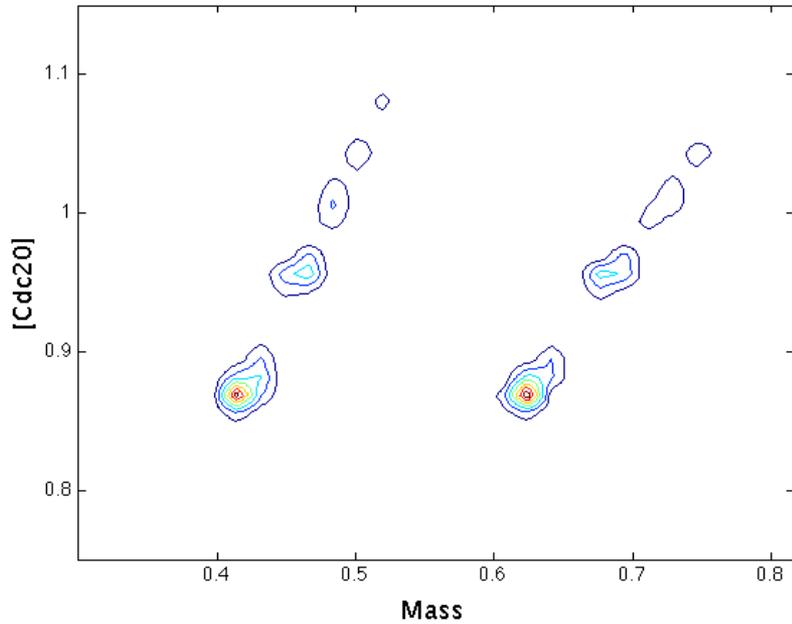
High flow-through rate of medium: ($D = 0.01$)



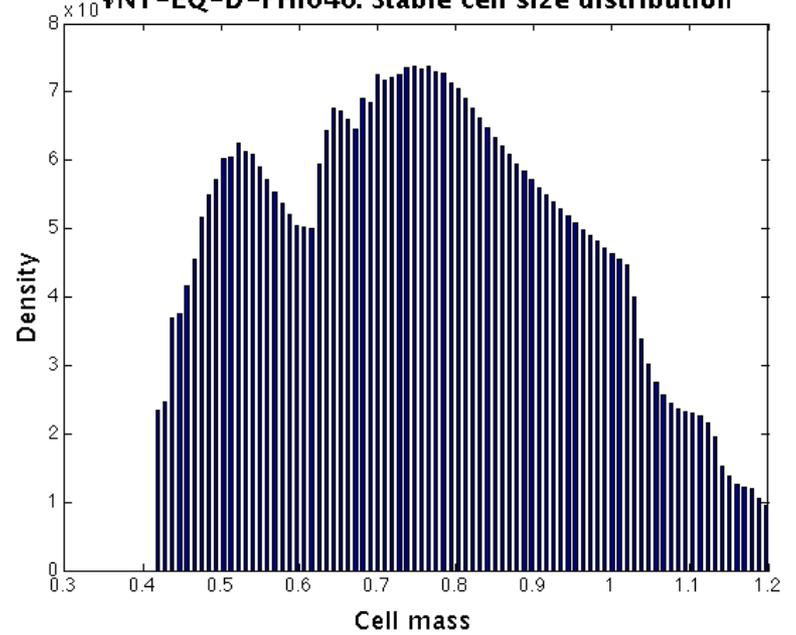


High flow-through rate of medium: ($D = 0.01$)

TNT-EQ-D-PHI040: Stable birth distribution

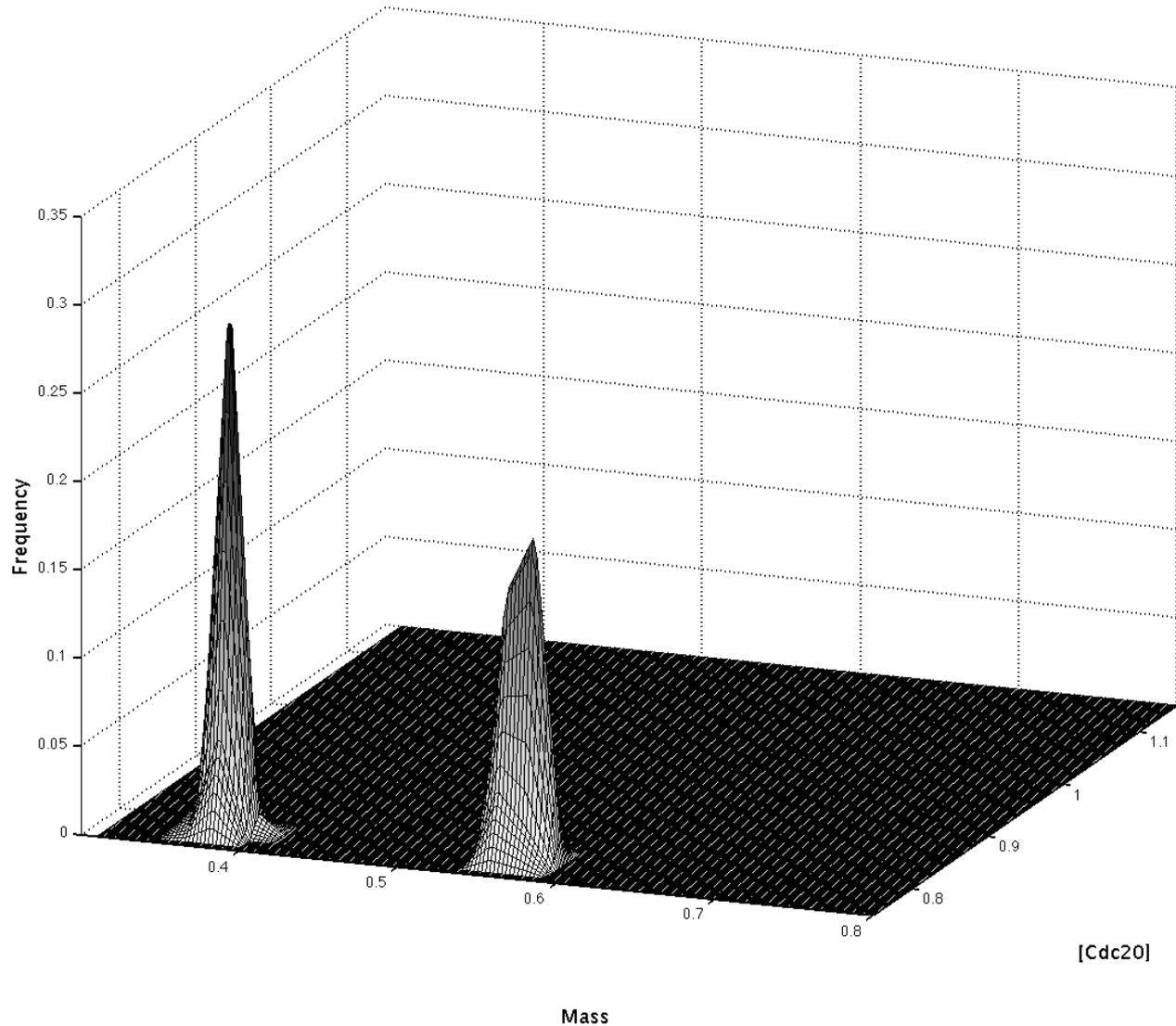


TNT-EQ-D-PHI040: Stable cell size distribution





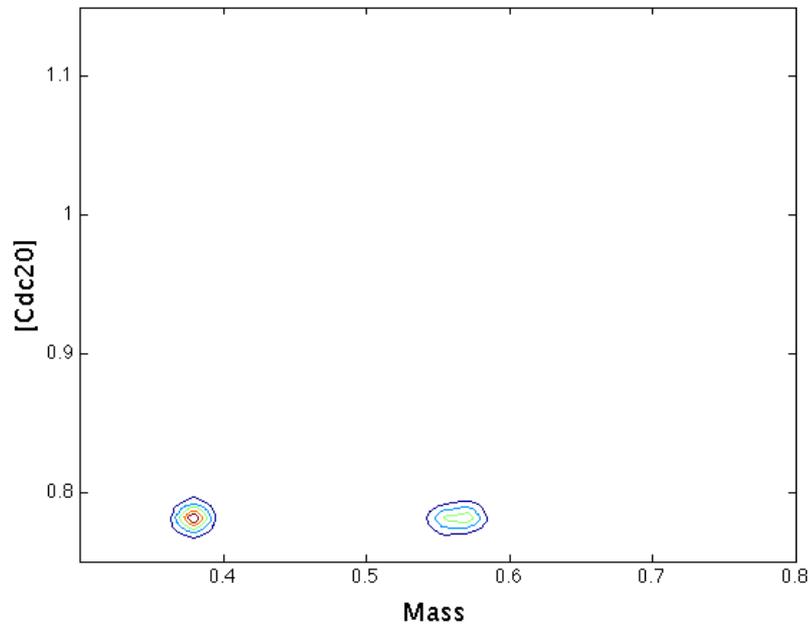
Low flow-through rate of medium ($D = 0.006$)





Low flow-through rate of medium ($D = 0.006$)

TNT-EQ-D-PHI040: Stable birth distribution



TNT-EQ-D-PHI040: Stable cell size distribution

