

# THEORY-BASED ECOLOGY

*A Darwinian approach*

$$SN = \alpha^{-1} \delta \tau$$
$$s_i = (s_{i1}, s_{i2}) = \left( \frac{\partial r_i}{\partial R_1}, \frac{\partial r_i}{\partial R_2} \right) \text{ and } l_j = (l_{j1}, l_{j2}) = \left( \frac{\partial R_1}{\partial N_j}, \frac{\partial R_2}{\partial N_j} \right)$$
$$a_{ij} = -\frac{\partial r_i}{\partial N_j} = -\frac{\partial r_i}{\partial R} \frac{\partial R}{\partial N_j} = -s_i \cdot l_j$$
$$\det a = \det S \det T$$
$$\frac{dR}{dt} = a(R - R^*) - q(R)N$$
$$\frac{dN}{dt} = r(R)N = (r(R) - w)N$$
$$\text{por}(w, m, x)$$

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# Theory in ecology?

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What to do, if Real World  
is more complicated, than  
Lotka-Volterra?

More complicated  
models will be  
even worse!  
Forget theory!

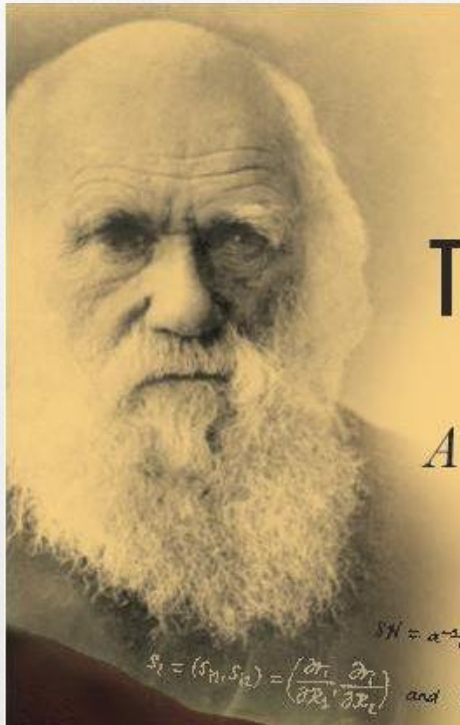
Plethora of  
sophisticated  
models, integrated  
verbally.

Theory, that  
integrates!  
**???**



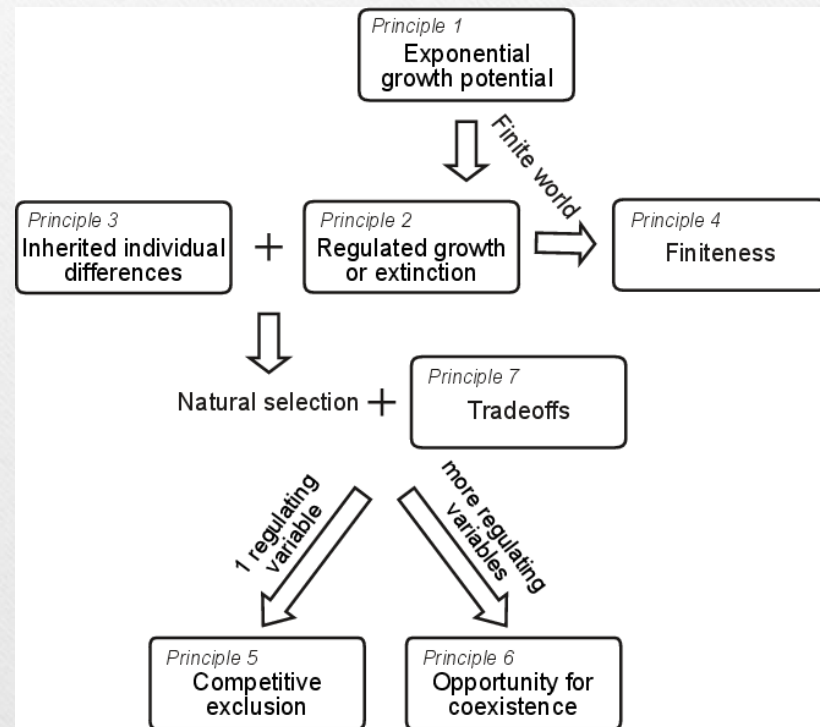
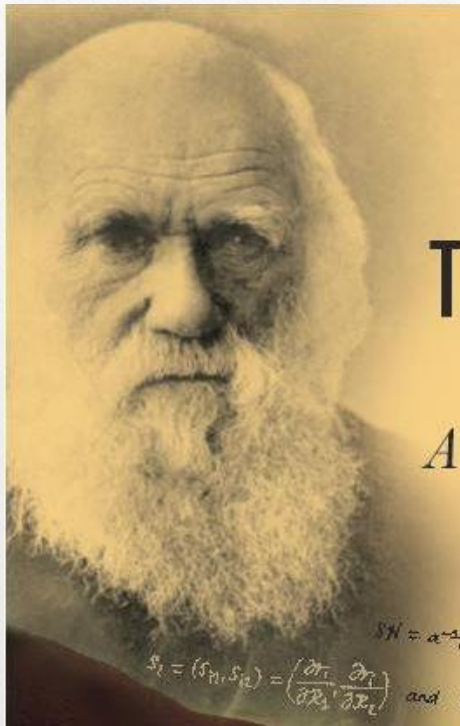
# Darwinian principles

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- Exponential growth.
- Growth regulation.
- Inherited differences.
- Survival of the fittest.
- Constraints and tradeoffs.
- Robust coexistence.
- Finiteness of populations.

# Darwinian principles



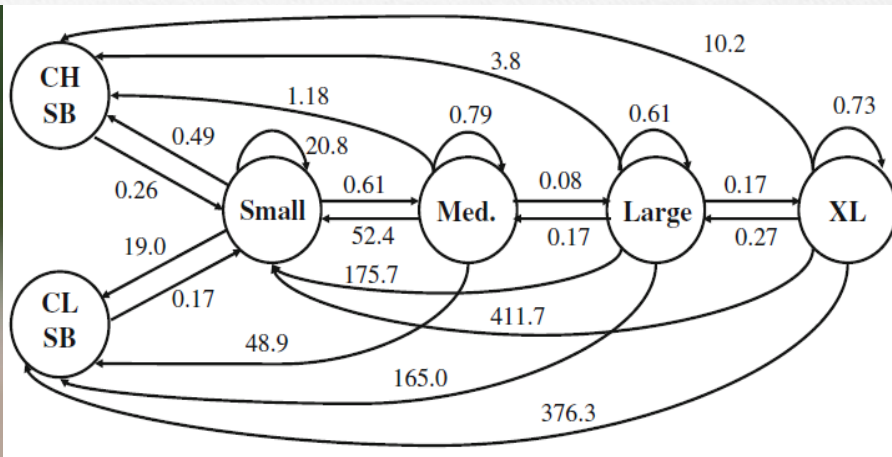


# Sources of complexity

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- Stochasticity of life histories
- *i*-states and structured populations
- Complexity of interactions between individuals
- Complexity of population dynamics
- Environments changing in space and time
- Complexity of communities
- Linking theory and data

# Structured population: an example from the many

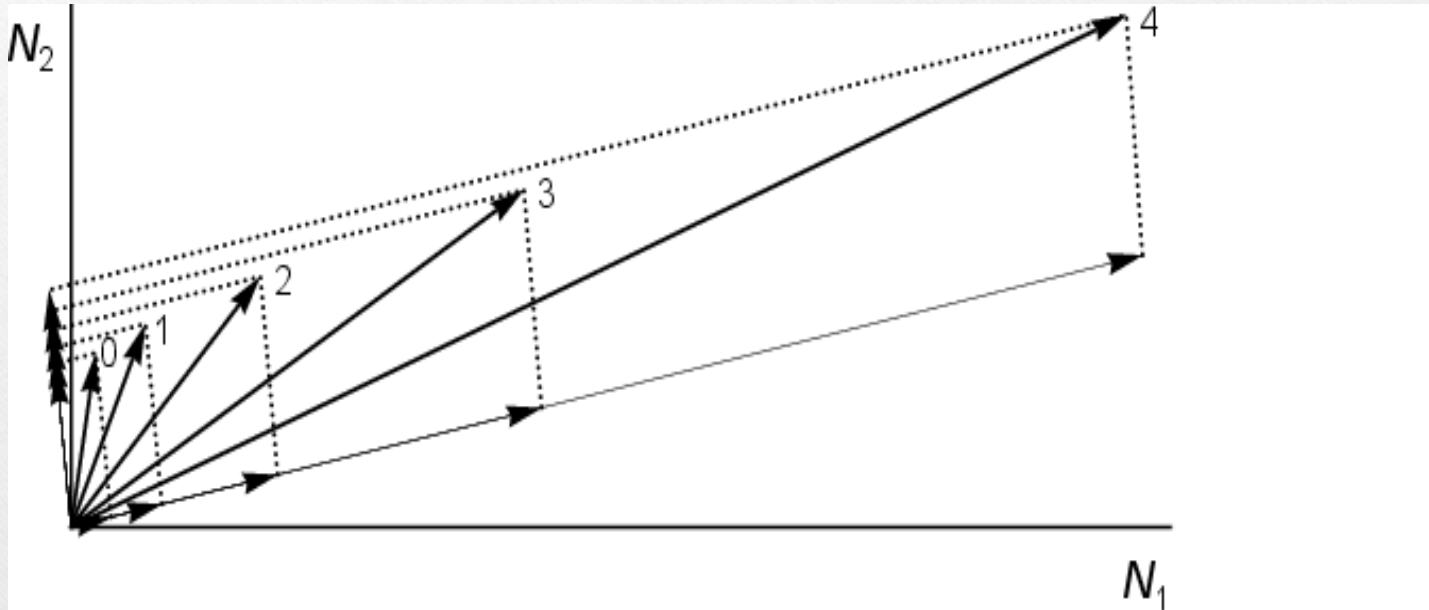


*Lespedeza cuneata* (Schutzenhofer et al. 2009)



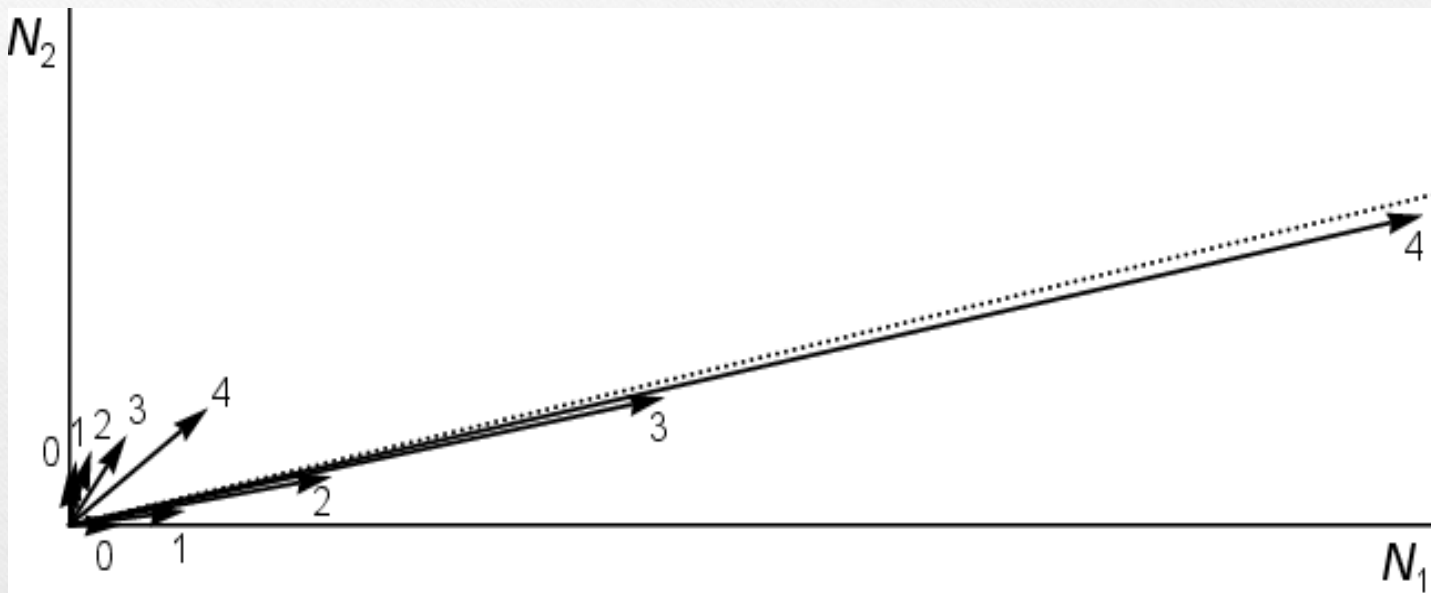
# Population structure: Matrix & eigenvector/value

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Unifying concept for *any* kinds of population structure!

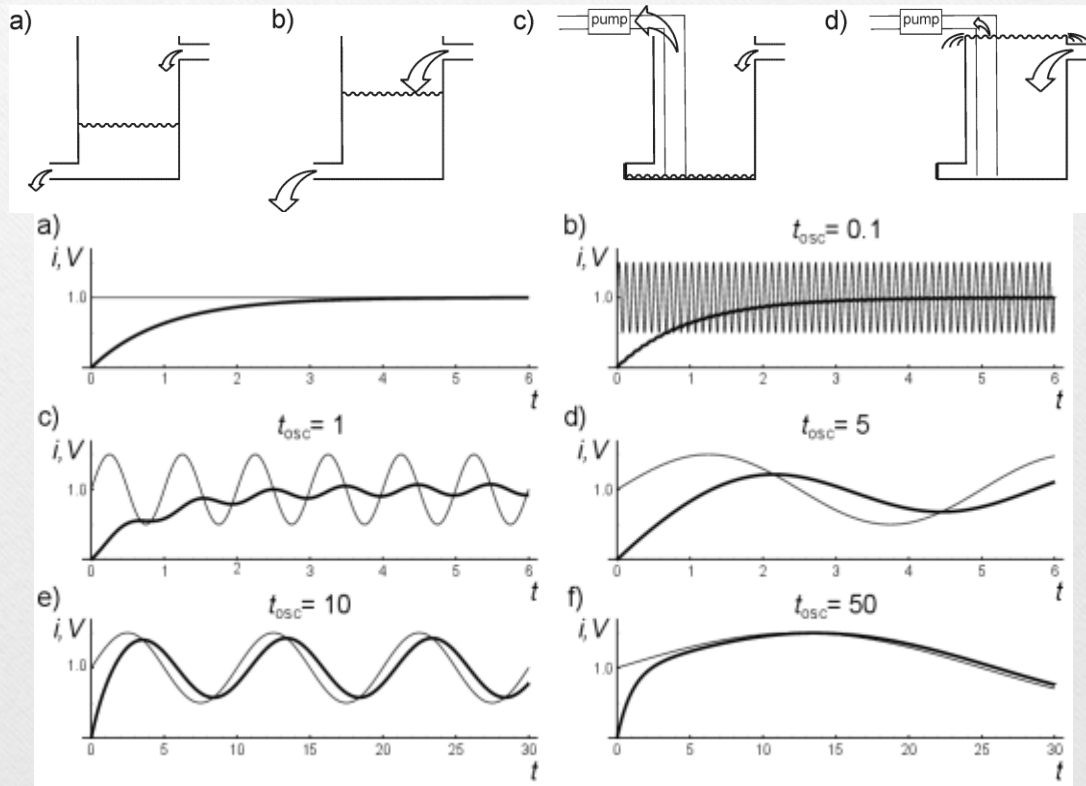
# Reproductive value



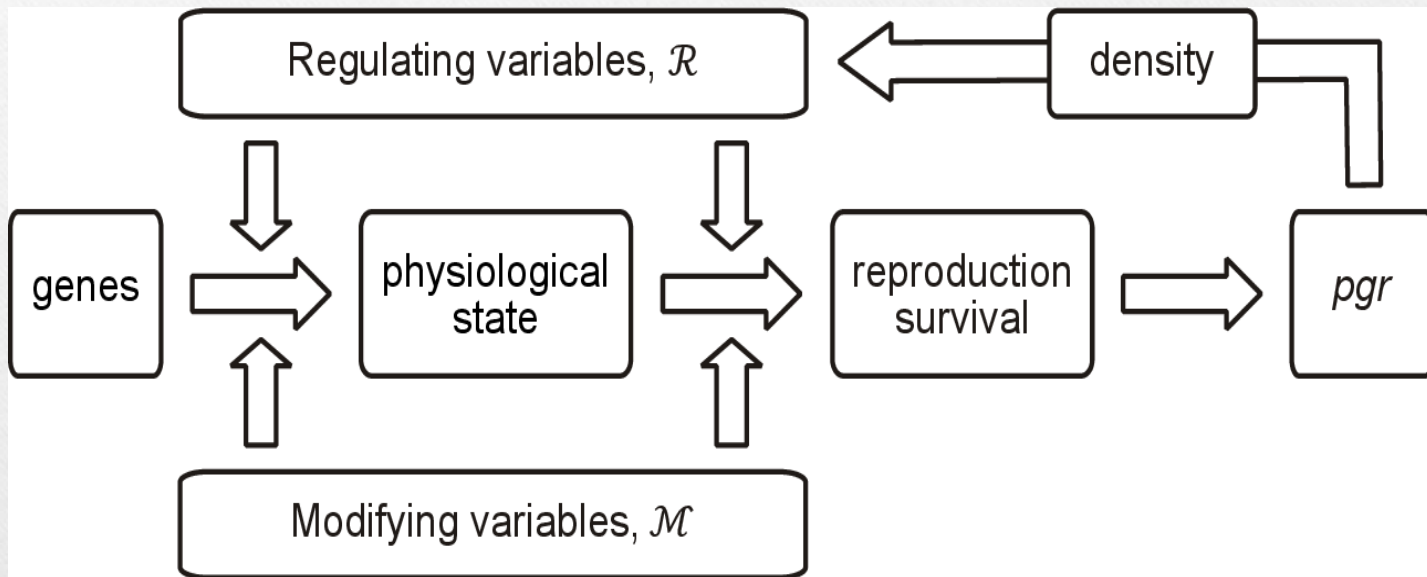
Advantage of starting in the better patch is retained indefinitely.



# Negative feedback & time-scale separation

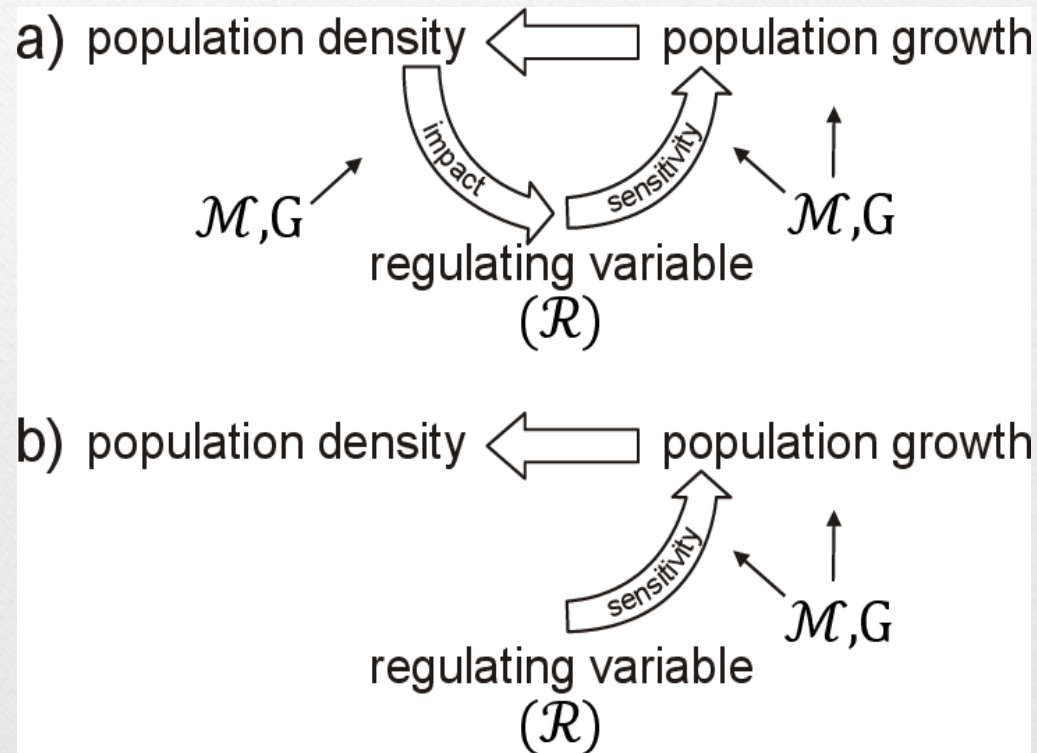


# Chain of effects and the environmental feedback

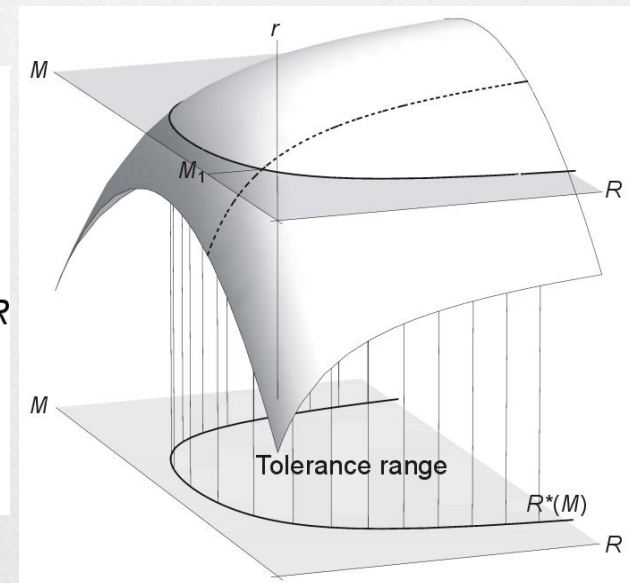
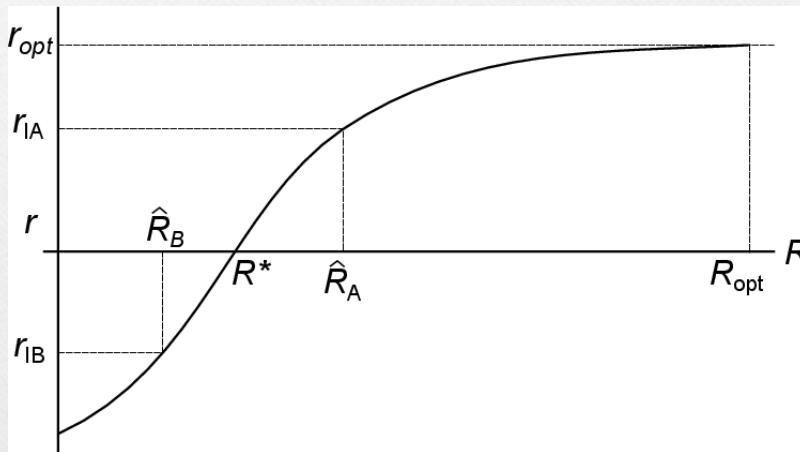




# Open and closed loop of regulation

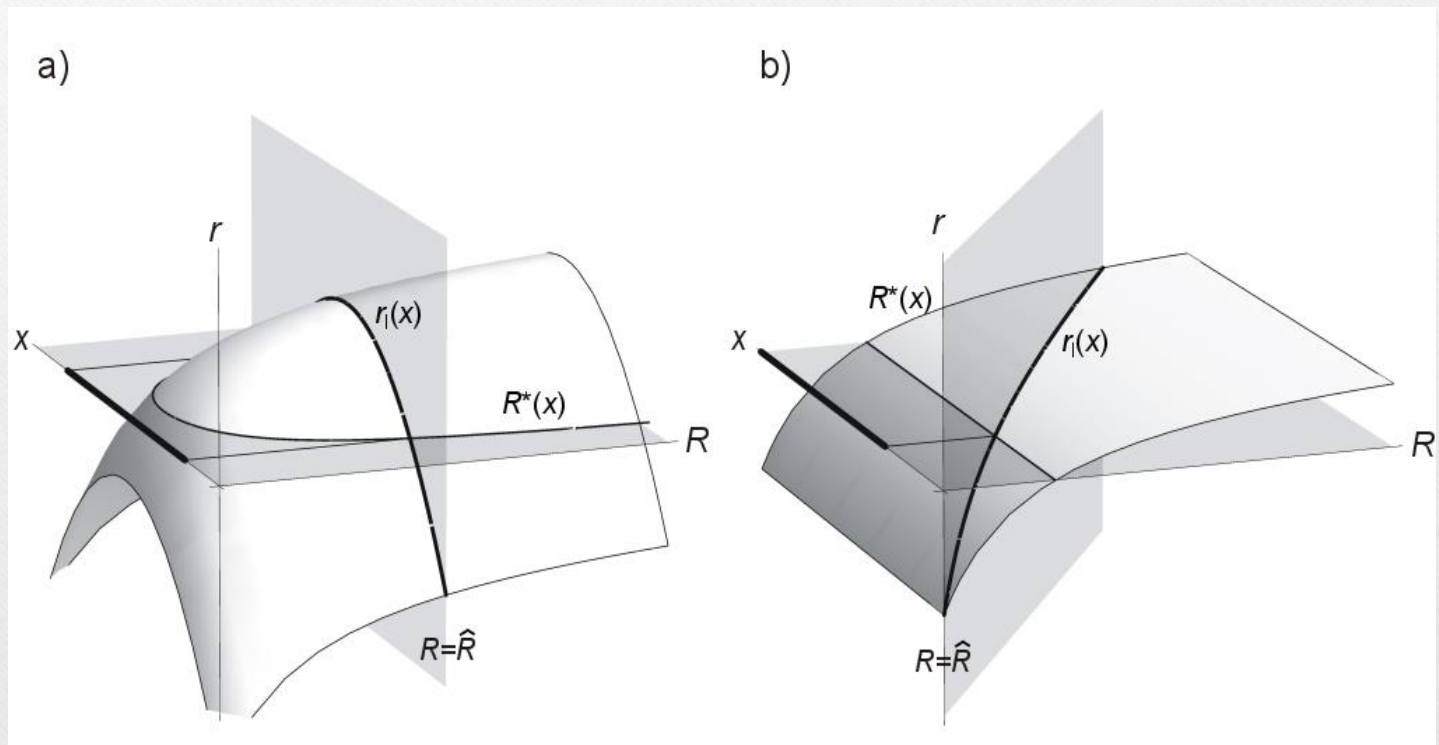


# Response function of a population





# Spatial distribution



# Bottom-up control

*Dynamics.*

$$\frac{dR}{dt} = \alpha(\hat{R} - R) - \varrho(R)N$$

$$\frac{dN}{dt} = r(R)N = (\gamma\varrho(R) - u)N$$

*Equilibrium.*

$$N = \frac{\alpha}{\rho(R^*)}(\hat{R} - R^*)$$

$$R = R^*$$

*Holling I, R is fast:*

$$R = \bar{R}(N) = \frac{\alpha}{\alpha + \beta N} \hat{R}$$

$$I = \frac{d\bar{R}(N)}{dN} = -\frac{\alpha\beta}{(\alpha + \beta N)^2} \hat{R}$$

$$\bar{r}(N) = \frac{\alpha\beta\gamma}{\alpha + \beta N} \hat{R} - u$$

$$S = \frac{dr(R)}{dR} = \gamma\beta$$

$$a = -\frac{d\bar{r}(N)}{dN} = -S \cdot I = \frac{\alpha\beta^2\gamma}{(\alpha + \beta N)^2} \hat{R}$$



# Top-down control

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*Dynamics:*

$$\frac{dR}{dt} = \alpha(\hat{R} - R) - \beta^N RN$$

$$\frac{dN}{dt} = (\gamma^N \beta^N R - u^N)N - \beta^P NP$$

$$\frac{dP}{dt} = (\gamma^P \beta^P N - u^P - bP)P$$

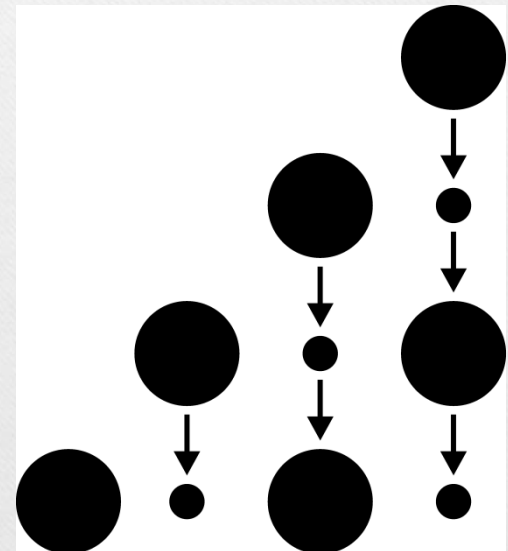
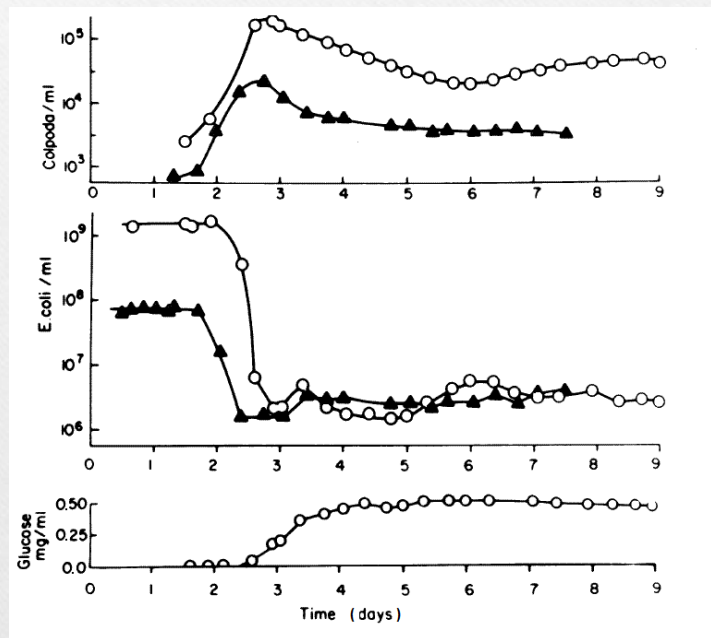
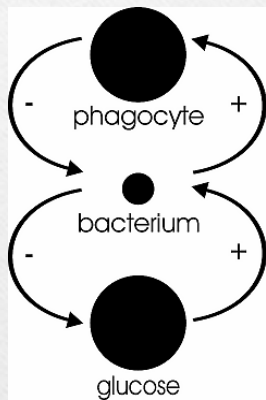
*Regulation:*

$$a = -\frac{d\bar{r}}{dN} = -\frac{\partial r}{\partial R} \frac{d\bar{R}}{dN} - \frac{\partial r}{\partial P} \frac{d\bar{P}}{dN} = a^R + a^P$$

$$a^P = -S^P \cdot I^P = \frac{\gamma^P (\beta^P)^2}{b} \rightarrow \infty \quad \text{when } b \rightarrow 0$$

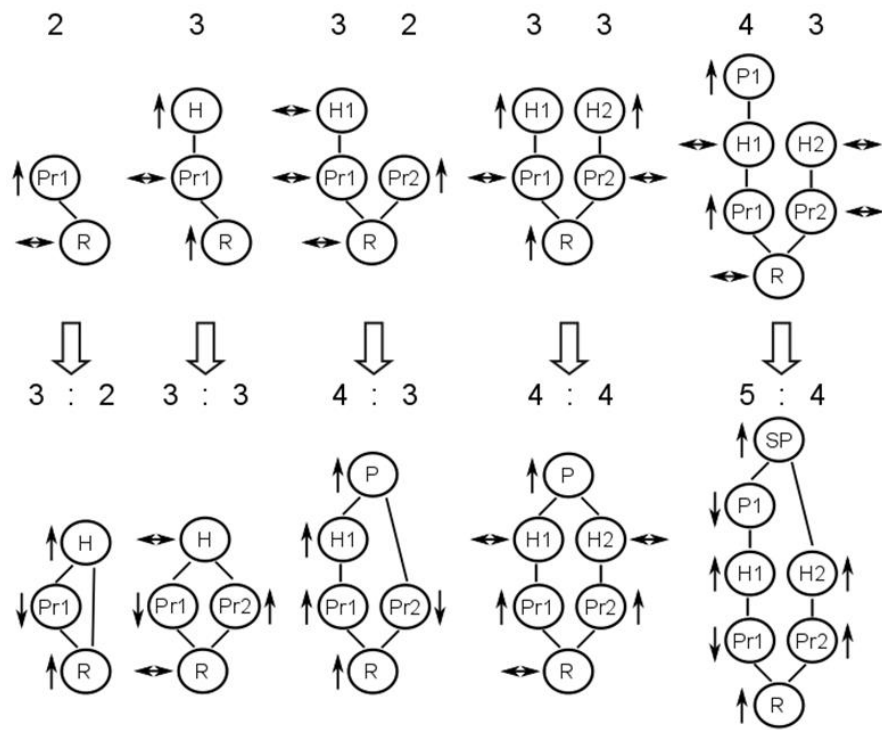
Rule of exclusive  
resource limitation  
(Fretwell 1977)

# Exclusive resource limitation





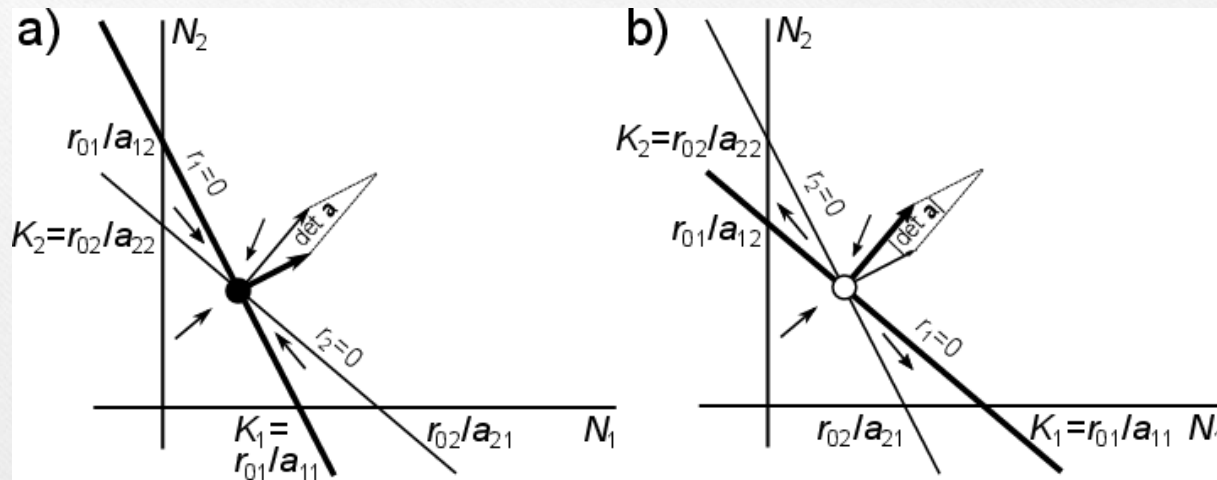
## Consequence for trophic networks



How does the network  
react to an increase  
of resource input?

(Wallrab, Diehl, de Roos, 2012)

# Coexistence in Lotka-Volterra

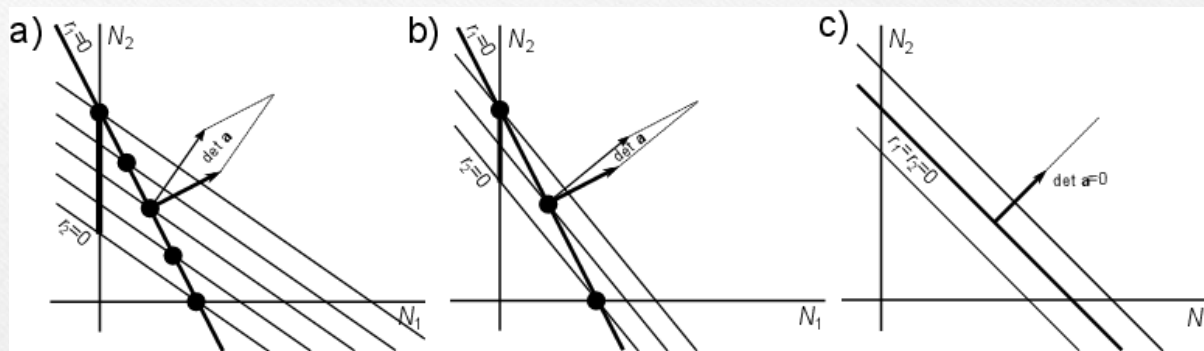


$$\frac{1}{N_1} \frac{dN_1}{dt} = r_{01} - a_{11}N_1 - a_{12}N_2$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_{02} - a_{21}N_1 - a_{22}N_2$$



# Robustness of coexistence



$$r(N) = r_0 - aN = 0$$

$$N = a^{-1}r_0$$

$$a^{-1} = \frac{1}{\det a} \begin{pmatrix} a_{22} & -a_{12} \\ -a_{21} & a_{11} \end{pmatrix}$$

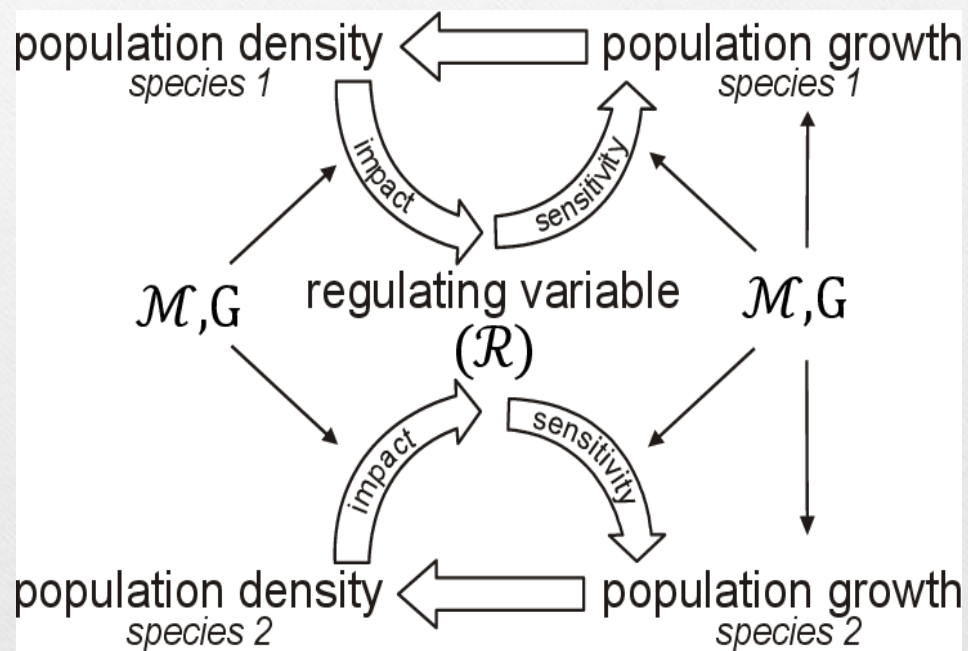
$\det \mathbf{a}$  small



Coexistence is not robust.

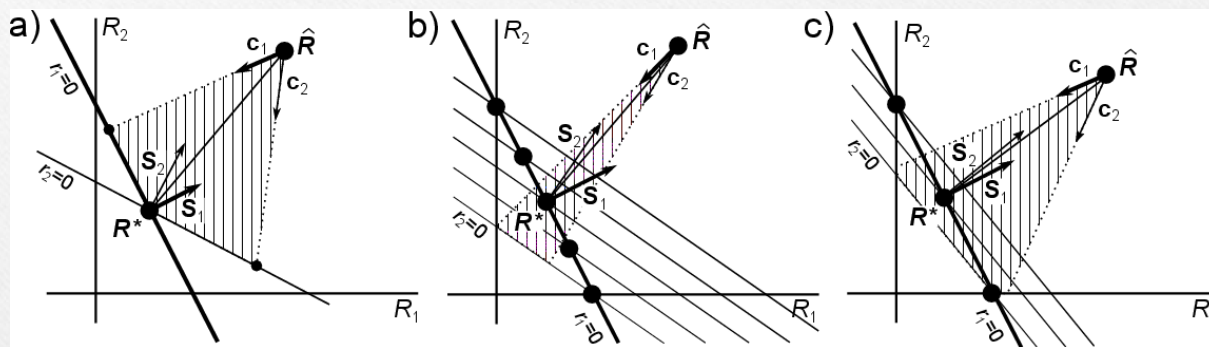
# Interactions through regulating variables

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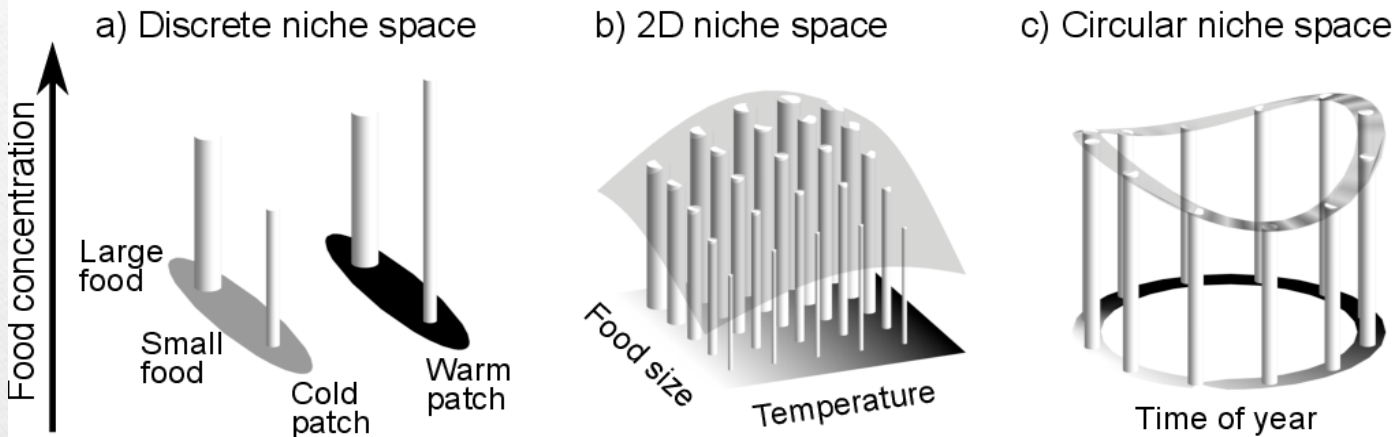
# Robustness of coexistence



$$a_{ij} = -\frac{\partial r_i}{\partial N_j} = -\frac{\partial r_i}{\partial \mathcal{R}} \cdot \frac{\partial \mathcal{R}}{\partial N_j} = -\frac{\partial r_i}{\partial \mathcal{R}_1} \cdot \frac{\partial \mathcal{R}_1}{\partial N_j} - \frac{\partial r_i}{\partial \mathcal{R}_2} \cdot \frac{\partial \mathcal{R}_2}{\partial N_j} = -\mathbf{S}_i \cdot \mathbf{I}_j$$

Robust coexistence: Populations must differ sufficiently in both  $\mathbf{I}$  and  $\mathbf{S}$ !

# Niche space



**Niche space** := index space of the regulating variables  
 $\neq$  space spanned by the regulating variables

**Niche space** : discrete, or continuous



# Mathematics of ecology $\subset$ Mathematics of life

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- We suggest an integrated theory of ecology.
- It is tautologic, as any math; not a replacement for understanding your specific system..
- Without such integration, ecology would remain stuck in hopeless debates.
- We tried to keep math as minimalist, as possible in the book.
- Still, the integration would not be possible without deep mathematics.



We thank Hans & *Mats* & the adaptive  
dynamics people for helping some authors  
to write many papers and a book on us.

Giant Tortoise community  
(Galapagos)

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