

Fajok eredete és Darwin igaza

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Statisztikus Fizika Szeminárium, 2013

Outline

1 Intro: ecology vs. evolution

2 Niche theory

3 Divergent evolution

Darwin vs. Mayr on origin of species



Charles Darwin
(1809-1882):
Origin of species (1859)
diverging evolution



Ernst Mayr
(1904-2005):
Systematics and the origin of species (1942)
biological species, allopatric speciation

Darwinian speciation with Darwin's word

“But the struggle will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers.”

“..the more diversified the descendants of any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers.”

The allopatric alternative by Mayr

Deus ex machina:

- Assume that an **external factor** splits the population into two.
- Independent evolution in the two subpopulations before recontact.
- At recontact they are so different that cannot interbreed – maybe, some reinforcement is needed.
- At recontact they will occupy different niches – maybe, some character shifting is needed.

Counter arguments:

- Darwin's picture was more parsimonious.
- Many examples for sympatric speciation exist by now.
- Strong evidence for gene flow during speciation.

The allopatric alternative by Mayr

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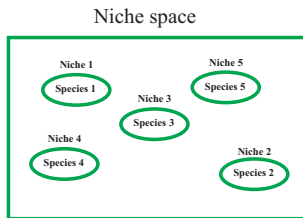
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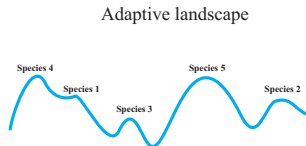
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Why are there so many kinds of animals?

Different pictures in ecology and evolution:
we need a mathematical unification.



Species occupy different
niches.



Species occupy different
peaks of landscape.

Tension: “wittest wins” *versus* “coexistence with reduced competition”

Complication: biological species concept of Mayr

Reduced competition – what is it?

Lotka-Volterra:

$$\frac{1}{n_i} \frac{dn_i}{dt} = r_i = r_{0i} - \sum_j a_{ij} n_j$$

strength of competition



In general:

$$a_{ij} = -\frac{dr_i}{dn_j}$$

Strength of competition is related to density/frequency dependence, i.e. population regulation!

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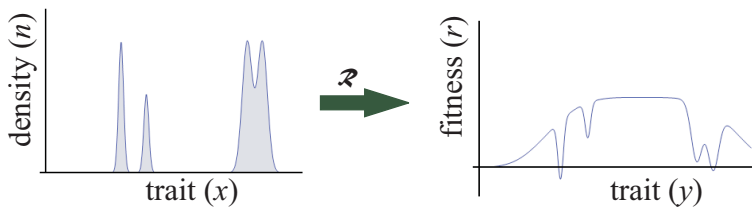
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In general:

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Regulated landscape



Strength of competition:

$$a(x, y) = -\frac{\delta r(y)}{\delta n(x)} = -\frac{\delta r(y)}{\delta \mathcal{R}} \frac{\delta \mathcal{R}}{\delta n(x)}$$

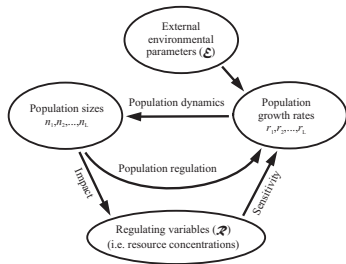
Physics notation for functional derivative.

If n is a distribution, instead of a continuous function, then this is a special kind of derivative by Mats.

Strength of competition (reduced competition) makes evolutionary sense only on a *regulated landscape!*

Niche theory

Population regulation – robust coexistence



Small $|J|$

⇒ weak regulation

⇒ sensitivity towards
perturbation

Long-term equilibrium:

$$r_i(\mathcal{E}, \mathcal{R}(n_1, n_2, \dots, n_L)) = 0$$

Effect of perturbation:

$$\frac{dn}{d\mathcal{E}} = - \left(\frac{\partial r}{\partial n} \right)^{-1} \cdot \frac{\partial r}{\partial \mathcal{E}} = - \frac{M}{\det \left(\frac{\partial r_i}{\partial n_j} \right)} \cdot \frac{\partial r}{\partial \mathcal{E}}$$

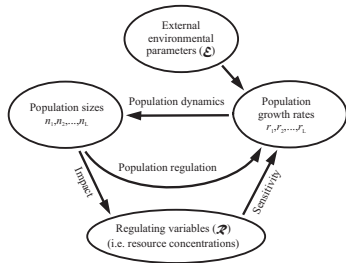
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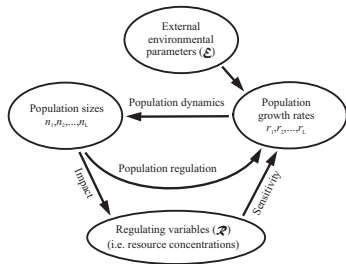
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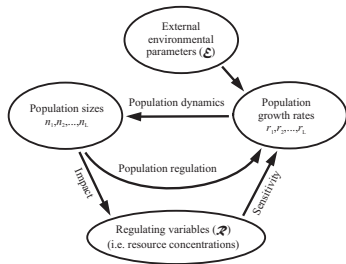
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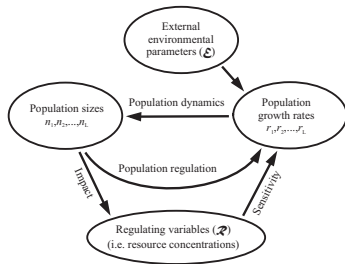
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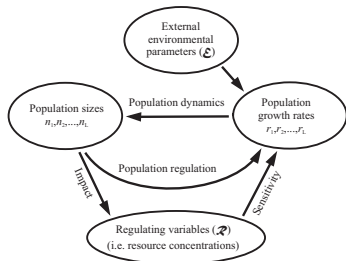
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Weak regulation : unlikely coexistence



Similar I or S vectors

⇒ small \mathcal{V}_I or \mathcal{V}_S

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Sensitivity niche vector:

Impact niche vector:

S_i

I_j

Strength of regulation

expressed in terms of niches:

$$|J| \leq \mathcal{V}_S \cdot \mathcal{V}_I$$

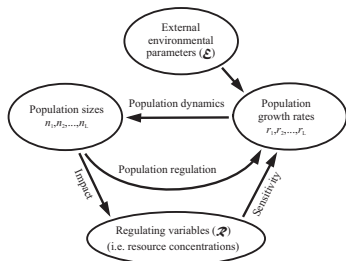
Volumes of parallelepipeds:

$$\mathcal{V}_S = |S_1 \wedge S_2 \wedge \dots \wedge S_L|$$

$$\mathcal{V}_I = |I_1 \wedge I_2 \wedge \dots \wedge I_L|$$

Robust coexistence requires segregation in I and S – niche segregation.

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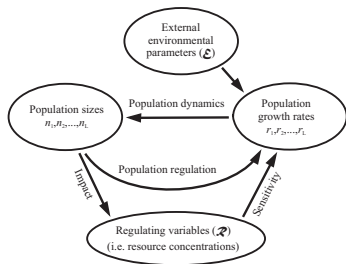
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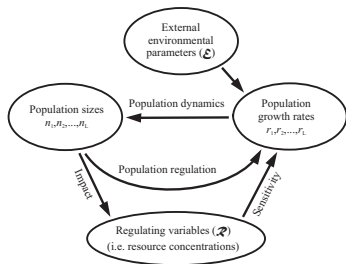
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Robust coexistence requires segregation in I and S – niche segregation.

What is niche space?

Niche space \equiv set of regulating factors

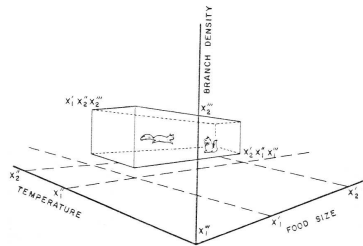
Niche of a species $\equiv (I, S)$ (cf. resource utilisation function)

The niche space can be

- discrete
- continuous.

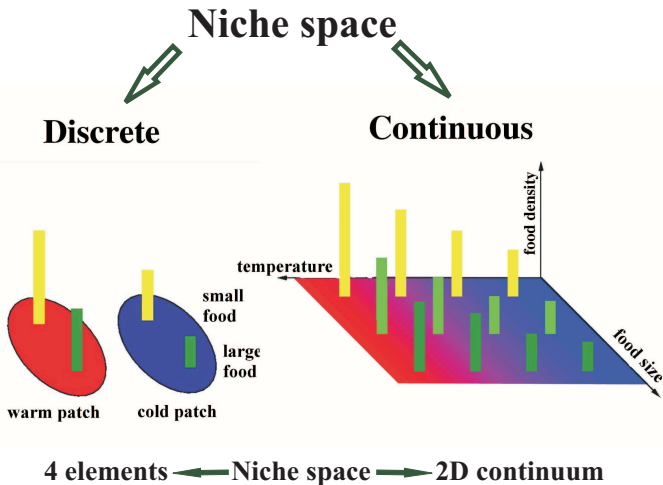
Niche segregation can be

- functional (local),
- habitat (spatial),
- temporal.

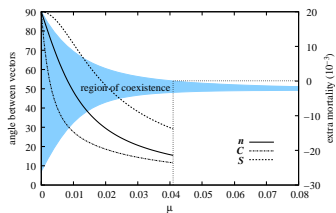
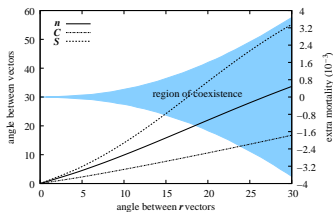
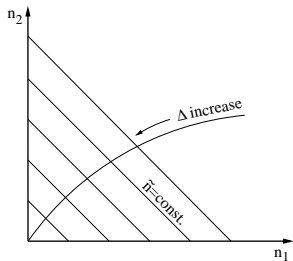
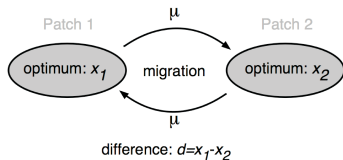


(Hutchinson, 1978)

Ways of niche segregation



Spatial niche segregation (Szilágyi & Mészéna, 2009)



Two regulating variables: total densities in the patches.

Általános strutúrált populáció

(Szilágyi & Mészéna, 2009; Barabás et al. in press)

$$\frac{dn_i}{d\mathbb{E}} = - \sum_{j=1}^S \left[\sum_{\mu,\nu} \underbrace{\left(\mathbf{v}_i \frac{\partial \mathbf{A}_i}{\partial \mathcal{R}_\mu} \mathbf{w}_i \right)}_{S_{i,\mu}} \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \underbrace{\frac{\partial \mathcal{R}_\nu}{\partial \mathbf{N}_j} \mathbf{p}_j}_{\mathcal{I}_{j,\nu}} \right]^{-1}$$

$$\times \left[\mathbf{v}_j \frac{\partial \mathbf{A}_j}{\partial \mathbb{E}} \mathbf{w}_j + \sum_{\sigma,\varrho} \left(\mathbf{v}_j \frac{\partial \mathbf{A}_j}{\partial \mathcal{R}_\sigma} \mathbf{w}_j \right) \left(\delta_{\sigma\varrho} - \frac{\partial \mathcal{G}_\sigma}{\partial \mathcal{R}_\varrho} \right)^{-1} \frac{\partial \mathcal{G}_\varrho}{\partial \mathbb{E}} \right]$$

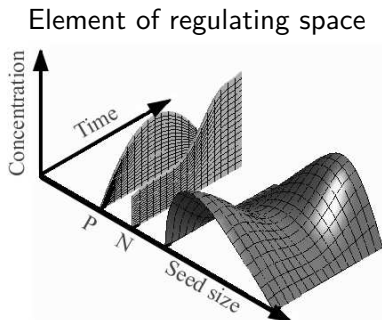
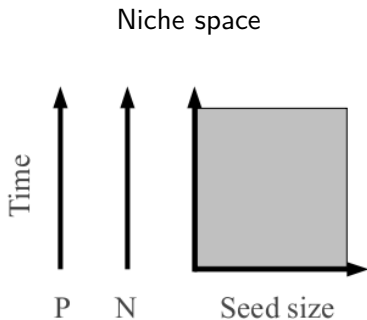
where $n_i = \mathbf{q}_i \cdot \mathbf{N}_i$ is total population size with weight vector \mathbf{q}_i and

$$\mathcal{G}_\mu(\mathcal{R}_\nu, \mathbb{E}) = \sum_{j=1}^S \left[\frac{n_j}{\mathbf{q}_j \mathbf{w}_j} \frac{\partial \mathcal{R}_\mu}{\partial n_j} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \left(\mathbf{w}_j^k - \frac{\mathbf{q}_j \mathbf{w}_j^k}{\mathbf{q}_j \mathbf{w}_j} \mathbf{w}_j \right) \otimes \mathbf{v}_j^k \right]$$

$$\times \mathbf{A}_j(\mathcal{R}_\nu, \mathbb{E}) \mathbf{w}_j.$$

Temporal niche segregation (Barabás & Meszéna, 2011)

Extension to cyclic (fluctuating) environment.



(Cyclic) time becomes niche axis.

Periódikus környezet (Barabás et al., 2012)

$$\begin{aligned}
 \frac{dn_i(0)}{d\mathbb{E}} &= \\
 &= -n_i(0) \sum_{j=1}^S \left(\mathcal{T} \text{Exp} \left(\int_0^T \sum_{\mu} \underbrace{\frac{\partial r_i(\tau)}{\partial \mathcal{R}_{\mu}(\tau)}}_{\mathcal{S}_{i,\mu}(\tau)} \underbrace{\frac{\partial \mathcal{R}_{\mu}(\tau)}{\partial n_j(\tau)}}_{\mathcal{I}_{j,\mu}(\tau)} n_j(\tau) d\tau \right) - \delta_{ij} \right)^{-1} \\
 &\quad \times \int_0^T \frac{\partial r_j(t)}{\partial \mathbb{E}} dt
 \end{aligned}$$

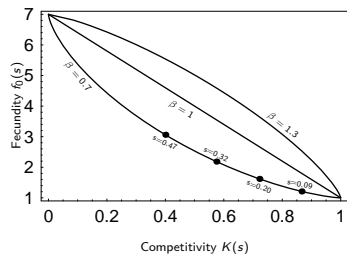
(\mathcal{T} : időrendezés)

Successional niche segregation

Structured metapopulation:

local population size has a dynamics also!

Random local catastrophes with rate μ .



Strategy: s

Trade-off:

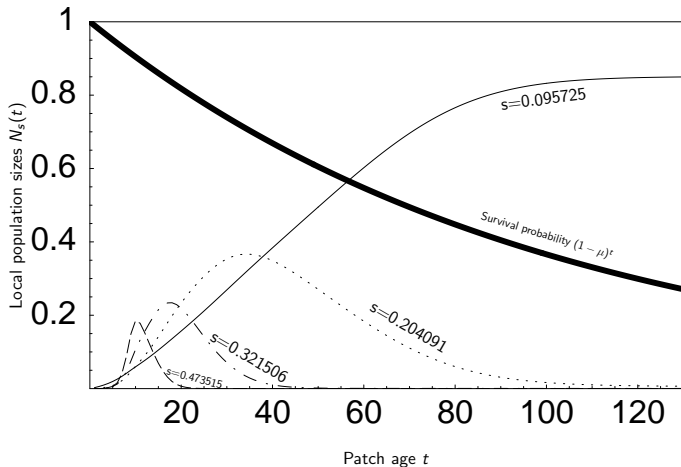
Competitivity: $K(s) = (1 - s)^{1/\beta}$

Fecundity: $f_0(s) = 1 + \gamma s^{1/\beta}$

Density dependent fecundity:

$$f\left(s, \sum N\right) = f_0(s) \exp\left(-\frac{\sum N}{K(s)} \ln f_0(s)\right)$$

Local succession



Regulating variable: local density – for all patch ages.
Niche axis: patch age.

Gross (2008) model of facilitation (Barabás et al., in prep)

$$\frac{1}{N_1} \frac{dN_1}{dt} = f_1(\mathcal{R}_1) - m_1^0,$$

$$\frac{1}{N_i} \frac{dN_i}{dt} = f_i(\mathcal{R}_1) - m_i^0 + d_i \mathcal{R}_i \quad (i = 2 \dots S),$$

$$\frac{d\mathcal{R}_1}{dt} = g(\mathcal{R}_1) - \sum_{i=1}^S c_i f_i(\mathcal{R}_1) N_i,$$

$$\mathcal{R}_\mu = 1 - \exp\left(-\theta \sum_{k < \mu} N_k\right) \quad (\mu = 2 \dots S).$$

With $S \rightarrow \infty$, each new species contributes a new regulating variable!

Unlimited coexistence? **NO!**

After some work:

$$\sqrt[S]{\mathcal{V}_S \mathcal{V}_I} \sim \exp\left(-\frac{\theta N}{2} S\right) \rightarrow 0 \quad \text{with } S \rightarrow \infty$$

Continuous coexistence: Lotka-Volterra

Continuous niche variable: x

Population dynamics:

$$\frac{dn_i}{dt} = r_i n_i = \left[r_0(x_i) - \sum_j a(x_i, x_j) n_j \right] n_i$$

$$r_0(x) = e^{-\frac{x^2}{2\omega^2}}$$

Gaussian carrying capacity

$$a(x_i, x_j) = e^{-\frac{(x_i - x_j)^2}{2\sigma^2}}$$

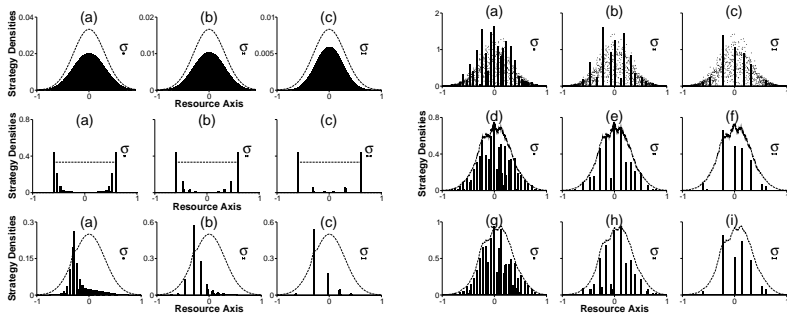
Gaussian competition kernel.

$$n(x) = \frac{\omega/\sigma}{\sqrt{2\pi(\omega^2 - \sigma^2)}} e^{-\frac{x^2}{2(\omega^2 - \sigma^2)}}$$

Continuous coexistence.

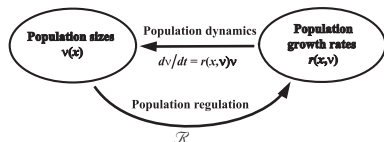
Structural instability of continuous coexistence

Lotka-Volterra:



(Szabó & Mészéna, *Oikos*, 2006)

Structural instability of continuous coexistence: General



Theorems by Mats:

- Compactness of the operator of regulation: coexistence of infinitely many *fixed* types is structurally unstable.
- + analicity in 1D: the *possibility* of a coexistence with limit point is structurally unstable


(Meszéna & Gyllenberg, JMB, 2005; Barabás et al., 2012, EER)

Scheffer & Nes: Self-organized similarity (PNAS 2006)

Claim: coexistence of similars!!!!

Model:

$$r(y) = r_0 \left(1 - \frac{\int \alpha(y, x) n(x) dx}{K(y)} \right) - g \frac{n(y)}{[n(y)]^2 + H^2} \quad (2)$$

apparent competition 

Generalized competition:

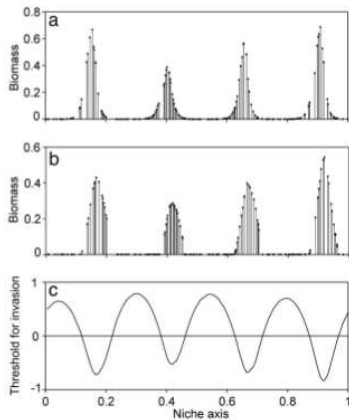
$$\frac{\delta r(y)}{\delta n(x)} = -\frac{r_0}{K(y)} \alpha(y, x) - g \delta(y - x) \dots \quad (3)$$

Degeneracies:

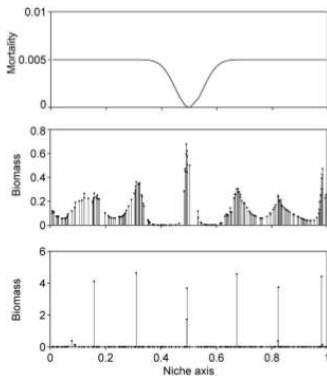
- They choose $K(y) = \text{const.}$
- Delta function for apparent competition!

Scheffer & Nes: Self-organized similarity (PNAS 2006)

Original model



Degeneracies removed



No degeneracies \Rightarrow No coexistence of similars at $t = \infty!$

Divergent evolution

Example: Lotka-Volterra

Continuous strategy variable: x

Population dynamics:

$$\frac{dn_i}{dt} = r_i n_i = \left[r_0(x_i) - \sum_j a(x_i, x_j) n_j \right] n_i$$

$$r_0(x) = K(1 - x^2)$$

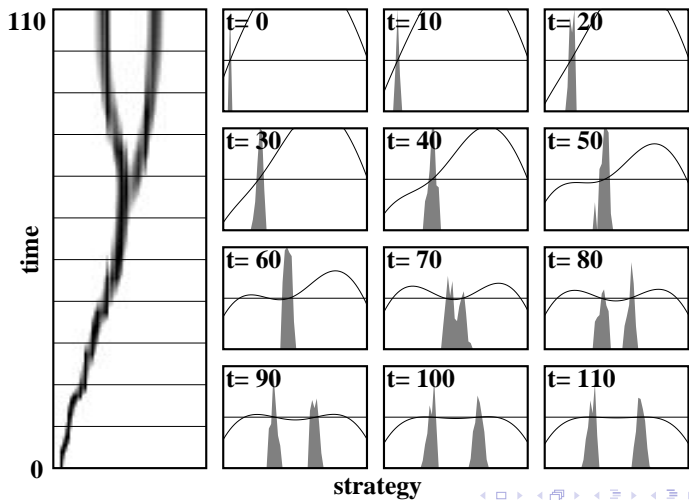
Optimising selection

$$a(x_i, x_j) = e^{-\frac{(x_i - x_j)^2}{2\sigma^2}}$$

Decreasing competition
with increasing difference

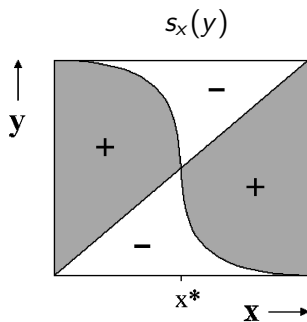
Stochastic mutation process is added with small mutational steps.

Evolutionary branching

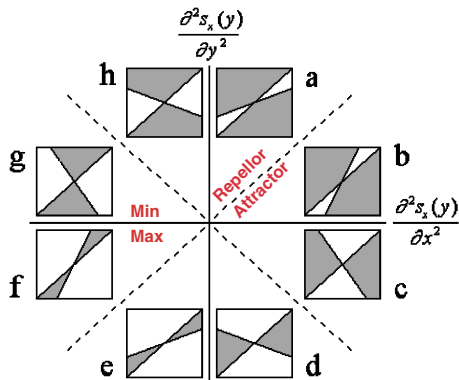


AD: invasion and fixed point

Pairwise invasibility plot



Singular point classification

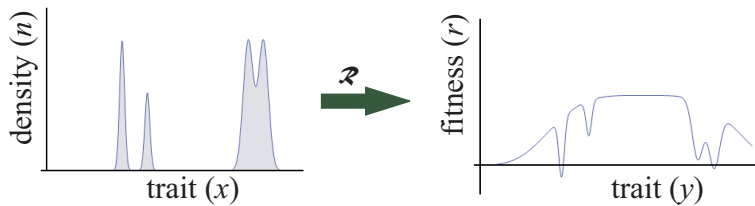


Geritz, Metz, Kisdi & Meszéna, Phys. Rev. Lett., 1997

Geritz, Kisdi, Meszéna & Metz, Evol. Ecol., 1998

Why invasion control everything? Two dynamics are confused!

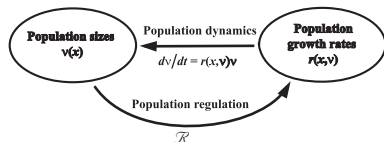
Central concept: Regulated landscape, again



Strength of competition:

$$a(x, y) = -\frac{\delta r(y)}{\delta n(x)} = -\frac{\delta r(y)}{\delta \mathcal{R}} \frac{\delta \mathcal{R}}{\delta n(x)}$$

Theory of regulated landscape



General population regulation:

$$v(x) \rightarrow r(y, v)$$

General competition:

$$a_v(y, x) = -\frac{\delta r(y, v)}{\delta v(x)}$$

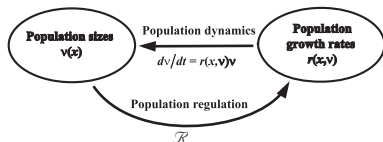
Discrete distribution: $\nu = \sum_{i=1}^L n_i \delta_{x_i} \implies$

$$\frac{\partial r(y, v)}{\partial n_i} = \int \frac{\delta r(y, v)}{\delta v(x)} \cdot \frac{\partial v(x)}{\partial n_i} dx = - \int a(y, x) \delta_{x_i}(x) dx = -a(y, x_i),$$

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Meszána, Gyllenberg, Jacobs, & Metz, Phys. Rev. Lett., 2005

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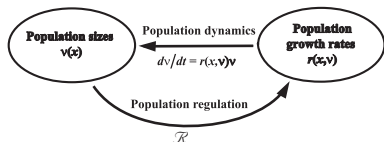
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Time-scale separation

Similar strategies:

$$x_i = x_0 + \varepsilon \xi_i, \quad \varepsilon \rightarrow 0$$

New variables:

Aggregated density: $N = \sum_i n_i$

Relative densities: $p_i = n_i / N$

Aggregated dynamics:

$$\frac{dN}{dt} = N \sum_i p_i r(x_i, \nu) \quad \text{FAST}$$

Relative dynamics:

$$\begin{aligned} \frac{d}{dt} \left(\frac{p_i}{p_j} \right) &= \frac{d}{dt} \left(\frac{n_i}{n_j} \right) = \frac{p_i}{p_j} [r(x_i, \nu) - r(x_j, \nu)] \propto \varepsilon \quad \text{SLOW} \\ &\approx \frac{p_i}{p_j} \langle r(x_i, \nu) - r(x_j, \nu) \rangle \quad \text{ergodic average} \end{aligned}$$

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Expansion of growth rates

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Taylor in ε :

$$\begin{aligned} r(y, \nu(N, \mathbf{p}, \varepsilon)) &= r(y, N\delta_0) - \varepsilon N \sum_{i=1}^L p_i \partial_2 a_\nu(y, 0) [\xi_i] \\ &\quad + \frac{\varepsilon^2}{2} (\text{quadratic in } p_i) + \dots \\ &= r\left(y, N\delta \sum_i p_i x_i\right) + o(\varepsilon) \end{aligned}$$

Coupling of orders in ε and in p_i !

In ε order, ν is equivalent to a monomorphic population!!

ASSUME: ergodic averages inherit this equivalence.

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Pairwise invasion fitness:

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Taylor expansion:

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(Partials at $y = x = x_0$.)

Only the second order term is frequency dependent!

Even this dependence is linear.

⇒ Density-independent directional evolution

⇒ LV-type frequency-dependence at the singular point.

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Modified from Dieckmann & Doebeli (1999):

Multilocus traits:

- Ecological trait: 2×32 loci
- Mating trait: 2×16 loci

Two alleles per locus (0, or 1), additive, random recombination.

Assortative mating according to the ecological trait:

- Hermaphrodite individuals choose a mate in their female role.
- The larger the mating trait of the mother, the smaller the trait difference she accept between herself and her mate.

Individual-based simulation in continuous time:

- Constant birth rate
- Death rate determined by Lotka-Volterra competition

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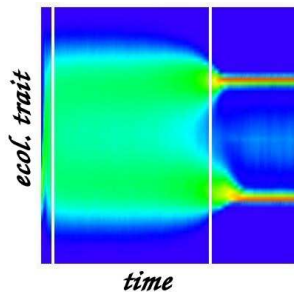
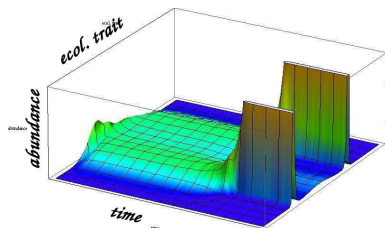
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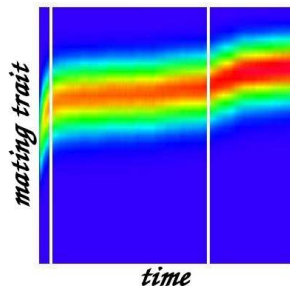
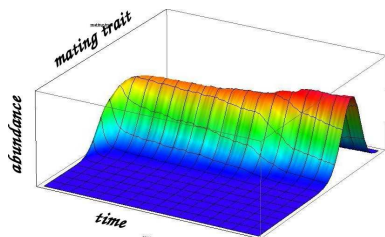
Reference simulation: Ecological trait



Three phases

- First: fast to the middle, widened trait distribution
- Second: slow, gradual transition to bimodality
- Third: fast completion of segregation

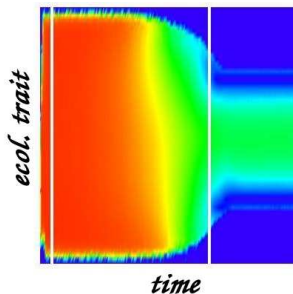
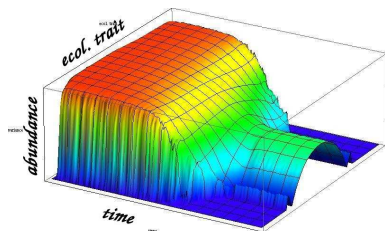
Reference simulation: Mating trait



Three phases

- First: fast increase of assortativity
- Second: minimal additional change
- Third: fast further increase of assortativity

Reference simulation: Additive variance

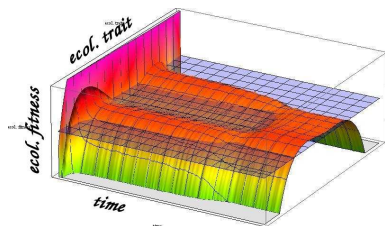


Three phases

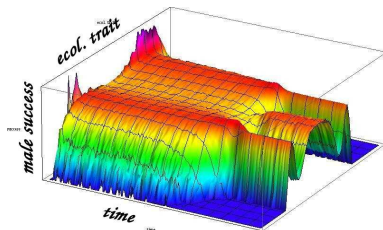
- First: no significant change of variance
- Second: accelerating loss of genetic variance
- Third: seems to be initiated by the loss of genetic variance

Reference simulation: Sources of selection

Ecological selection



Sexual selection



Ecological selection diminishes and sexual selection takes over for the third phase.

Problems with Darwinian speciation – answered

■ I. What is reduced competition?

Reduced competition can be defined only on the regulated landscape! – It leads to branching evolution.

■ II. Spatial segregation.

Functional and habitat segregations are complementary ways of niche-segregation; both of them can drive evolutionary branching.

■ III. Reproductive isolation.

As branching is driven by fitness minimum, it is advantageous to be isolated.

Caution: Emergence of reproductive isolation is a distinct and complicated evolutionary issue!

Still: Ecological selection makes isolation advantageous.

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- Dynamical theory of evolution on a regulated landscape was developed. It leads to adaptive dynamics and evolutionary branching in a natural way.
- The theory mathematizes the Darwinian idea of adaptive diversification.
- *Deep & clean mathematics is the route for deep biological understanding.*

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Many thanks for the coauthors!

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- Stefan Geritz (University of Helsinki)
- Mats Gyllenberg (University of Helsinki)
- Éva Kisdi (University of Helsinki)
- Hans Metz (University of Leiden)
- Kalle Parvinen (University of Turku)
- Liz Pásztor (Eötvös University)
- András Szilágyi (Eötvös University)
- Péter Szabó (Szent István University)

Thanks for your attention!