Towards a first-principles theory for evolutionary diversification

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Modelling Biological Evolution
Leichester, 2013

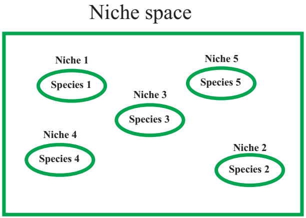
I argue for:

- Integrate theories of ecology and evolution!
- Darwin's, instead of Mayr's, is the parsimonious speciation theory!

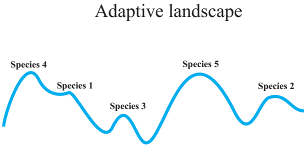
Outline

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"

Reduced competition – what is it?

Lotka-Volterra:

$$\frac{1}{n_i}\frac{\mathrm{d}n_i}{\mathrm{d}t} = r_i = r_{0i} - \sum_j a_{ij} n_j$$

strength of competition

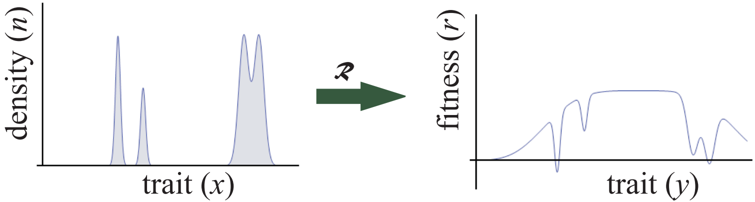
In general:

$$a_{ij} = -\frac{\partial r_i}{\partial n_j}$$

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

Unified theory?

Staring point: regulated landscape



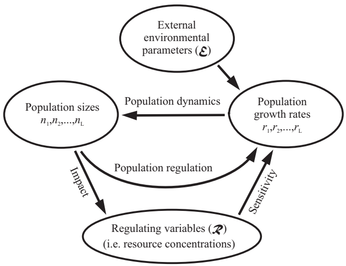
Strength of competition:

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

Functional derivative in function (Banach) space OR (if n is a distribution) a special kind of derivative by Mats Gyllenberg in topological vector space.

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

Ecology: robustness of coexistence?



Small $|\mathbf{J}|$

$\Rightarrow$ week regulation

$\Rightarrow$ sensitivity towards perturbation

Long-term equilibrium:

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

Effect of perturbation:

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

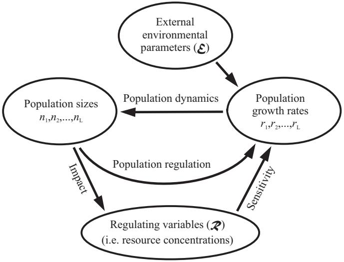
Strength of regulation:

$$J = \det\left(\frac{\partial r_i}{\partial n_j}\right) = \det\left(\frac{\partial r_i}{\partial \mathcal{R}} \cdot \frac{\partial \mathcal{R}}{\partial n_j}\right)$$

Strength of competition:

$$a_{ij} = -\frac{\partial r_i}{\partial n_j} \qquad (1)$$

Limiting similarity



Similar $\boldsymbol{I}$ or $\boldsymbol{S}$ vectors

$\Rightarrow$ small $\mathcal{V}_{\boldsymbol{I}}$ or $\mathcal{V}_{\boldsymbol{S}}$

$\Rightarrow$ small $|J|$

$\Rightarrow$ week regulation

$\Rightarrow$ high sensitivity

Strength of regulation:

$$J = \det\left(\frac{\partial r_i}{\partial n_j}\right) = \det\left(\frac{\partial r_i}{\partial \boldsymbol{\mathcal{R}}} \cdot \frac{\partial \boldsymbol{\mathcal{R}}}{\partial n_j}\right)$$

Sensitivity niche vector: $\boldsymbol{S}_i$
Impact niche vector: $\boldsymbol{I}_j$

Strength of regulation expressed in terms of niches:

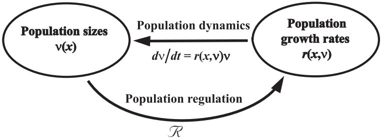
$$|J| \leq \mathcal{V}_{\boldsymbol{S}} \cdot \mathcal{V}_{\boldsymbol{I}}$$

Volumes of paralellopipeds:

$$\mathcal{V}_{\boldsymbol{S}} = |\boldsymbol{S}_1 \wedge \boldsymbol{S}_2 \wedge \cdots \wedge \boldsymbol{S}_L|$$
$$\mathcal{V}_{\boldsymbol{I}} = |\boldsymbol{I}_1 \wedge \boldsymbol{I}_2 \wedge \cdots \wedge \boldsymbol{I}_L|$$

Robust coexistence requires segregation in $\boldsymbol{I}$ and $\boldsymbol{S}$ – niche segregation.

Structural instability of continuous coexistence

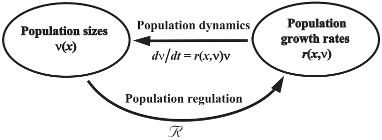


Theorems proven:

- 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)

Evolution on the regulated landscape



Regulated landscape:

$$\nu(x) \to r(y, \nu)$$

General competition:

$$a_\nu(y,x) = -\frac{\delta r(y,\nu)}{\delta \nu(x)}$$

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

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

$$\frac{\partial r\,(y,\nu)}{\partial x_i} = \int \frac{\delta r(y,\nu)}{\delta \nu(x)} \cdot \frac{\partial \nu(x)}{\partial x_i} dx = -\int a(y,x)\left(-n_i\delta'_{x_i}(x)\right) dx = -n_i\partial_2 a(y,x_i)$$

Connection between the dynamical variable and the strategy!
From population dynamics to strategy dynamics!

Relative dynamics of similar strategies

Pairwise invasion fitness:

$$s_x(y) = \langle r\,(y, n\delta_x)\rangle \qquad \text{ergodic average}$$

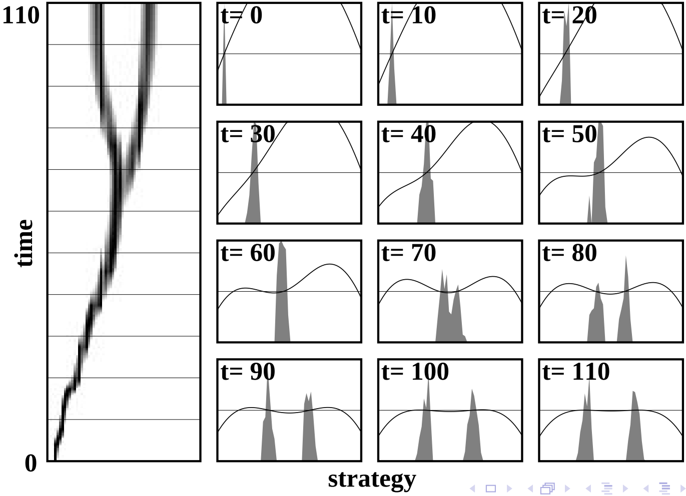
Taylor expansion:

$$\frac{d}{dt}\left(\ln\frac{n_i}{n_j}\right) = \varepsilon\frac{\partial s_x(y)}{\partial y}\left[\xi_i - \xi_j\right] + \frac{\varepsilon^2}{2}\left(\frac{\partial^2 s_x(y)}{\partial y^2}\left[\xi_i\right]\left[\xi_i\right] - \frac{\partial^2 s_x(y)}{\partial y^2}\left[\xi_j\right]\left[\xi_j\right] + \right.$$
$$\left. +2\frac{\partial^2 s_x(y)}{\partial y \partial x}\left[\xi_i - \xi_j\right]\left[\sum_i \frac{n_i}{n}\xi_i\right]\right) + \text{h.o.t.}$$

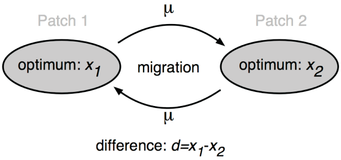
(Partials at $y = x = x_0$.)

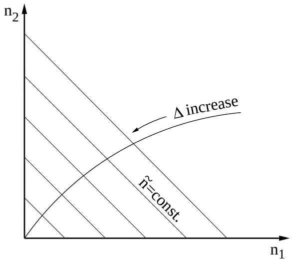
ε scales similarity of strategies. No linearisation in the dynamics!
Linear term: directional evolution. Quadratic term: frequency dep.
Possible branching, only at the singular points!

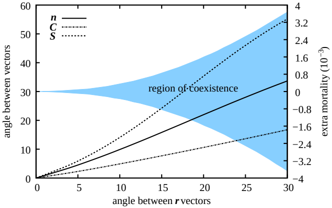
Evolutionary branching

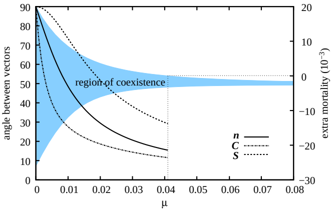


Spatial niche segregation (Szilágyi & Meszéna 2009)



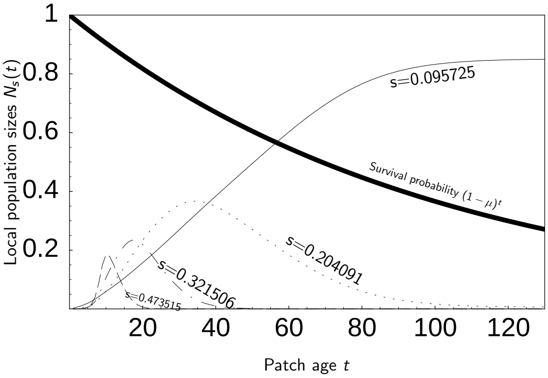






Two regulating variables: total densities in the patches.

Successional niche segregation (Parvinen & Meszéna 2009)



Regulating variable: local density – for all patch ages.
Niche axis: patch age.
Strategies are endpoints of branching evolution.

Unified biological picture?

What the heck is niche theory?

Niche space $\equiv$ *set* of regulating factors

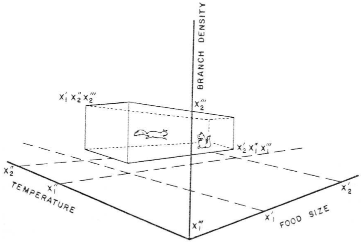
Niche of a species $\equiv (\boldsymbol{I}, \boldsymbol{S})$ (cf. resource utilisation function)

The niche space can be

- discrete
- continuous.

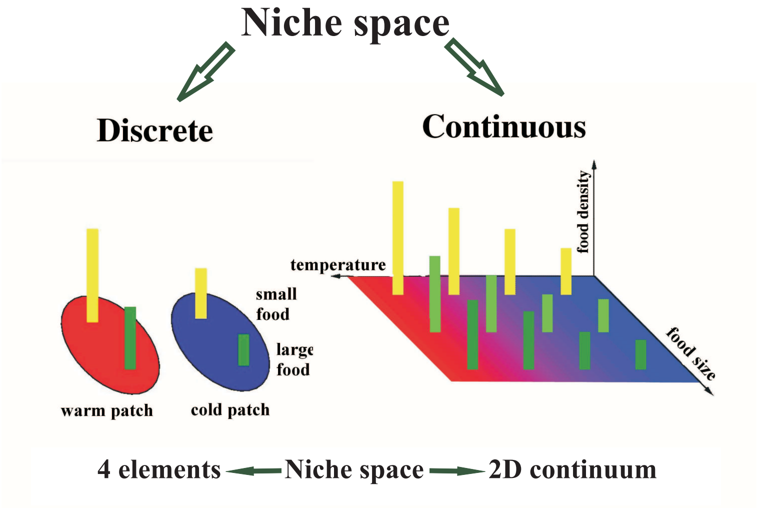
Niche segregation can be

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



(Hutchinson, 1978)

Ways of niche segregation



What is speciation? Darwin vs. Mayr

- Darwin: gradual differentiation
  - Gradual transformation from within-species diversity to between species one.
  - Driven by the fitness-advantage of reduced competition.
- Mayr: allopatric theory
  - An external factor splits the population into two.
  - Independent evolution in the two subpopulations.

Cf. Mallet (2008)

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 evolutionry 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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Take Home

- Niche segregation is segregation with respect to the ways of regulation.
- Evolutionary theory must incorporate regulating feedback from the start to explain diversity.
- Clean mathematics leads to clean biological picture.

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Many thanks for the coauthors!

- György Barabás (University of Michigan)
- Ulf Dieckmann (IIASA)
- Michel Durinx (University of Leiden)
- Stefan Geritz (University of Helsinki)
- Mats Gyllenberg (University of Helsinki)
- Frans Jacobs (University of Leiden)
- 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!