Continuity of adaptive dynamics

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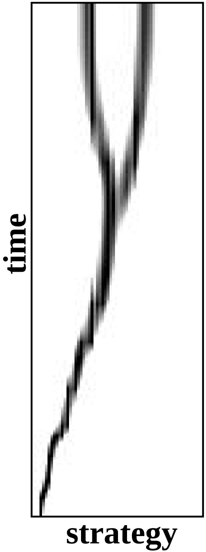
Outline

AD: what is it?



Frequency-dependence:
fitness landscape is affected by the populations itself.
(Otherwise: the fittest win, and that's all.)

Nicest: evolutionary branching.

AD: the central constructs

Continuous strategy variable:
describes the inherited properties

Invasion fitness:

$s_{x_1,x_2,\ldots,x_L}(y)$: long-term growth rate of a rare strategy y in the ergodic environment determined by the resident populations $x_1, x_2, \ldots, x_L$

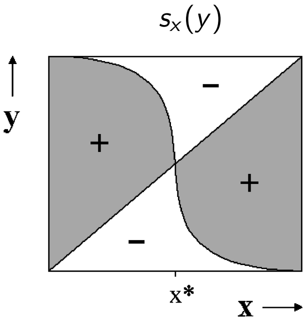
Pairwise invasion fitness:
$s_x(y)$: mutant y invade resident x

Metz, Nisbet & Geritz, TREE, 1992

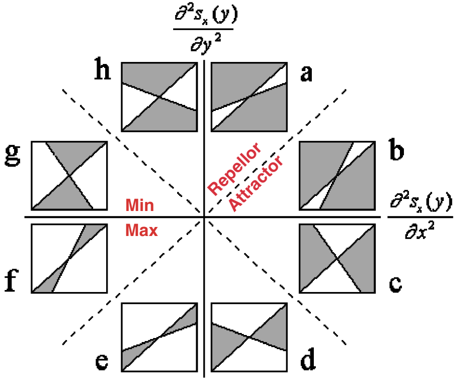
Metz, Geritz, Meszéna, Jacobs & Heerwaarden, 1996

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?

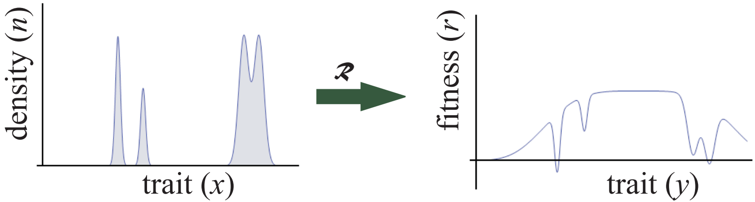
AD from first principles?

- When does invasion imply fixation? Answered by Stefan's tube theorem: when strategies are similar. Attractor inheritance.
- What if more than one mutant?
- What is the connection between monomorphic and polimorphic dynamics?

We need a coherent mathematical framework, in which we can derive AD from population dynamics .

Intuitive treatment

Regulated landscape



Continuity tenet

Relative abundance of similar strategies has little effect on the adaptive landscape.

It is self-evident!

See the consequences!

Meszéna, J. Evol. Biol. 2005

Example: Lotka-Volterra

Continuous strategy variable: x

Population dynamics:

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

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

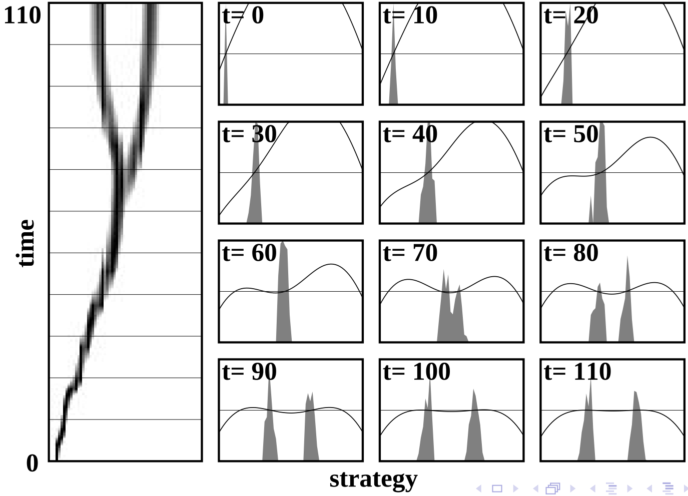
Optimising selection

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

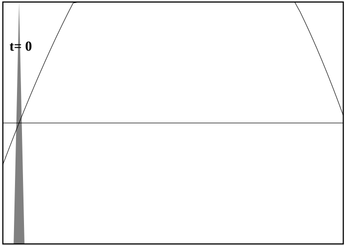
Decreasing competition
with increasing difference

Stochastic mutation process is added with small mutational steps.

Evolutionary branching



Directional evolution

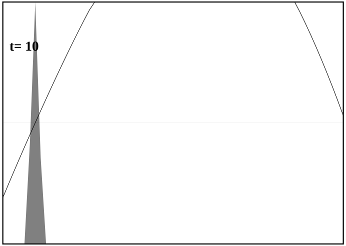


There is no reason
to restrict ourselves
to invasion
by a single mutant!

Continuity Tenet $\Longrightarrow$ no swift change in the selection gradient

An arbitrary cloud of mutants is evolving into the direction of fitness gradient, provided that the distribution is narrow.

Directional evolution



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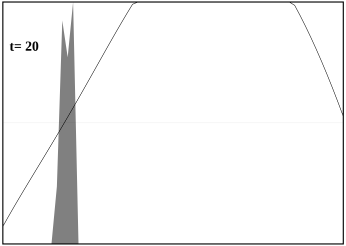

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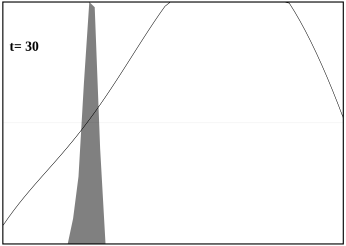

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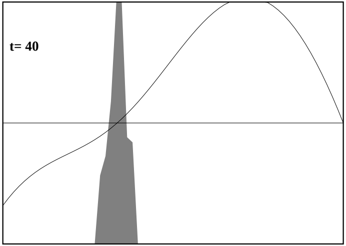

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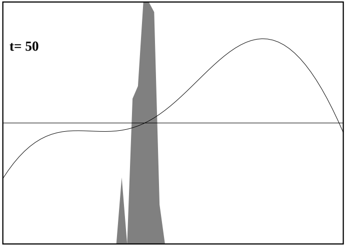

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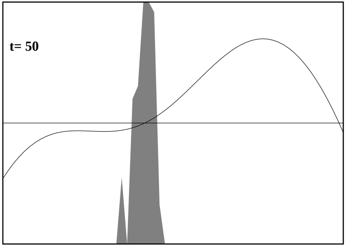

It arrives
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and branches there!

As the fitness gradient is around zero, an arbitrarily small change can change its sign.

Frequency dependence starts to matter!

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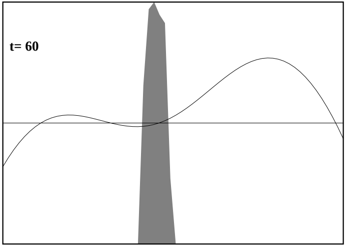

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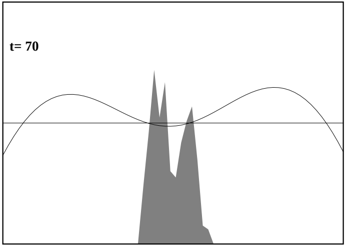

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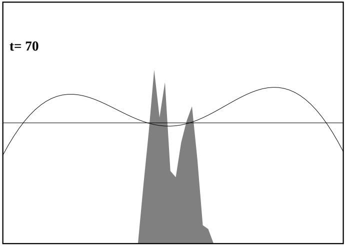

After branching, the populations evolves away!

Continuity Tenet $\Longrightarrow$ No swift change in the second derivative of the fitness.

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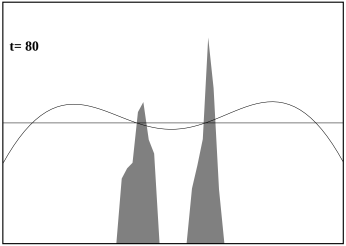

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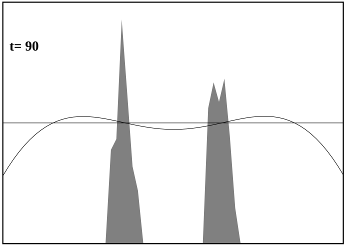

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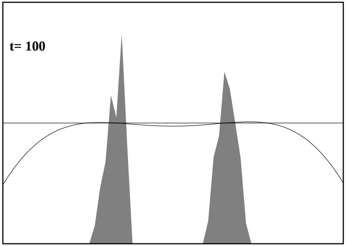

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Reason:
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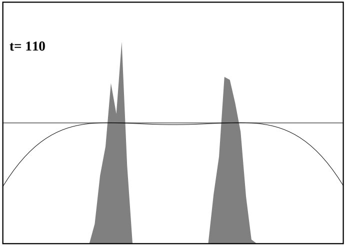

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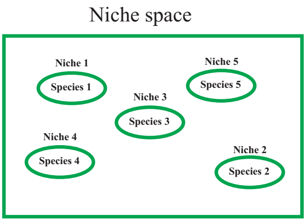
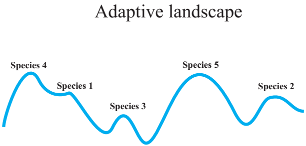
Niche connection

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:

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

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!

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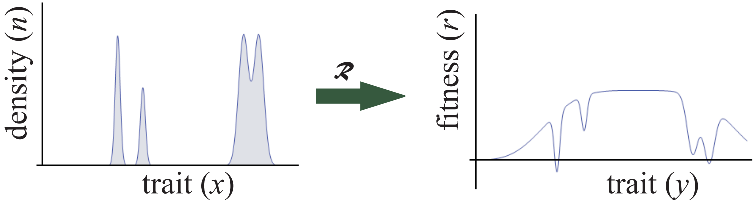
Regulated landscape: niche



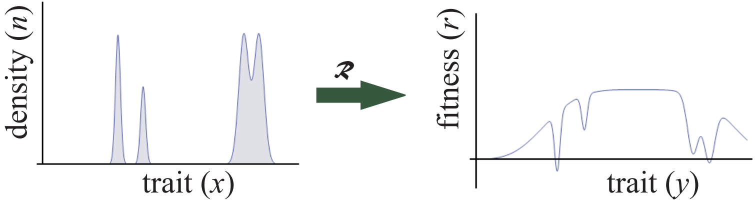
Strength of competition:

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

Niche segregation:
competition is reduced when a strategy impacts regulating variables different from the ones the other sensitive to.

Formal treatment

Regulated landscape: technical version



Multiple dimensional trait space allowed. Strength of competition:

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

(Functional derivative for continuous n; a special kind of derivative by Mats, for distribution.)

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

Derivatives of competition function

General population regulation:

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

General competition:

$$a_n(y, x) = -\frac{\delta r(y, n)}{\delta n(x)}$$

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

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

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Connection between pop. din. and trait space continuity!
Functional analysis ends here :-).

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Time-scale separation

Similar strategies:

$$x_i = x_0 + \varepsilon\xi_i, \qquad \varepsilon \to 0$$

New variables:

Aggregated density: $N = \sum_i n_i$
Relative densities: $p_i = n_i/N$

Aggregated dynamics:

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

Relative dynamics:

$$\frac{d}{dt}\left(\frac{p_i}{p_j}\right) = \frac{d}{dt}\left(\frac{n_i}{n_j}\right) = \frac{p_i}{p_j}\left[r(x_i, n) - r(x_j, n)\right] \propto \varepsilon \qquad \text{SLOW}$$

$$\approx \frac{p_i}{p_j}\langle r(x_i, n) - r(x_j, n)\rangle \qquad \text{ergodic average}$$

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Expansion of growth rates

Similar strategies:

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Taylor in ε:

$$r\left(y, n(N, \boldsymbol{p}, \varepsilon)\right) = r\left(y, N\delta_0\right) - \varepsilon N \sum_{i=1}^{L} p_i \partial_2 a_n(y, 0)\left[\xi_i\right] + \frac{\varepsilon^2}{2}(\text{quadratic in } p_i) + \dots$$

$$= r\left(y, N\delta_{\sum_i p_i x_i}\right) + o(\varepsilon)$$

Coupling of orders in ε and in p_i!

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

ASSUME: ergodic averages inherit this equivalence.

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Taylor expansion:

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

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

Only the second order term is frequency dependent!
Even this dependence is linear.
$\Longrightarrow$ Density-independent directional evolution
$\Longrightarrow$ LV-type frequency-dependence at the singular point.

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$\Longrightarrow$ Density-independent directional evolution
$\Longrightarrow$ LV-type frequency-dependence at the singular point.

Expansion of relative dynamics

Pairwise invasion fitness:

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

Taylor expansion:

$$\frac{d}{dt}\left(\ln\frac{p_i}{p_j}\right) = \varepsilon\frac{\partial s_x(y)}{\partial y}\left[\xi_i - \xi_j\right] + \frac{\varepsilon^2}{2}\left(\frac{\partial^2 s_x(y)}{\partial y^2}\left[\xi_i\right]\left[\xi_i\right] - \frac{\partial^2 s_x(y)}{\partial y^2}\left[\xi_j\right]\left[\xi_j\right] + \right.$$

$$\left. +2\frac{\partial^2 s_x(y)}{\partial y \partial x}\left[\xi_i - \xi_j\right]\left[\sum_i p_i \xi_i\right]\right) + \text{h.o.t.}$$

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

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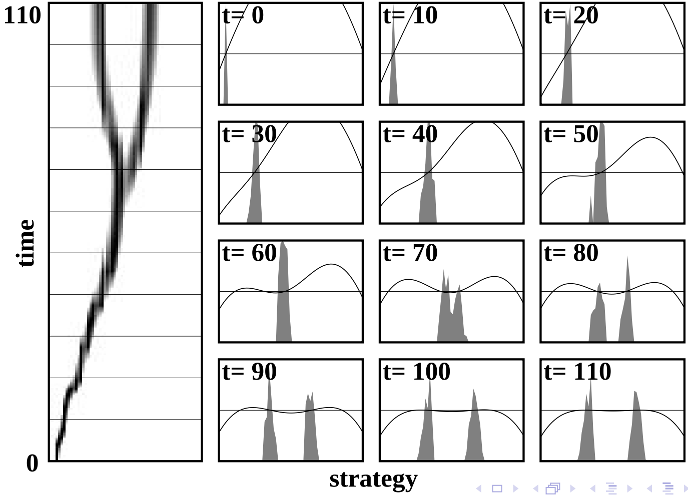
Branching, 2nd look



What have we learned?

- Relative dynamics of similar populations is
  - simple;
  - decoupled from the aggregated dynamics;
  - fully controlled by the pairwise invasion fitness.
- Therefore, we formalized the continuity tenet and its consequences.
- No need for an infinite cascade of s functions with unclear relationships to each other.
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Clonal reproduction.	WAS NOT DISCUSSED.
Small mutational steps.	This is the essence of AD!
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takehome

Don't be afraid of deeper math, if it represents the essence more cleanly!

Many thanks for the coauthors!

- Ulf Dieckmann (IIASA)
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- 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)

Thanks for your attention!