Outline

1. Introduction
2. Intuitive treatment
3. Niche connection
4. Formal treatment
5. Conclusions
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
Continuity of adaptive dynamics

Introduction

AD: invasion and fixed point

Pairwise invasibility plot

$\begin{aligned} s_x(y) \\
\uparrow & \quad \downarrow \\
\uparrow & \quad y \\
\downarrow & \quad \downarrow \\
x & \quad x^* \end{aligned}$

Singular point classification


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 polymorphic dynamics?

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

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

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 $\implies$ 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.
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Arrival to a minimum

It arrives to a fitness minimum, and branches there!

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

Frequency dependence starts to matter!
Arrival to a minimum

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It arrives to a fitness minimum, and branches there!

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Branching away

After branching, the populations evolves away!

Continuity Tenet $\implies$ No swift change in the second derivative of the fitness.
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Reason:
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After branching, the populations evolves away!

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

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

In general:

\[
a_{ij} = - \frac{\partial r_i}{\partial n_j}
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Strength of competition is related to density/frequency dependence, i.e. population regulation!
Reduced competition – what is it?

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Regulated landscape: niche

Strength of competition:

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

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

Derivatives of competition function

General population regulation:

\[ n(x) \rightarrow r(y, n) \]

General competition:

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

Discrete distribution: \( n = \sum_{i=1}^{L} n_i \delta x_i \) \( \Rightarrow \)

\[
\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),
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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:

\[ x_i = x_0 + \varepsilon \xi_i, \quad \varepsilon \rightarrow 0 \]

New variables:
- Aggregated density: \( N = \sum_i n_i \)
- Relative densities: \( p_i = n_i / N \)

Aggregated dynamics:

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

Relative dynamics:

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

\[ \approx \frac{p_i}{p_j} \langle r(x_i, n) - r(x_j, n) \rangle \quad \text{ergodic average} \]
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Expansion of growth rates

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Taylor in \( \varepsilon \):

\[
\begin{align*}
    r(y, n(N, p, \varepsilon)) &= r(y, N\delta_0) - \varepsilon N \sum_{i=1}^{L} p_i \partial_2 a_n(y, 0) [\xi_i] \\
    &\quad + \frac{\varepsilon^2}{2} \text{(quadratic in } p_i) + \ldots \\
    &= r\left(y, N\delta \sum_i p_i x_i\right) + o(\varepsilon)
\end{align*}
\]

**Coupling of orders in \( \varepsilon \) and in \( p_i \)!**

In \( \varepsilon \) order, \( n \) is equivalent to a monomorphic population!!

**ASSUME:** ergodic averages inherit this equivalence.
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Expansion of relative dynamics

Pairwise invasion fitness:

\[ s_x(y) = \langle r(y, n\delta_x) \rangle \]  

ergodic average

Taylor expansion:

\[
\frac{d}{dt} \left( \ln \left( \frac{p_i}{p_j} \right) \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] + 
\right.

\left. + 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.}
\]

(Partial at \( y = x = x_0 \).)

Only the second order term is frequency dependent!
Even this dependence is linear.
\( \implies \) Density-independent directional evolution
\( \implies \) LV-type frequency-dependence at the singular point.
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(Partials at \( y = x = x_0 \).)

Only the second order term is frequency dependent!
Even this dependence is linear.
\( \Rightarrow \) Density-independent directional evolution
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Branching, 2\textsuperscript{nd} 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.

- Directly applicable to multidimensional strategy spaces.

- Directly connected to niche theory.
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Assumptions of AD: second look

Clonal reproduction.

Small mutational steps.

Rare mutations.

The fate of a mutant is determined by the mutual invasion fitnesses.

WAS NOT DISCUSSED.

This is the essence of AD!

NOT NEEDED!

It is a consequence!
Assumptions of AD: second look

- Clonal reproduction. WAS NOT DISCUSSED.
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It is a consequence!
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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Thanks for your attention!