

# Continuity of adaptive dynamics

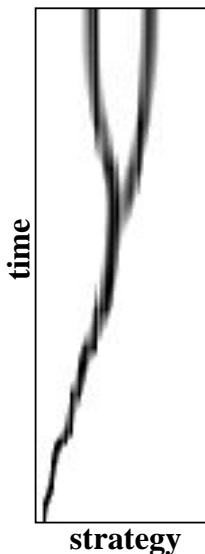
Géza Meszéna  
Eötvös University, Budapest

MAICP workshop, Milano, 2014

# 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:

$$s_{x_1, x_2, \dots, x_L}(y):$$

long-term growth rate of a rare strategy  $y$  in the ergodic environment determined by the resident populations  $x_1, x_2, \dots, x_L$

## Pairwise invasion fitness:

$$s_x(y):$$

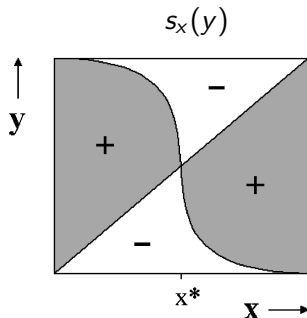
mutant  $y$  invade resident  $x$

Metz, Nisbet & Geritz, TREE, 1992

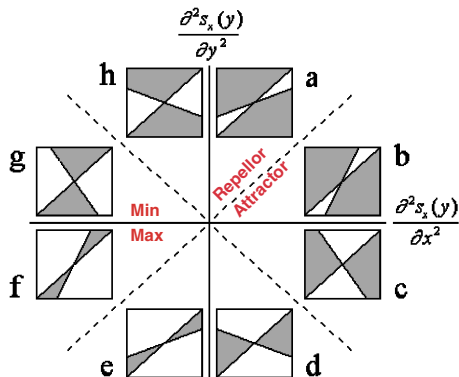
Metz, Geritz, Meszéna, Jacobs & Heerwaarden, 1996

## AD: invasion and fixed point

Pairwise invasibility plot



Singular point classification



Geritz, Metz, Kisdi & Meszena, Phys. Rev. Lett., 1997

Geritz, Kisdi, Meszena & Metz, Evol. Ecol., 1998

Why invasion control everything?

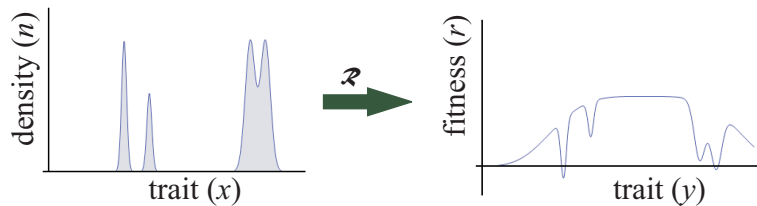
# AD from first principles?

- 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 polymorphic 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!

# Example: Lotka-Volterra

Continuous strategy variable:  $x$

Population dynamics:

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

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

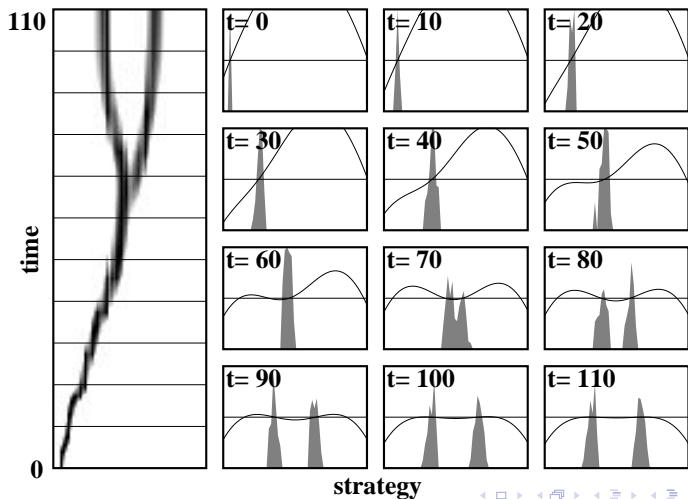
Optimising selection

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

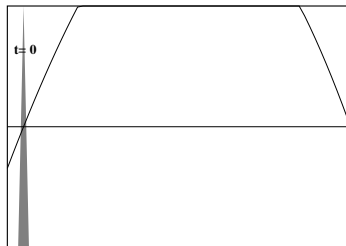
Decreasing competition  
with increasing difference

Stochastic mutation process is added with small mutational steps.

# Evolutionary branching



# Directional evolution

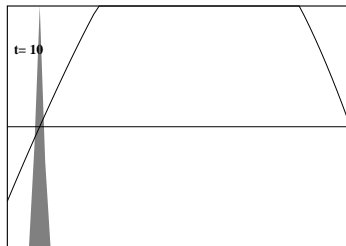


There is no reason  
to restrict ourselves  
to invasion  
by a single mutant!

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.

# Directional evolution

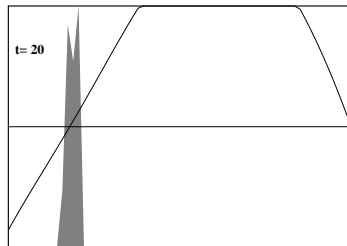


There is no reason  
to restrict ourselves  
to invasion  
by a single mutant!

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.

# Directional evolution

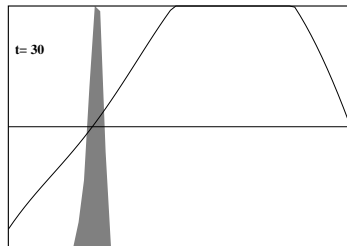


There is no reason  
to restrict ourselves  
to invasion  
by a single mutant!

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.

# Directional evolution

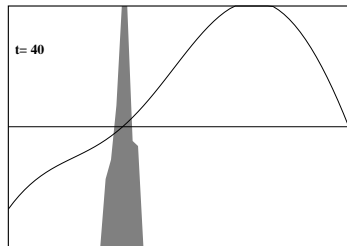


There is no reason  
to restrict ourselves  
to invasion  
by a single mutant!

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.

# Directional evolution



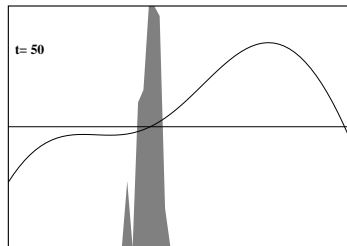
There is no reason  
to restrict ourselves  
to invasion  
by a single mutant!

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.



# Directional evolution

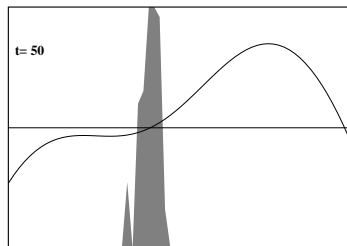


There is no reason  
to restrict ourselves  
to invasion  
by a single mutant!

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.

## Arrival to a minimum

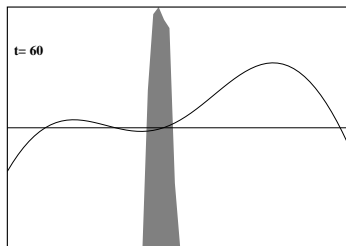


It arrives  
to a fitness minimum,  
and branches there!

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

Frequency dependence starts to matter!

## Arrival to a minimum

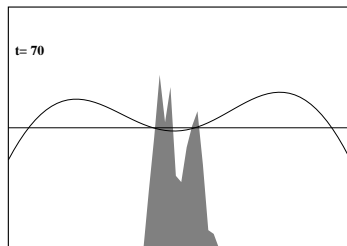


It arrives  
to a fitness minimum,  
and branches there!

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

Frequency dependence starts to matter!

## Arrival to a minimum

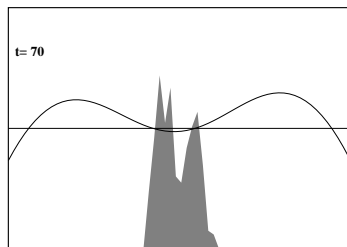


It arrives  
to a fitness minimum,  
and branches there!

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

Frequency dependence starts to matter!

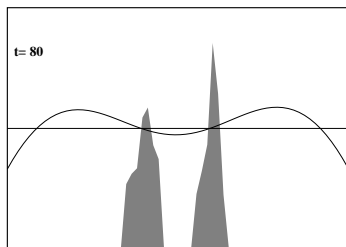
# Branching away



After branching,  
the populations  
evolves away!

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

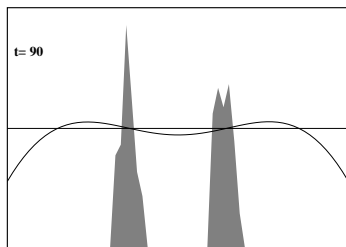
# Branching away



After branching,  
the populations  
evolves away!

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

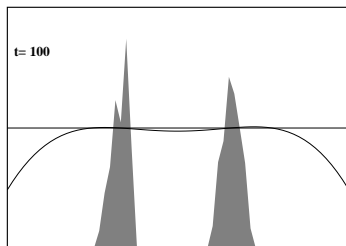
# Branching away



After branching,  
the populations  
evolves away!

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

# Branching away



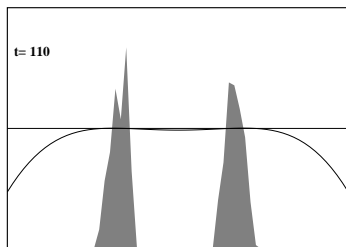
After branching,  
the populations  
evolves away!

Reason:

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



# Branching away



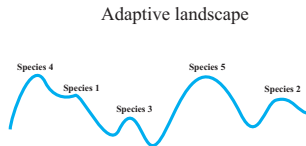
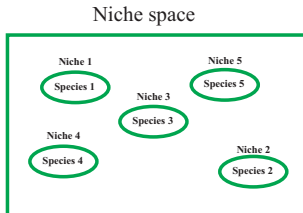
After branching,  
the populations  
evolves away!

Continuity Tenet  $\implies$  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.



Tension: “fittest 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:

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

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

# 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:

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

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

# Reduced competition – what is it?

Lotka-Volterra:

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

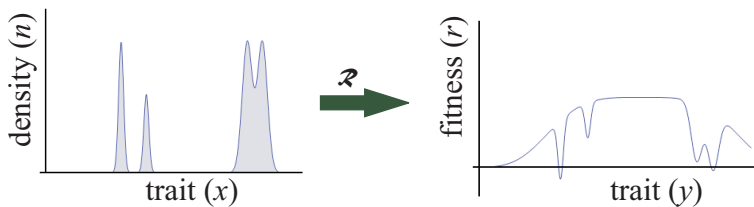
strength of competition

In general:

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

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

## Regulated landscape: niche



Strength of competition:

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

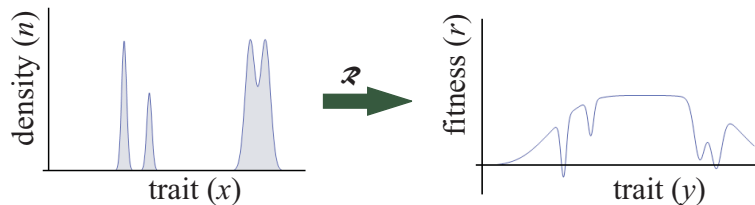
Niche segregation:

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:

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

General competition:

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

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

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

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

Connection between pop. din. and trait space continuity!

Functional analysis ends here :-).

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

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

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

Connection between pop. din. and trait space continuity!

Functional analysis ends here :-).

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

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

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

**Connection between pop. din. and trait space continuity!**

Functional analysis ends here :-).

# 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:

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

# 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:

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

# 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:

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

# 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:

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



# Expansion of growth rates

Similar strategies:

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

Taylor in  $\varepsilon$ :

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

**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.

# Expansion of growth rates

Similar strategies:

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

Taylor in  $\varepsilon$ :

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

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.

# Expansion of growth rates

Similar strategies:

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

Taylor in  $\varepsilon$ :

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

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.

# Expansion of relative dynamics

Pairwise invasion fitness:

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

Taylor expansion:

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

(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.

# Expansion of relative dynamics

Pairwise invasion fitness:

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

Taylor expansion:

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

(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.

# Expansion of relative dynamics

Pairwise invasion fitness:

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

Taylor expansion:

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

(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.

# Expansion of relative dynamics

Pairwise invasion fitness:

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

Taylor expansion:

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

(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.

# Expansion of relative dynamics

Pairwise invasion fitness:

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

Taylor expansion:

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

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

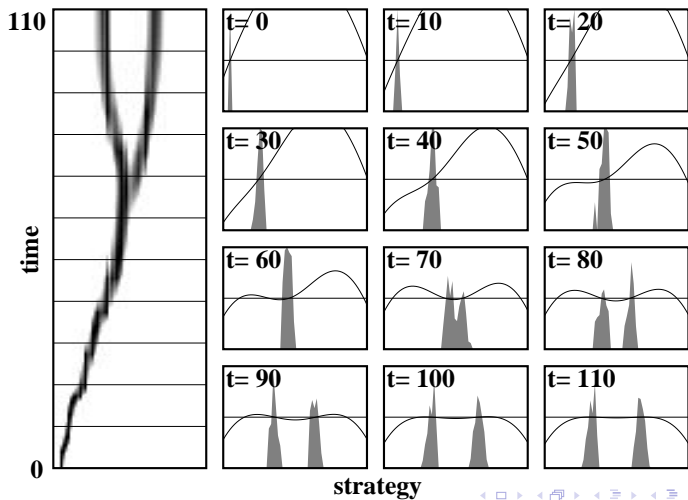
Only the second order term is frequency dependent!

Even this dependence is linear.

⇒ Density-independent directional evolution

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



Branching, 2<sup>nd</sup> 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.

# 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.

# 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.

# 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.

# 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.

# Assumptions of AD: second look

Clonal reproduction.

WAS NOT DISCUSSED.

Small mutational steps.

This is the essence of AD!

Rare mutations.

NOT NEEDED!

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

It is a consequence!

# Assumptions of AD: second look

Clonal reproduction.

WAS NOT DISCUSSED.

Small mutational steps.

This is the essence of AD!

Rare mutations.

NOT NEEDED!

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

It is a consequence!



# Assumptions of AD: second look

Clonal reproduction.

WAS NOT DISCUSSED.

Small mutational steps.

This is the essence of AD!

Rare mutations.

NOT NEEDED!

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

It is a consequence!

# Assumptions of AD: second look

Clonal reproduction.

WAS NOT DISCUSSED.

Small mutational steps.

This is the essence of AD!

Rare mutations.

NOT NEEDED!

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

It is a consequence!

## takehome

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

# Many thanks for the coauthors!

- 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)

Thanks for your attention!