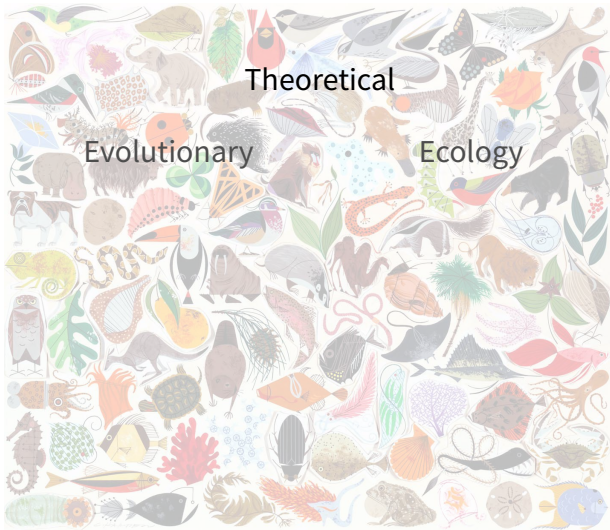


Lecture I: Introduction of Methods and Concepts

January 2017



(c) Charley Harper, "Tree of Life"

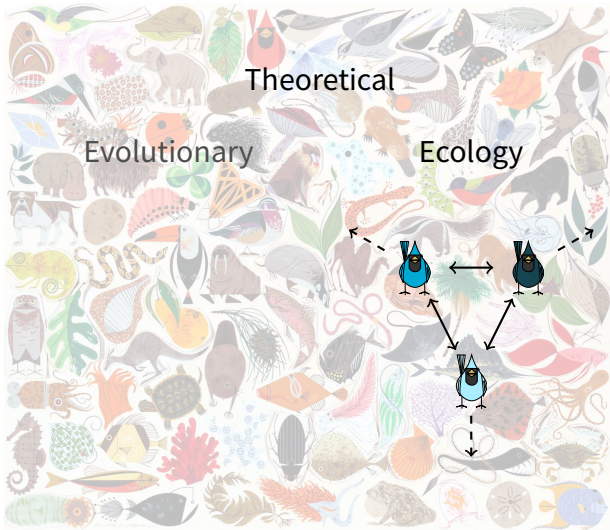


Theoretical

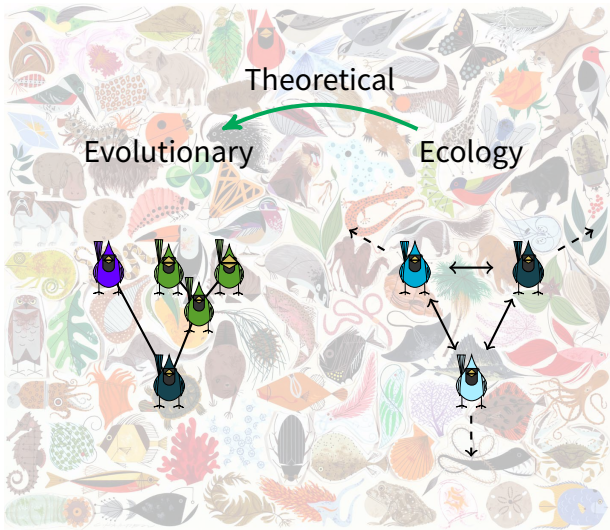
Evolutionary

Ecology

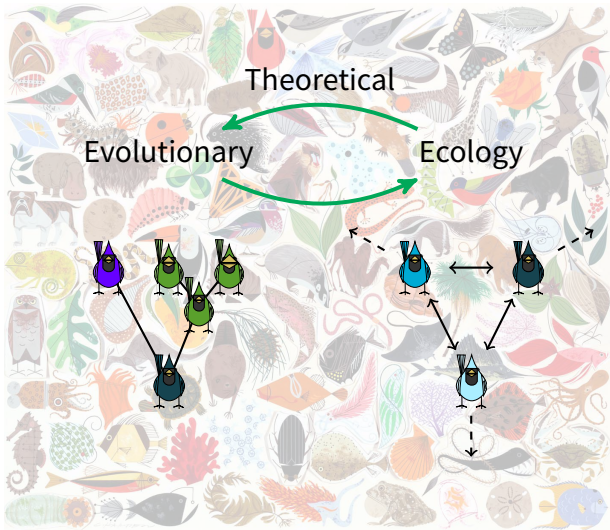
(c) Charley Harper, "Tree of Life"



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Seven steps to modelling a biological problem

[Otto and Day, 2007]

Seven steps to modelling a biological problem

1 Formulate the question

[Otto and Day, 2007]

Seven steps to modelling a biological problem

1 Formulate the question

What do you want to know?

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients

[more soon]

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients
- 3 Qualitatively describe the system

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients
- 3 Qualitatively describe the system

Life-cycle, flow diagram

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients
- 3 Qualitatively describe the system
- 4 Quantitatively describe the system

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients
- 3 Qualitatively describe the system
- 4 Quantitatively describe the system

Write down the equations

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients
- 3 Qualitatively describe the system
- 4 Quantitatively describe the system
- 5 Analyze the equations

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients
- 3 Qualitatively describe the system
- 4 Quantitatively describe the system
- 5 Analyze the equations
 - ▶ *Graphical analysis*
 - ▶ *Simulations*
 - ▶ *Equilibrium and stability analyses*
 - ▶ *Deriving general solutions*
 - ▶ *Determining long-term or asymptotic behavior*

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients
- 3 Qualitatively describe the system
- 4 Quantitatively describe the system
- 5 Analyze the equations
- 6 Checks and balances

[Otto and Day, 2007]

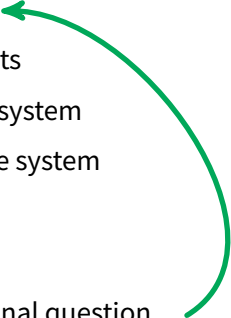
Seven steps to modelling a biological problem

- 1 Formulate the question
- 2 Determine basic ingredients
- 3 Qualitatively describe the system
- 4 Quantitatively describe the system
- 5 Analyze the equations
- 6 Checks and balances

Generality, alternative models

[Otto and Day, 2007]

Seven steps to modelling a biological problem

- 1 Formulate the question
 - 2 Determine basic ingredients
 - 3 Qualitatively describe the system
 - 4 Quantitatively describe the system
 - 5 Analyze the equations
 - 6 Checks and balances
 - 7 Relate results back to original question
- 

[Otto and Day, 2007]

Outline

Introduction

Defining a model

Basic ingredients

Features of evolutionary models

Discrete traits

Quantitative traits

Basic ingredients of a model

Variables

- ▶ Define the variables

[Otto and Day, 2007]

Basic ingredients of a model

Variables

- ▶ Define the variables

e.g., $p_i(t)$, frequency of individuals of type i at time t

$N_j(z, t)$, number of individuals of type z in deme j at time t

$X_j(t)$, indicator of whether there is a mutant at site j at time t

[Otto and Day, 2007]

Basic ingredients of a model

Variables

- ▶ Define the variables

e.g., $p_i(t)$, frequency of individuals of type i at time t

$N_j(z, t)$, number of individuals of type z in deme j at time t

$X_j(t)$, indicator of whether there is a mutant at site j at time t

- ▶ Identify constraints on the variables

e.g., $0 \leq p \leq 1$

[Otto and Day, 2007]

Basic ingredients of a model

Variables

- ▶ Define the variables
- ▶ Identify constraints on the variables

Time

[Otto and Day, 2007]

Basic ingredients of a model

Variables

- ▶ Define the variables
- ▶ Identify constraints on the variables

Time

- ▶ Is time continuous or discrete?

[Otto and Day, 2007]

Basic ingredients of a model

Variables

- ▶ Define the variables
- ▶ Identify constraints on the variables

Time

- ▶ Is time continuous or discrete?
- ▶ What is the time scale?

[Otto and Day, 2007]

Basic ingredients of a model

Variables

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- ▶ Identify constraints on the variables

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- ▶ Is time continuous or discrete?
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Parameters

[Otto and Day, 2007]

Basic ingredients of a model

Variables

- ▶ Define the variables
- ▶ Identify constraints on the variables

Time

- ▶ Is time continuous or discrete?
- ▶ What is the time scale?

Parameters

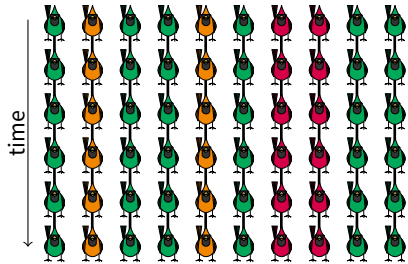
- ▶ Define the model's parameters;
- ▶ Identify constraints.

[Otto and Day, 2007]

Some features of evolutionary models

Reproduction

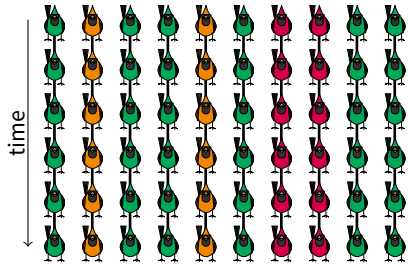
Clonal or sexual, with or without mate choice.



Some features of evolutionary models

Reproduction

Clonal or sexual, with or without mate choice.



[Fisher, 1930, Wright, 1931]; F. Massol

Some features of evolutionary models



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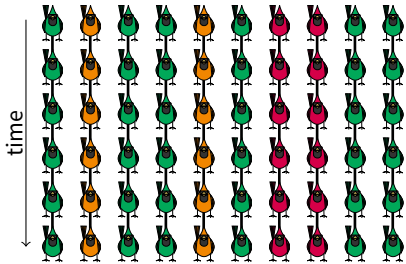
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Clonal or sexual, with or without mate choice.

Evolutionary forces

- ▶ Drift
- ▶ Selection
- ▶ Migration
- ▶ Mutation



[Fisher, 1930, Wright, 1931]; F. Massol

Some features of evolutionary models



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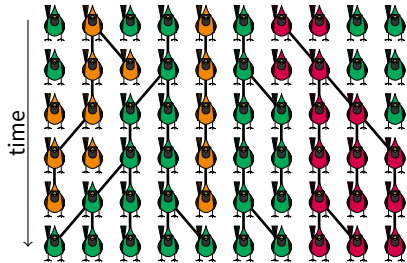
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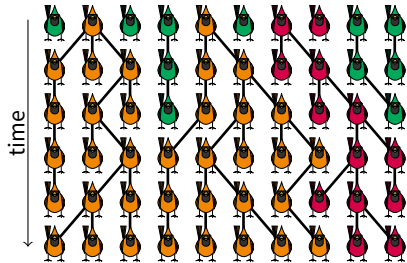
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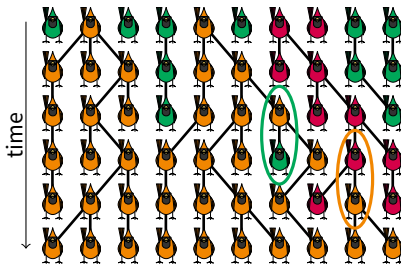
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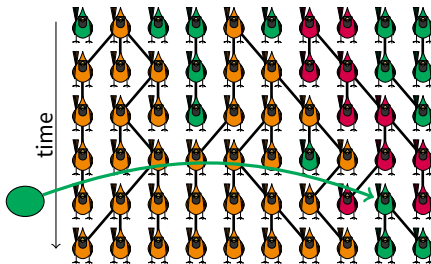
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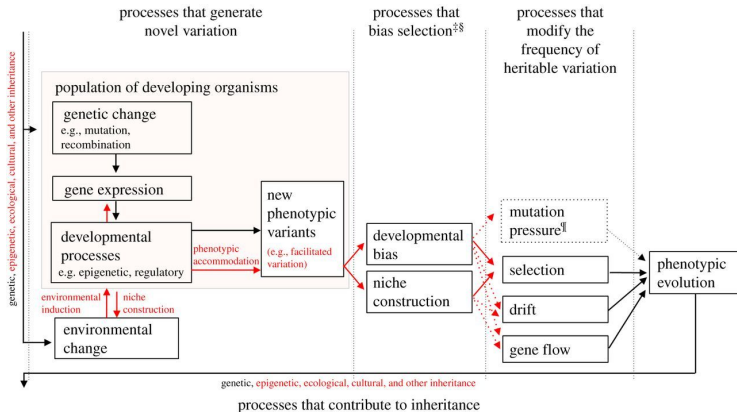
Evolutionary forces

- ▶ Drift
- ▶ Selection
- ▶ Migration
- ▶ Mutation



[Fisher, 1930, Wright, 1931]; F. Massol

Some other features...



... that we won't consider here.

[Laland et al., 2015]

A key concept: fitness

This survival of the fittest [...] is that which Mr. Darwin has called 'natural selection, or the preservation of favoured races in the struggle for life.'

Herbert Spencer, *The principles of biology* (1864)

A key concept: fitness

This survival of the fittest [...] is that which Mr. Darwin has called 'natural selection, or the preservation of favoured races in the struggle for life.'

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What is “fitness”?

A key concept: fitness

This survival of the fittest [...] is that which Mr. Darwin has called 'natural selection, or the preservation of favoured races in the struggle for life'

Herbert Spencer, *The principles of biology* (1864)

What is “fitness”?

not this:

Dear Dr. Florence Débarre,
Warm Greetings from [Journal of Aerobics and Fitness](#).
We greatly appreciate your valuable contribution towards the scientific community.
We would like to invite you to contribute 1 page **Letter to Editor (Research, Review, Case Reports, Short Commentary of 1or 2**

Outline

Introduction

Defining a model

Discrete traits

- Discrete time

- Continuous time

- Fitness components

Quantitative traits

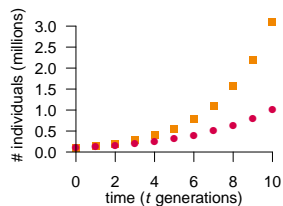
Discrete traits – I) Discrete generations

Geometric population growth

$$A_t = (1 + a)^t A_0$$

$$B_t = (1 + b)^t B_0$$

$a = 0.41$ and $b = 0.26$.



[Hartl and Clark, 2007]

Discrete traits – I) Discrete generations

Geometric population growth

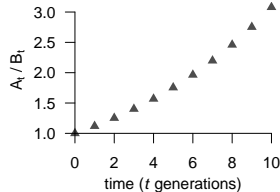
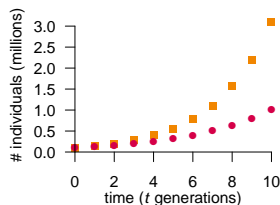
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Ratio of the number of A individuals to B individuals

$$\frac{A_t}{B_t} = \left(\frac{1 + a}{1 + b} \right)^t \frac{A_0}{B_0}$$

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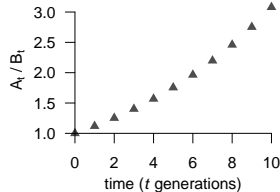
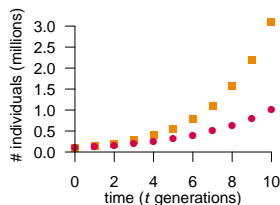
$$B_t = (1 + b)^t B_0$$

Ratio of the number of A individuals to B individuals

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Relative fitness

$a = 0.41$ and $b = 0.26$.



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Geometric population growth

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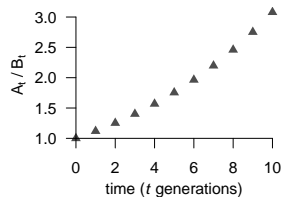
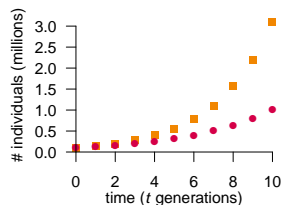
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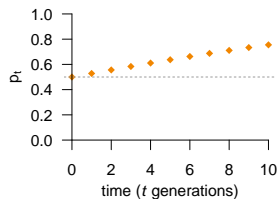


[Hartl and Clark, 2007]

Discrete traits – I) Discrete generations (*continued*)

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$$p_t = \frac{A_t}{A_t + B_t}$$



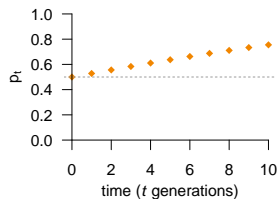
Discrete traits – I) Discrete generations (*continued*)

Proportion of A individuals

$$p_t = \frac{A_t}{A_t + B_t}$$

Change in the proportion of A individuals:

$$\Delta p_t = \frac{(w - 1)p_t(1 - p_t)}{wp_t + 1 - p_t}$$



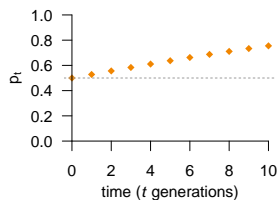
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$$\begin{aligned}\Delta p_t &= p_{t+1} - p_t \\ &= \frac{(1 + a)A_t}{(1 + a)A_t + (1 + b)B_t} - p_t \\ &= \frac{wp_t}{wp_t + 1 - p_t} - p_t = \frac{(w - 1)p_t(1 - p_t)}{\bar{w}_t}\end{aligned}$$

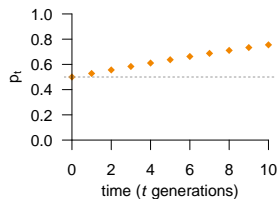
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Discrete traits – II) Continuous Time

Exponential population growth

$$A(t) = A_0 \exp(\alpha t)$$

$$B(t) = B_0 \exp(\beta t)$$

Discrete traits – II) Continuous Time

Exponential population growth

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Ratio of the number of A individuals to B individuals

$$\frac{A(t)}{B(t)} = \frac{A_0}{B_0} \exp((\alpha - \beta) t)$$

Discrete traits – II) Continuous Time

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Relative fitness

Discrete traits – II) Continuous Time

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Relative fitness

Change in the proportion of A individuals

$$\frac{dp(t)}{dt} = (\alpha - \beta) p(t)(1 - p(t)).$$

Discrete traits – II) Continuous Time

Exponential population growth

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Relative fitness

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$$\frac{dp(t)}{dt} = mp(t)(1 - p(t)).$$

Comparing discrete and continuous time

Ratio of the number of A individuals to B individuals

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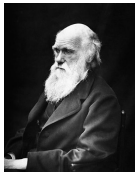
$$\frac{A(t)}{B(t)} = \exp(m t) \frac{A_0}{B_0}$$

Comparing discrete and continuous time

Ratio of the number of A individuals to B individuals

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Darwinian fitness



$$\frac{A(t)}{B(t)} = \exp(mt) \frac{A_0}{B_0}$$

Malthusian fitness

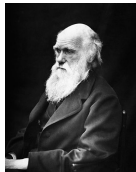


Comparing discrete and continuous time

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Darwinian fitness



$$\frac{A(t)}{B(t)} = \exp(mt) \frac{A_0}{B_0}$$

Malthusian fitness



$$m = \ln(w) \approx w - 1$$

(when w is close to 1).

Comparing discrete and continuous time

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(when w is close to 1).

Change in the frequency of A individuals

$$\Delta p = \frac{(w - 1) p (1 - p)}{wp + 1 - p}$$

$$\frac{dp}{dt} = m p (1 - p).$$

Comparing discrete and continuous time

Ratio of the number of A individuals to B individuals

$$\frac{A_t}{B_t} = w^t \frac{A_0}{B_0}$$

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$$\Delta p = \frac{(w-1)p(1-p)}{wp+1-p}$$

$$\approx (w-1)p(1-p)$$

(when w is close to 1).

$$\frac{dp}{dt} = mp(1-p).$$

Fitness components

Life stages at which selection can operate

[Bundgaard and Christiansen, 1972, Hedrick, 2011], with modifications

Fitness components

Life stages at which selection can operate

Fecundity selection

- ▶ Egg/seed production
- ▶ Sperm/pollen production

Viability selection

- ▶ Zygotic survival
- ▶ Rate of development
- ▶ Maternal-fetal interactions
- ▶ Sex-dependent survival

Sexual selection

- ▶ Assortative mating
- ▶ Male vigor
- ▶ Female choice

Gametic selection

- ▶ Nonrandom union of gametes
- ▶ Meiotic drive
- ▶ Self-incompatibility

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Fitness components

Life stages at which selection can operate

Fecundity selection

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Outline

Introduction

Defining a model

Discrete traits

Quantitative traits
Adaptive dynamics

Evolution of quantitative traits



vs.



Evolution of quantitative traits



Methods

- ▶ “Raw” model

No assumptions on the distribution.

e.g., use of integro-differential equations.

Evolution of quantitative traits



Methods

- ▶ “Raw” model

No assumptions on the distribution.

e.g., use of integro-differential equations.

- ▶ Quantitative genetics

Moment-based approaches

Evolution of quantitative traits



Methods

- ▶ “Raw” model
 - No assumptions on the distribution.*
 - e.g., use of integro-differential equations.*
- ▶ Quantitative genetics
 - Moment-based approaches*
- ▶ Adaptive dynamics

Evolution of quantitative traits



Methods

- ▶ “Raw” model
 - No assumptions on the distribution.*
 - e.g., use of integro-differential equations.*
- ▶ Quantitative genetics
 - Moment-based approaches*
- ▶ Adaptive dynamics

Adaptive dynamics (AD)

[Metz et al., 1992, Geritz et al., 1998, Doebeli, 2011]

Adaptive dynamics (AD)

Assumptions

- ▶ Mutations are rare,

[Metz et al., 1992, Geritz et al., 1998, Doebeli, 2011]

Adaptive dynamics (AD)

Assumptions

- ▶ Mutations are rare,

→ *Describe the evolution of a trait as a sequence of trait substitutions.*

[Metz et al., 1992, Geritz et al., 1998, Doebeli, 2011]

Adaptive dynamics (AD)

Assumptions

- ▶ Mutations are rare,
→ *Describe the evolution of a trait as a sequence of trait substitutions.*
- ▶ Mutations are of small effect.

[Metz et al., 1992, Geritz et al., 1998, Doebeli, 2011]

Adaptive dynamics (AD)

Assumptions

- ▶ Mutations are rare,
→ *Describe the evolution of a trait as a sequence of trait substitutions.*
- ▶ Mutations are of small effect.
→ *Local stability analysis*

[Metz et al., 1992, Geritz et al., 1998, Doebeli, 2011]

Adaptive dynamics (AD)

Assumptions

- ▶ Mutations are rare,
→ *Describe the evolution of a trait as a sequence of trait substitutions.*
- ▶ Mutations are of small effect.
→ *Local stability analysis*

A Key Concept: Invasion fitness

Tells us whether an initially rare mutant can invade.

[Metz et al., 1992, Geritz et al., 1998, Doebeli, 2011]

AD: Example

Model

- ▶ Lotka-Volterra dynamics:

AD: Example

Model

- ▶ Lotka-Volterra dynamics:

Carrying capacity

There is an optimal value of the trait, x_{opt}

$$K(x) = K_0 \exp\left(-\frac{(x - x_{opt})^2}{2v_K}\right),$$

AD: Example

Model

- ▶ Lotka-Volterra dynamics:

Carrying capacity

There is an optimal value of the trait, x_{opt}

$$K(x) = K_0 \exp\left(-\frac{(x - x_{opt})^2}{2v_K}\right),$$

Interaction term

Strongest when the traits are closest.

$$\alpha(x, y) = 1 - (x - y)^2.$$

AD: Example

Model

► Lotka-Volterra dynamics:

Carrying capacity

There is an optimal value of the trait, x_{opt}

$$K(x) = K_0 \exp\left(-\frac{(x - x_{opt})^2}{2v_K}\right),$$

Interaction term

Strongest when the traits are closest.

$$\alpha(x, y) = 1 - (x - y)^2.$$

► Mutation

Unbiased, of small variance.

$$\mu(x, z) = \frac{1}{\sigma_\mu \sqrt{2\pi}} \exp\left(-\frac{(x - z)^2}{2\sigma_\mu^2}\right).$$

AD: Example (2)

Full model

$$\frac{\partial N(x, t)}{\partial t} = \left(1 - \frac{\int \alpha(x, y) N(y, t) dy}{K(x)} \right) N(x, t) - \int \mu(x, z) dz N(x, t) + \int \mu(z, x) N(z, t) dz.$$

AD: Example (3)

When mutation is very rare...

“Resident” (with trait x_r) vs. “mutant” (with trait x_m)

- ▶ Resident alone

$$\frac{dN_r(t)}{dt} = \left(1 - \frac{N_r(t)}{K(x_r)}\right) N_r(t).$$

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- ▶ Resident + Mutant

$$\frac{dN_r(t)}{dt} = \left(1 - \frac{N_r(t) + \alpha(x_r, x_m)N_m(t)}{K(x_r)}\right) N_r(t),$$
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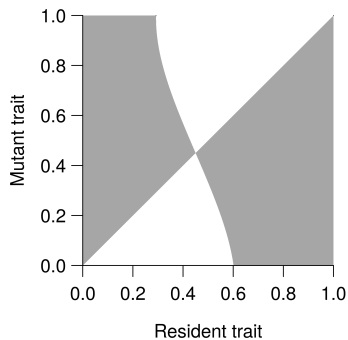
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Invasion fitness $w(x_m, x_r)$

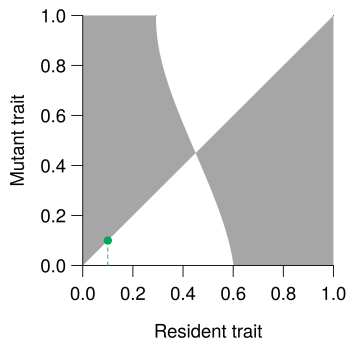
Pairwise Invasibility Plots (PIP)

Contour-plot of $w(x_m, x_r)$, showing regions where the mutant can invade.



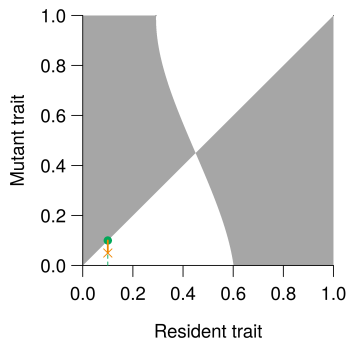
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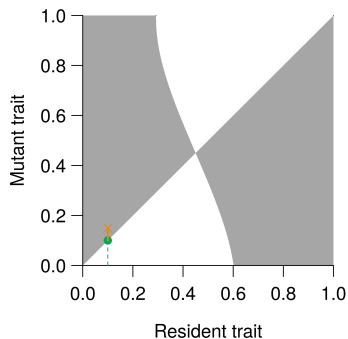


$$w(x_m, x_r) \approx$$

$$\underbrace{w(x_r, x_r)}_{=0} + (x_m - x_r) \underbrace{\left. \frac{\partial w(x_m, x_r)}{\partial x_m} \right|_{x_m=x_r}}_{\text{Selection gradient } D(x_r)}$$

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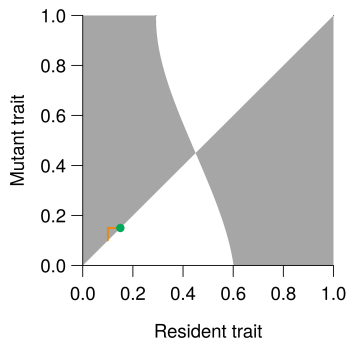


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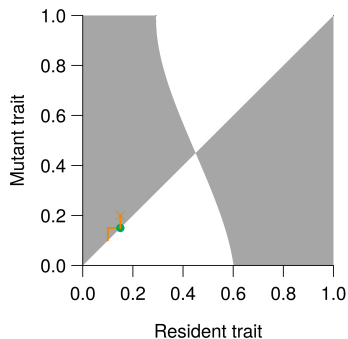


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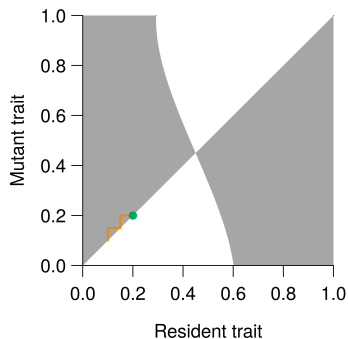


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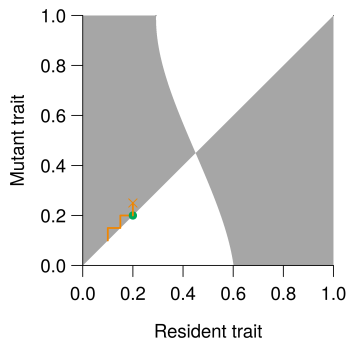


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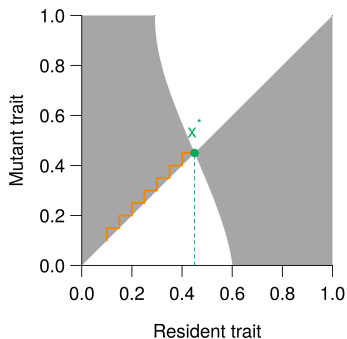


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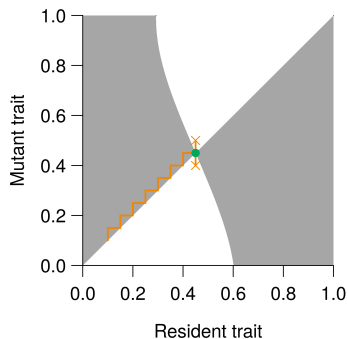


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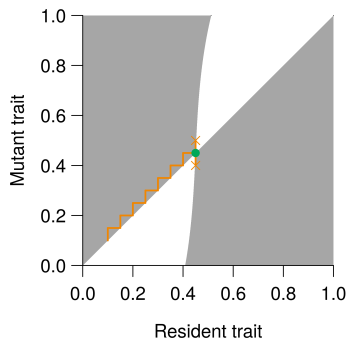


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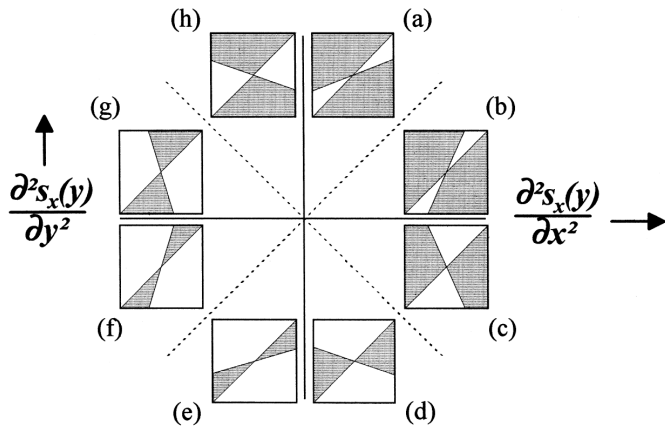
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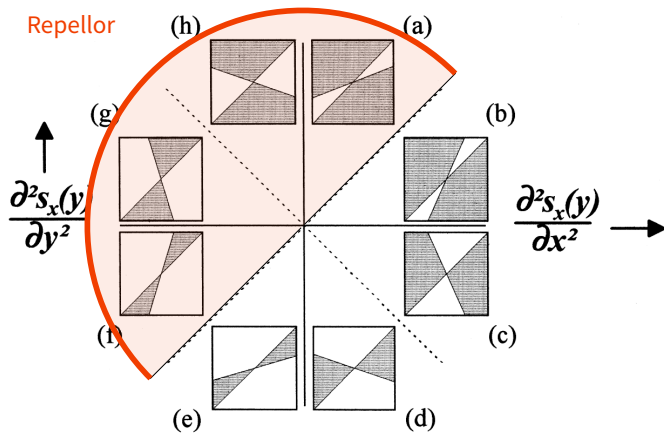
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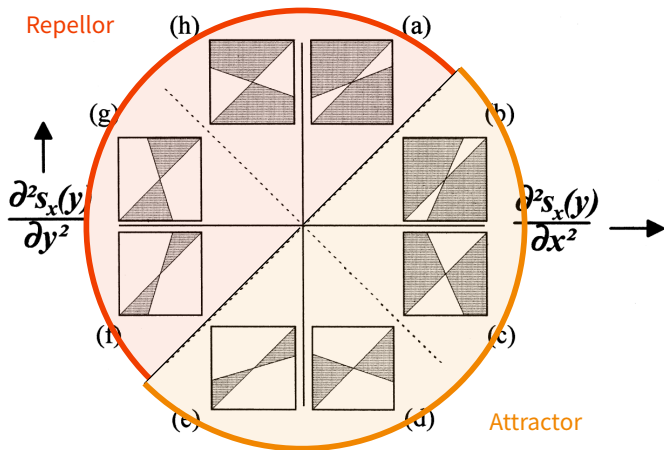
Pairwise Invasibility Plots (continued)



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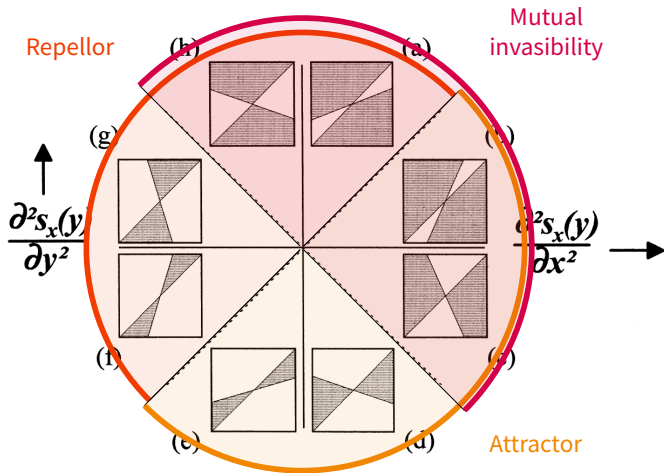


Pairwise Invasibility Plots (continued)



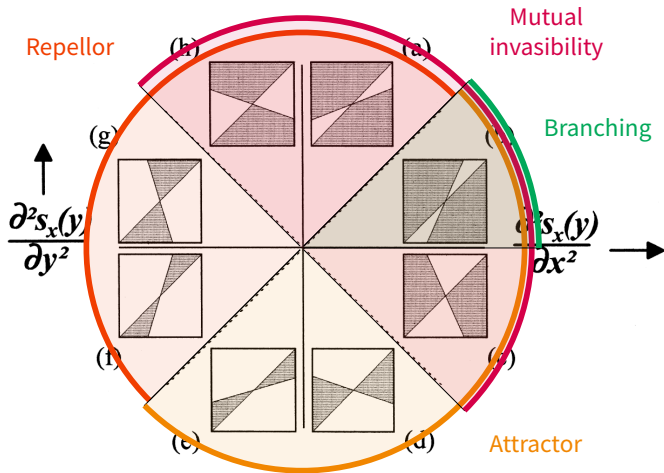
(c) [Geritz et al., 1998]

Pairwise Invasibility Plots (continued)



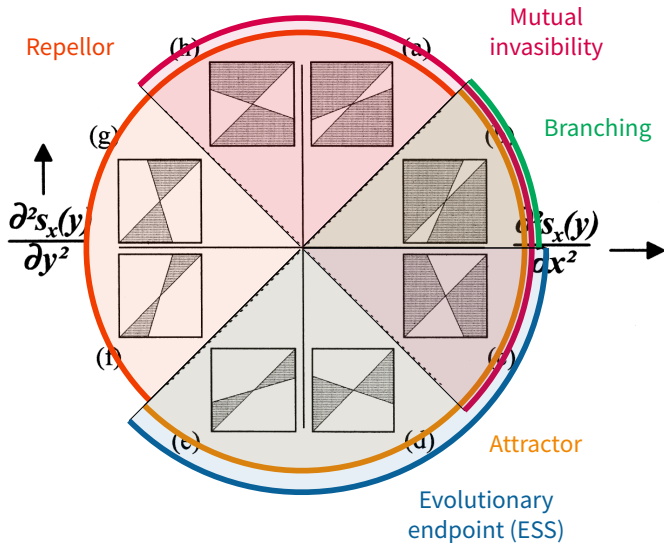
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Pairwise Invasibility Plots (continued)



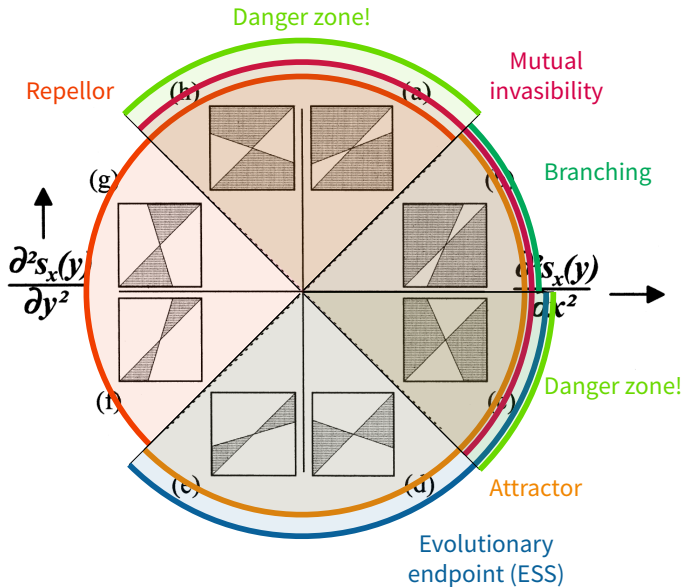
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Pairwise Invasibility Plots (continued)



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Pairwise Invasibility Plots (continued)



Back to the example

Adaptive dynamics

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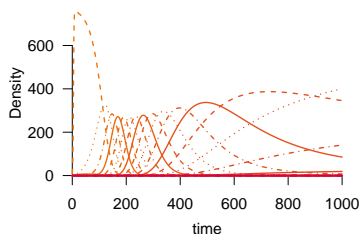
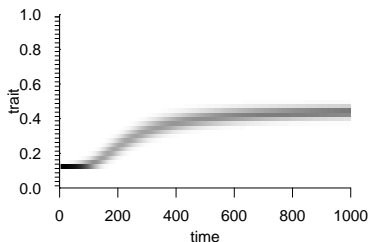
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Full model ($v_K = 0.2$)



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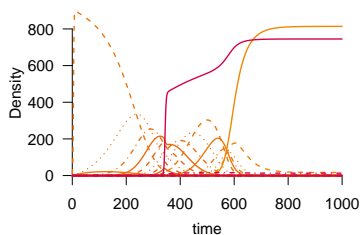
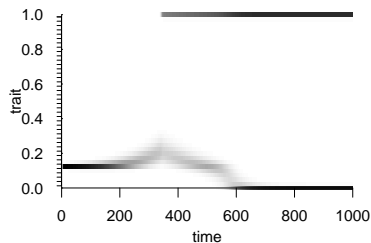
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Some take-home messages

Some dangers

- ▶ How do the model's results depend on the assumptions made?
- ▶ Do the results make sense biologically?

[Otto and Day, 2007]

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- ▶ How do the model's results depend on the assumptions made?
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And ultimately...

- ▶ Can you test the model with real data / experiments?
- ▶ How does the model help us better understand and interpret the world?

[Otto and Day, 2007]

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