Lecture I: Introduction of Methods and Concepts

January 2017

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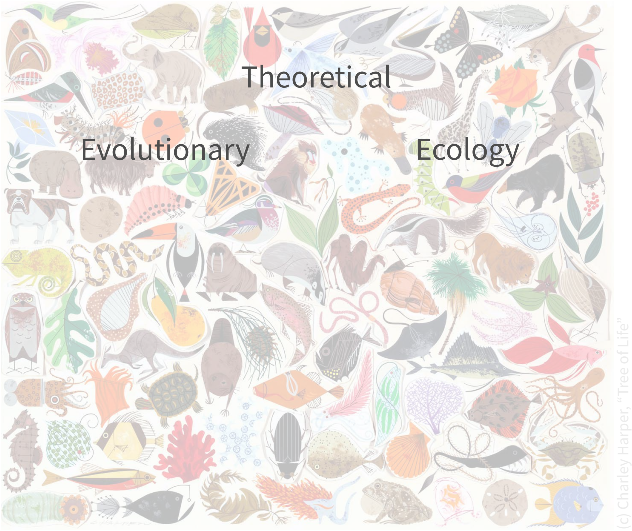
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Evolutionary
Ecology
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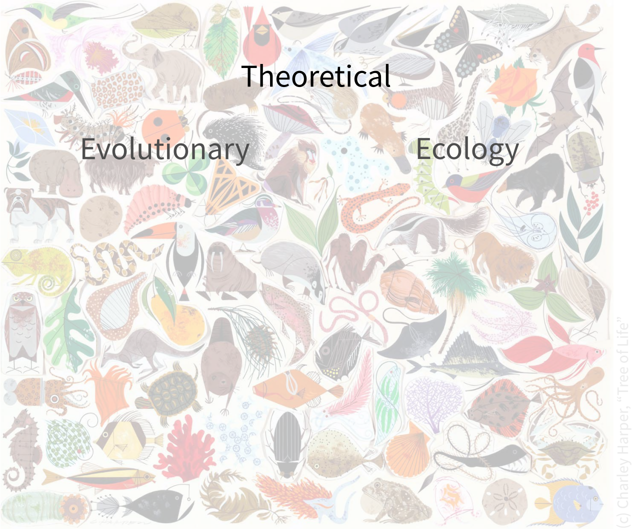
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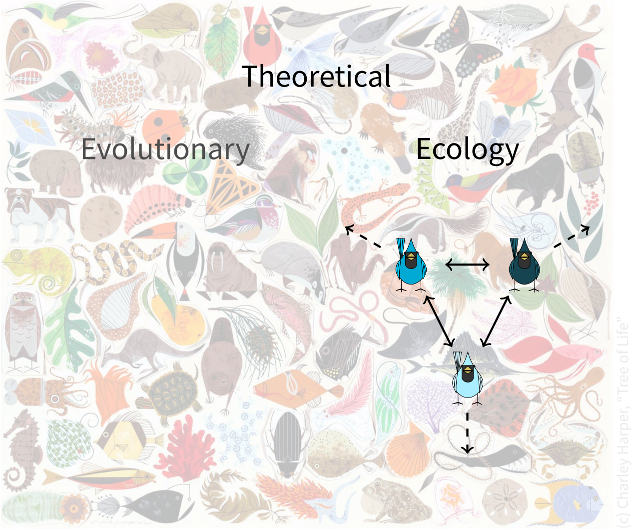
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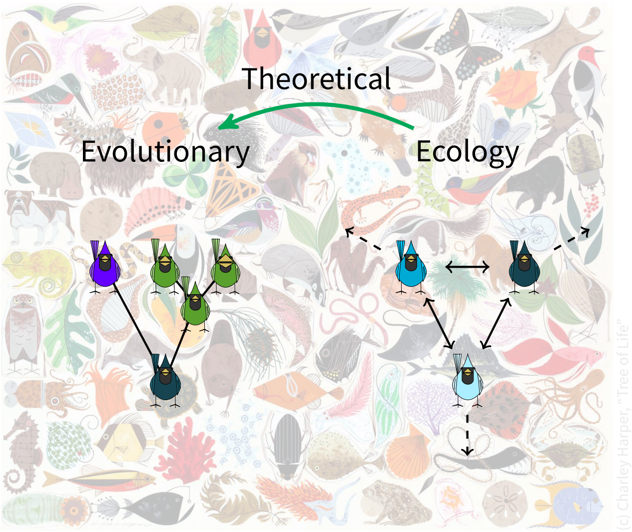
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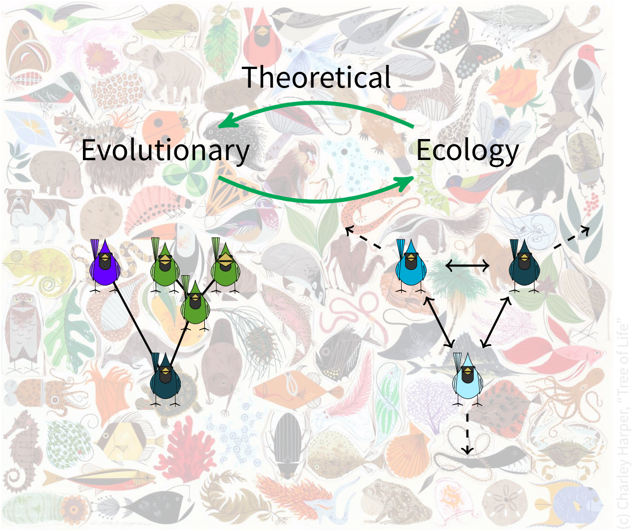
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Seven steps to modelling a biological problem

[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
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    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, altenative 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

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

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  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

- Define the variables
- Identify constraints on the variables

Time

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

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

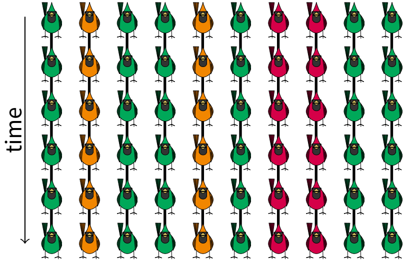
- Define the model's parameters;
- Identify constraints.

[Otto and Day, 2007]

Some features of evolutionary models

Reproduction

Clonal or sexual, with or without mate choice.



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

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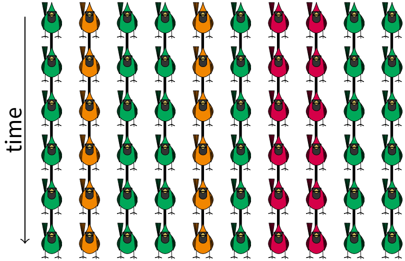

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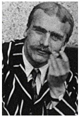
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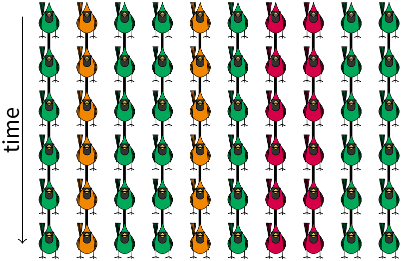
Reproduction

Clonal or sexual, with or without mate choice.

Evolutionary forces

- Drift
- Selection
- Migration
- Mutation



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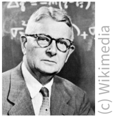

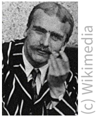

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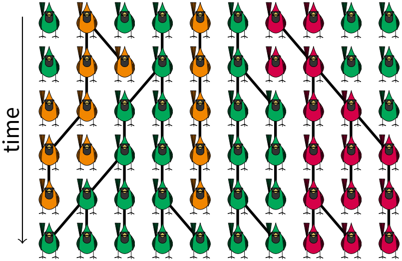

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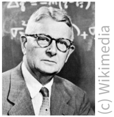

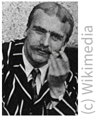

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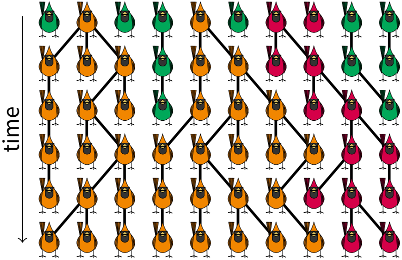

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Some features of evolutionary models


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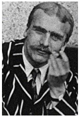
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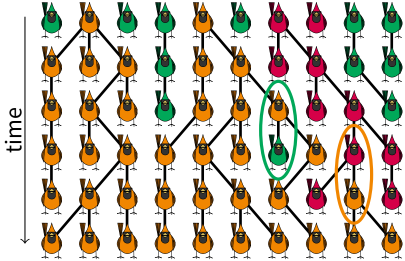

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Some features of evolutionary models


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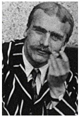
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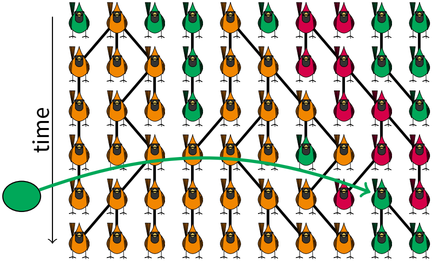

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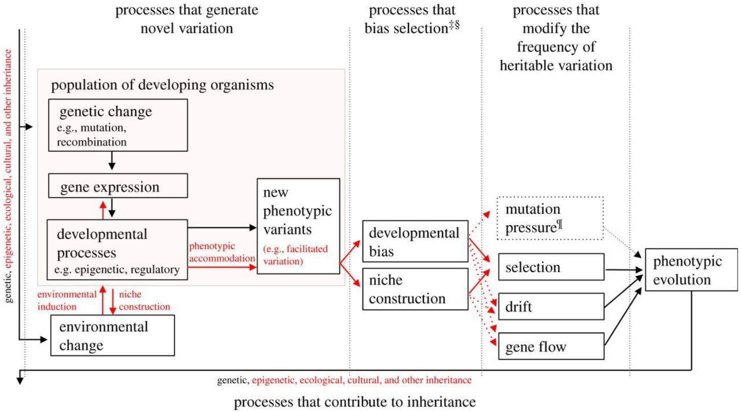
Some other features...



... 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)

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What is "fitness"?

A key concept: fitness

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

What is “fitness”?

not this:

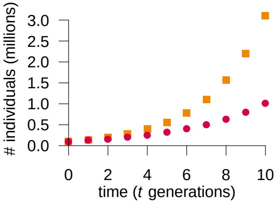
Dear Dr. Florence Débarre,
Warm Greetings from Journal of Aerobics and Fitness.
We greatly appreciate your valuable contribution towards the scientific community.
We would like to invite you to contribute 1 page **Letter to Editor (Research, Review, Case Reports, Short Commentary of 1or 2**

Outline

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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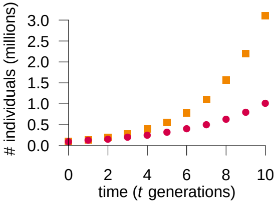
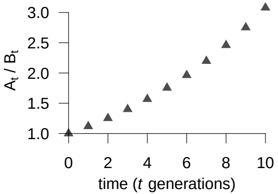


Ratio of the number of A individuals to B individuals

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



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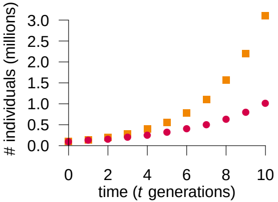
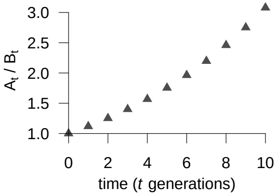


Ratio of the number of A individuals to B individuals

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

Relative fitness



[Hartl and Clark, 2007]

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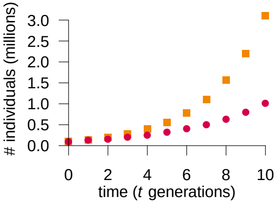

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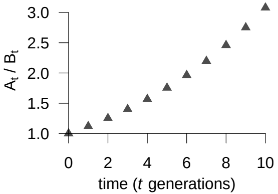
Relative fitness ★

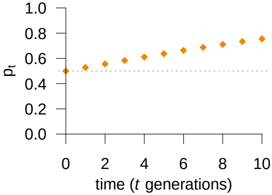


[Hartl and Clark, 2007]

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

Proportion of A individuals

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

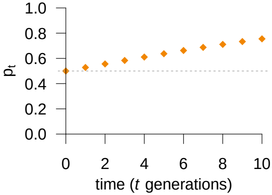


Proportion of A individuals

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

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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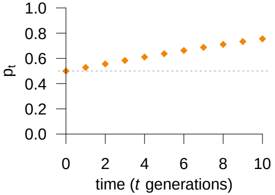

Change in the proportion of A individuals:

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

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

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

Proportion of A individuals

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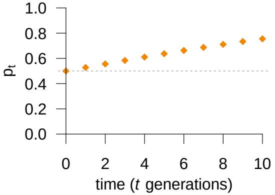

Change in the proportion of A individuals:

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Exponential population growth

$$A(t) = A_0 \exp(\alpha\, t)$$
$$B(t) = B_0 \exp(\beta\, t)$$

Exponential population growth

$$A(t) = A_0 \exp(\alpha\, t)$$
$$B(t) = B_0 \exp(\beta\, t)$$

Ratio of the number of A individuals to B individuals

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

Exponential population growth

$$A(t) = A_0 \exp(\alpha\, t)$$
$$B(t) = B_0 \exp(\beta\, t)$$

Ratio of the number of A individuals to B individuals

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

Relative fitness

Exponential population growth

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Ratio of the number of A individuals to B individuals

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

Relative fitness ★

Exponential population growth

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Ratio of the number of A individuals to B individuals

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

Relative fitness

Change in the proportion of A individuals

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

Exponential population growth

$$A(t) = A_0 \exp(\alpha\, t)$$
$$B(t) = B_0 \exp(\beta\, t)$$

Ratio of the number of A individuals to B individuals

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

Relative fitness

Change in the proportion of A individuals

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

Comparing discrete and continuous time

Ratio of the number of A individuals to B individuals

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

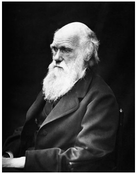
$$\frac{A(t)}{B(t)} = \exp(m\,t)\frac{A_0}{B_0}$$

Comparing discrete and continuous time

Ratio of the number of A individuals to B individuals

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

Darwinian fitness



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Malthusian fitness

Comparing discrete and continuous time

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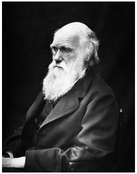

$$\frac{A(t)}{B(t)} = \exp(m\,t) \frac{A_0}{B_0}$$

Malthusian fitness

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

(when w is close to 1).

Comparing discrete and continuous time

Ratio of the number of A individuals to B individuals

$$\frac{A_t}{B_t} = w^t \frac{A_0}{B_0} \qquad \frac{A(t)}{B(t)} = \exp(m\,t)\frac{A_0}{B_0}$$

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

(when w is close to 1).

Change in the frequency of A individuals

$$\Delta p = \frac{(w-1)\,p\,(1-p)}{wp + 1 - p} \qquad \frac{dp}{dt} = m\,p(1-p).$$

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

(when w is close to 1).

Change in the frequency of A individuals

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

(when w is close to 1).

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

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

[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
- Offspring production

Viability selection

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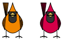
Outline

Evolution of quantitative traits



vs.

Evolution of quantitative traits

Methods

- “Raw” model

  No assumptions on the distribution.

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

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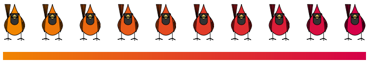

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Adaptive dynamics (AD)

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

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  → *Local stability analysis*

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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:

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  Carrying capacity

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

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

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- Mutation

  Unbiaised, 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

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

AD: Example (3)

When mutation is very rare...

"Resident" (with trait x_r) vs. "mutant" (with trait x_m)

- Resident alone

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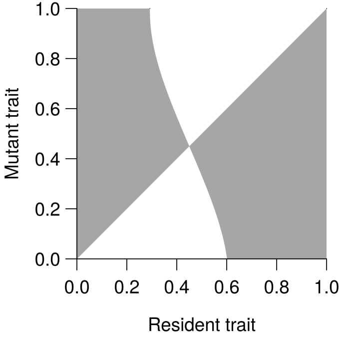
Pairwise Invasibility Plots (PIP)

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



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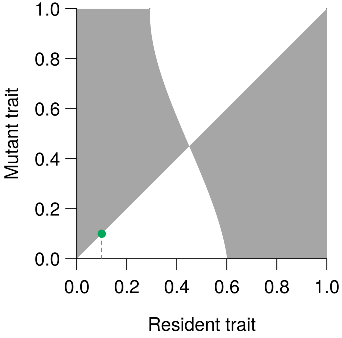

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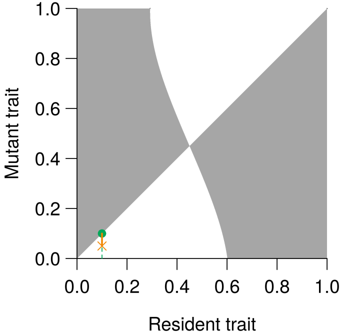

$$w(x_m, x_r) \approx$$

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

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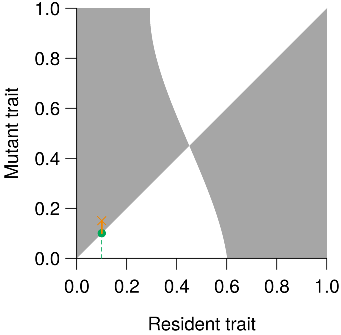

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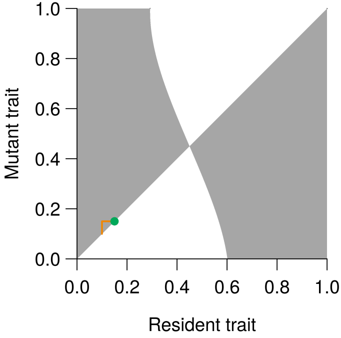

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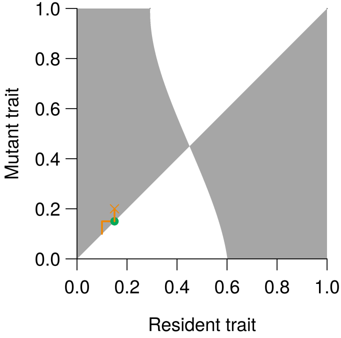

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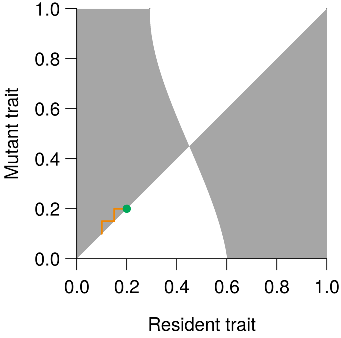

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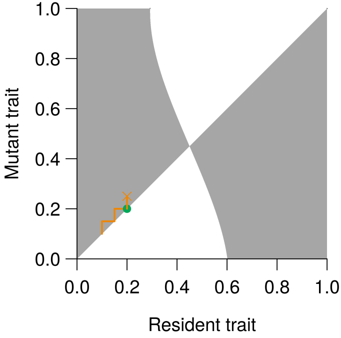

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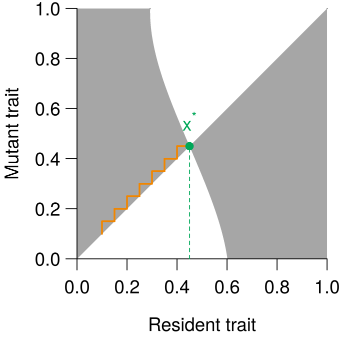

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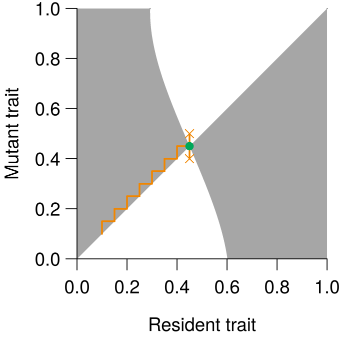

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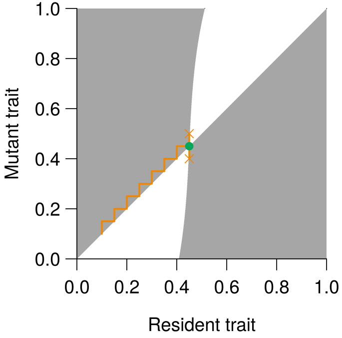

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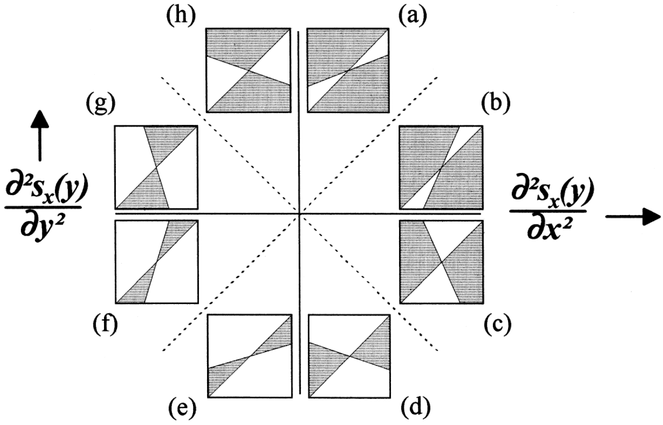

(c) [Geritz et al., 1998]

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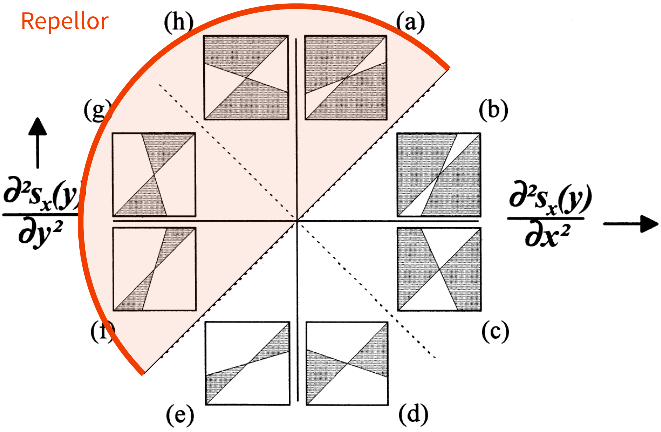

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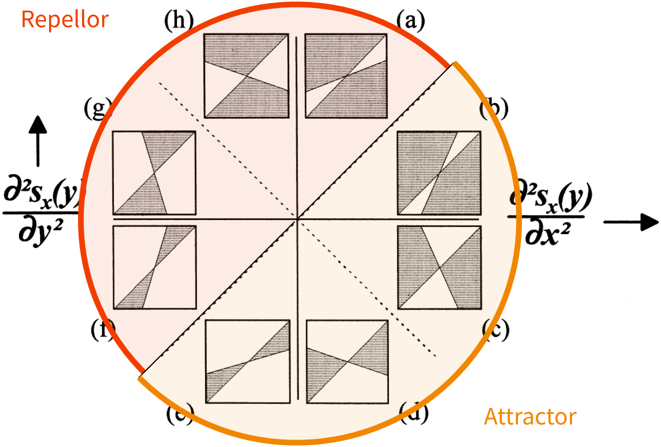

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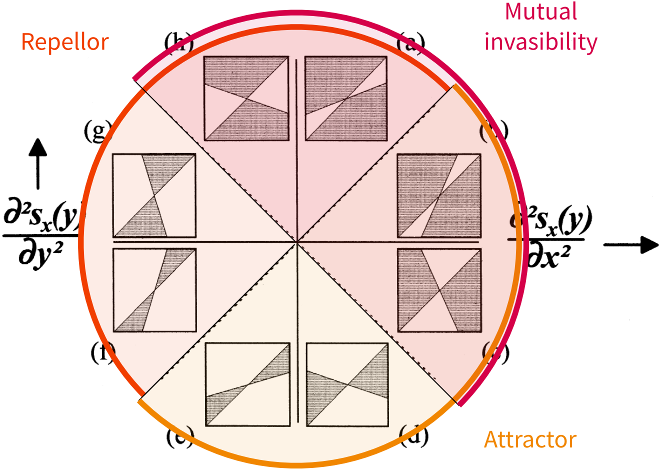

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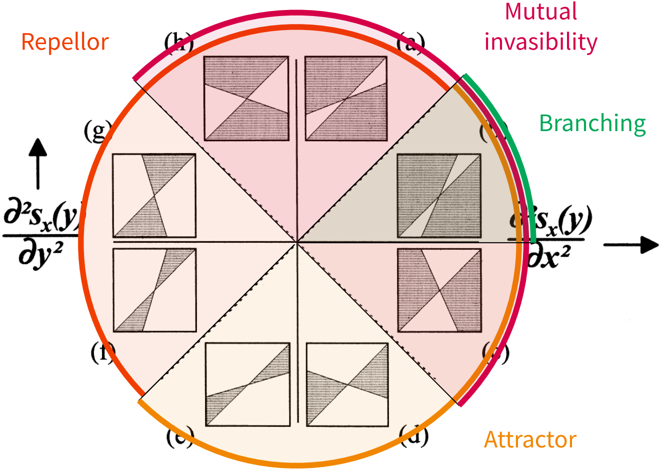

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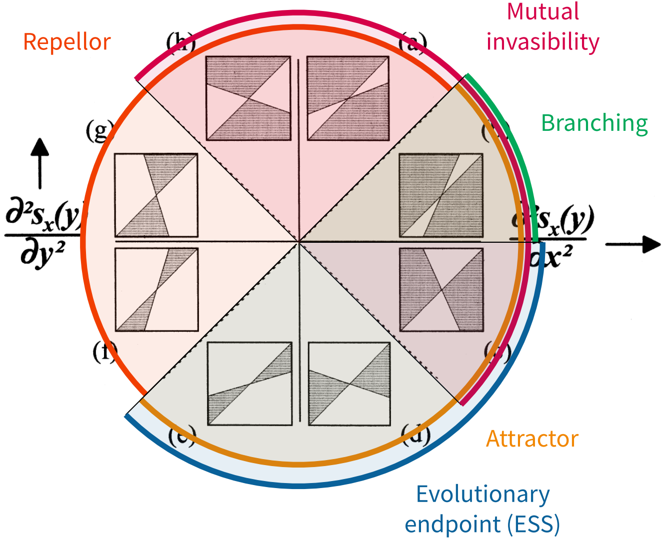

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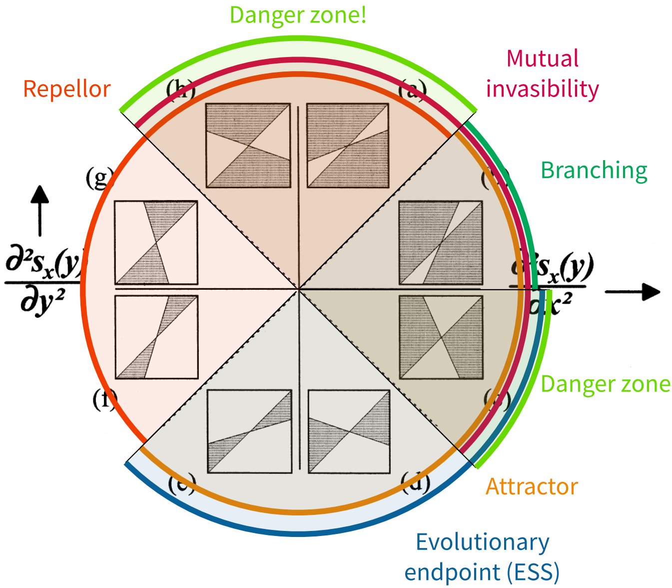

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Adaptive dynamics

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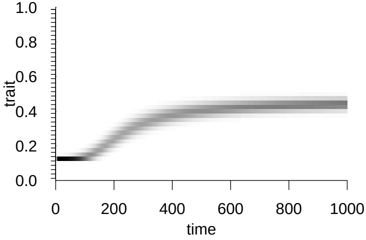
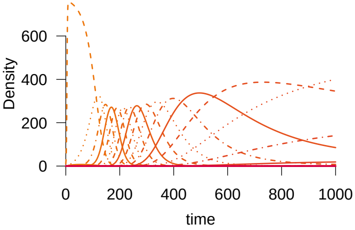
Full model ($v_K = 0.2$)





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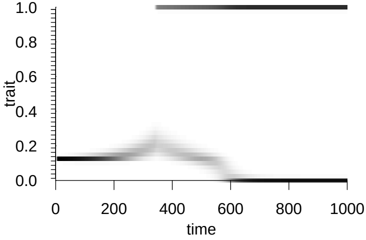

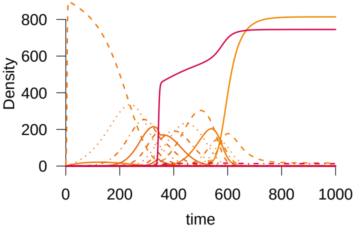

Some take-home messages

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- How do the model's results depend on the assumptions made?
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[Otto and Day, 2007]

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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]

References

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