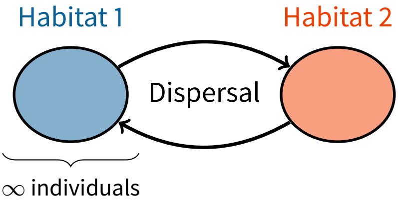
Lecture III: Heterogeneous environments

January 2017

Model



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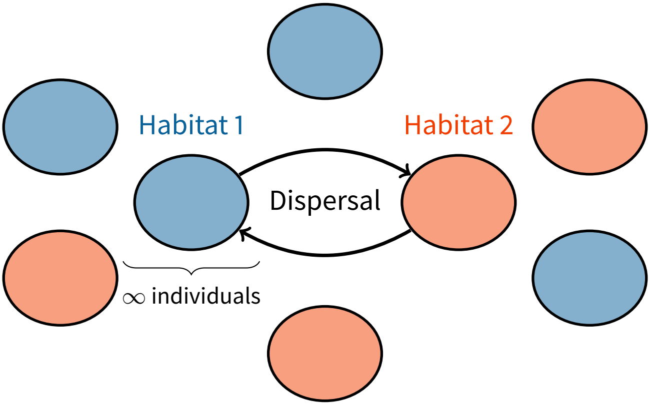

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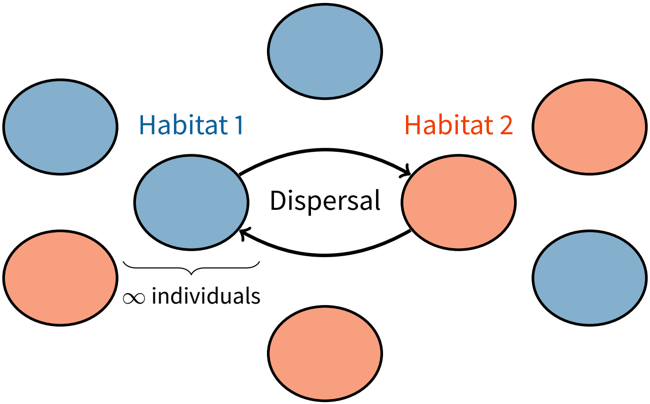
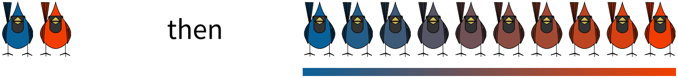




Outline

Introduction

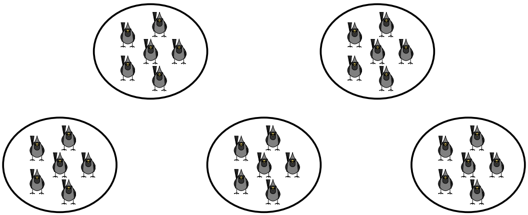
Discrete time models

- Soft selection
- Hard selection

Continuous time model

Discrete time models

Models with global pooling: all individuals join a pool of dispersers.



Discrete time models

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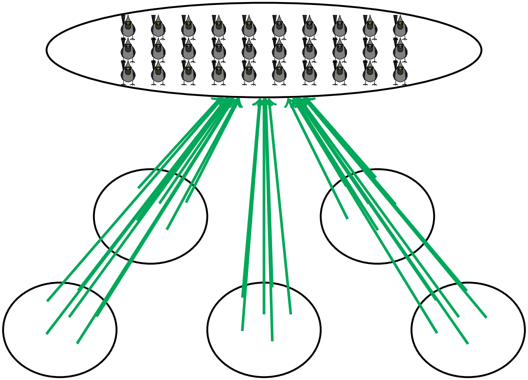

Discrete time models

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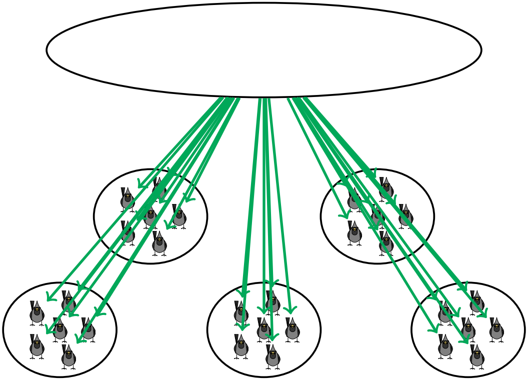

Discrete time models

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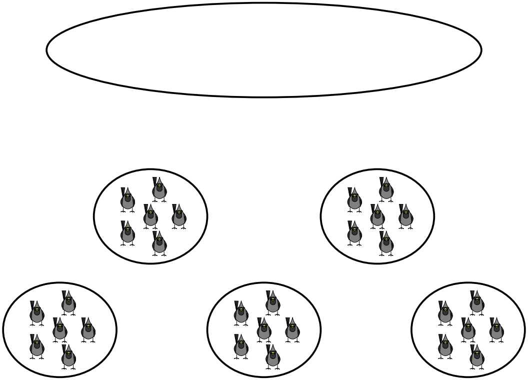
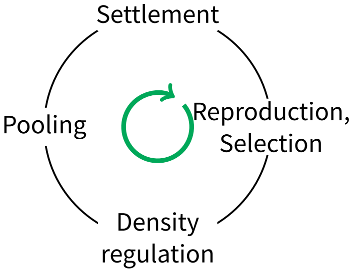


No drift: ∞ individuals in each deme.

“Levene model”

Or the importance of being clear about life-cycles...



[Levene, 1953, Ravigné et al., 2004]

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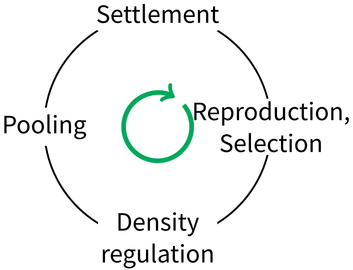

Viabilities:

	 A		 a
In habitat 1	w_1	$>$	v_1
In habitat 2	w_2	$<$	v_2

[Levene, 1953, Ravigné et al., 2004]

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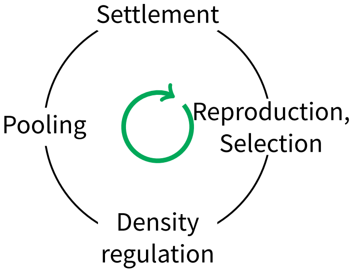

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Notation:

c Proportion of type-1 habitats

p Frequency of A in the population.

[Levene, 1953, Ravigné et al., 2004]

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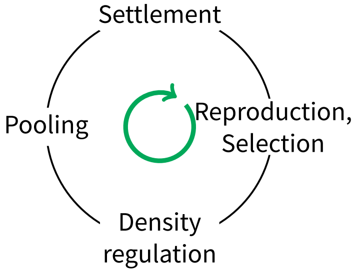

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Notation:

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p Frequency of A in the population.

$$\Delta p = p' - p$$

$$= c\frac{w_1 p}{w_1 p + v_1(1-p)} + (1-c)\frac{w_2 p}{w_2 p + v_2(1-p)} - p.$$

[Levene, 1953, Ravigné et al., 2004]

“Levene model” (2)

$$\Delta p = c \frac{w_1 p}{w_1 p + v_1(1-p)} + (1-c) \frac{w_2 p}{w_2 p + v_2(1-p)} - p.$$

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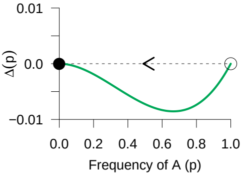
Equilibria:

“Levene model” (2)

$$\Delta p = c\frac{w_1 p}{w_1 p + v_1(1-p)} + (1-c)\frac{w_2 p}{w_2 p + v_2(1-p)} - p.$$

Equilibria:

$$c\frac{w_1}{v_1} + (1-c)\frac{w_2}{v_2} < 1$$



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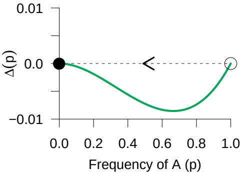
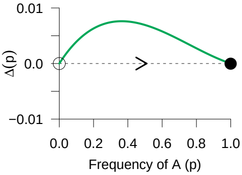


$$c\frac{v_1}{w_1} + (1-c)\frac{v_2}{w_2} < 1$$

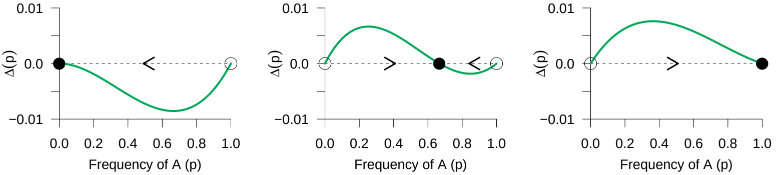


"Levene model" (2)

$$\Delta p = c\frac{w_1 p}{w_1 p + v_1(1-p)} + (1-c)\frac{w_2 p}{w_2 p + v_2(1-p)} - p.$$

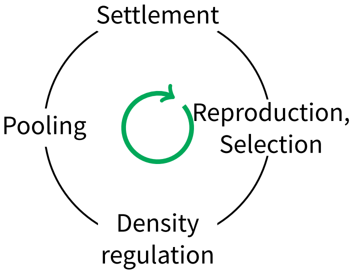
Equilibria:

$c\frac{w_1}{v_1} + (1-c)\frac{w_2}{v_2} < 1$ — otherwise — $c\frac{v_1}{w_1} + (1-c)\frac{v_2}{w_2} < 1$



$$p^* = c\frac{v_2}{v_2 - w_2} - (1-c)\frac{v_1}{w_1 - v_1}$$

“Levene model”



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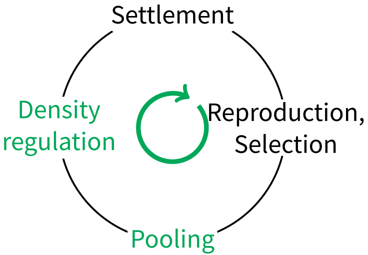
p Frequency of A in the population.

[Dempster, 1955, Ravigné et al., 2004]

"Dempster model"



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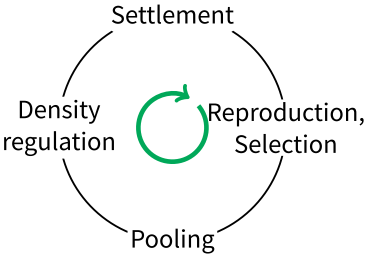

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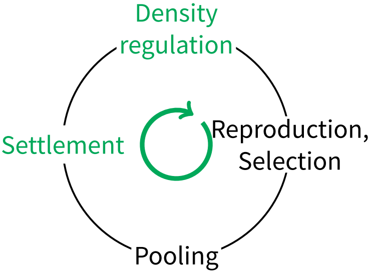
$$= \frac{[cw_1 + (1-c)w_2]\,p}{[cw_1 + (1-c)w_2]\,p + [cv_1 + (1-c)v_2]\,(1-p)} - p.$$

[Dempster, 1955, Ravigné et al., 2004]

“Dempster model”/“Model 3”



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“Dempster model”/“Model 3” (2)

$$\Delta p = \frac{\left[c w_1 + (1-c) w_2\right] p}{\left[c w_1 + (1-c) w_2\right] p + \left[c v_1 + (1-c) v_2\right](1-p)} - p.$$

Equilibria:

“Dempster model”/“Model 3” (2)

$$\Delta p = \frac{[cw_1 + (1-c)w_2]\, p}{[cw_1 + (1-c)w_2]\, p + [cv_1 + (1-c)v_2]\,(1-p)} - p.$$

Equilibria:

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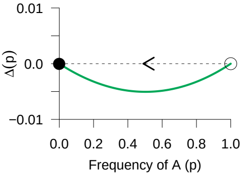

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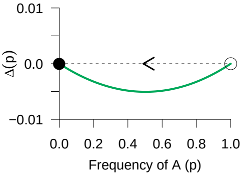

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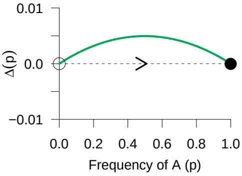

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Equilibria:

$$\frac{cw_1 + (1-c)w_2}{cv_1 + (1-c)v_2} < 1 \qquad \emptyset \qquad \frac{cw_1 + (1-c)w_2}{cv_1 + (1-c)v_2} > 1$$

Regimes of selection

Levene

$$\Delta p = c \frac{w_1 p}{w_1 p + v_1 (1-p)} + (1-c) \frac{w_2 p}{w_2 p + v_2 (1-p)} - p.$$

Dempster

$$\Delta p = \frac{[c w_1 + (1-c) w_2]\, p}{[c w_1 + (1-c) w_2]\, p + [c v_1 + (1-c) v_2]\,(1-p)} - p.$$

[Wallace, 1975]

Regimes of selection

Levene – Soft selection

$$\Delta p = c\frac{w_1 p}{w_1 p + v_1(1-p)} + (1-c)\frac{w_2 p}{w_2 p + v_2(1-p)} - p.$$

- Contribution from each habitat does not depend on their composition

  Proportion of individuals coming from type-1 habitats is c.

Dempster

$$\Delta p = \frac{\left[c w_1 + (1-c) w_2\right] p}{\left[c w_1 + (1-c) w_2\right] p + \left[c v_1 + (1-c) v_2\right](1-p)} - p.$$

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Regimes of selection

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- Contribution from each habitat does not depend on their composition

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Dempster – Hard selection

$$\Delta p = \frac{[cw_1 + (1-c)w_2]\,p}{[cw_1 + (1-c)w_2]\,p + [cv_1 + (1-c)v_2]\,(1-p)} - p.$$

- Contribution from each habitat depends on their composition

  Proportion of individuals coming from type-1 habitats is $c\frac{w_1 p + v_1(1-p)}{[cw_1+(1-c)w_2]\,p+[cv_1+(1-c)v_2]\,(1-p)}$.

[Wallace, 1975]

Soft selection, hard selection

Origin of the terms

[Wallace, 1968, Wallace, 1975, Débarre and Gandon, 2011]

Soft selection, hard selection

Origin of the terms

- International monetary exchange:
  soft vs. hard currencies.

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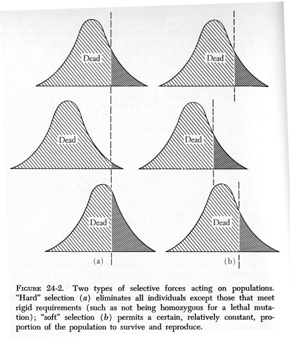
Soft selection, hard selection

Origin of the terms

- International monetary exchange: soft vs. hard currencies.
- Context: mutation load



(c) [Wallace, 1968, p. 428]

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Soft selection, hard selection

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- International monetary exchange: soft vs. hard currencies.
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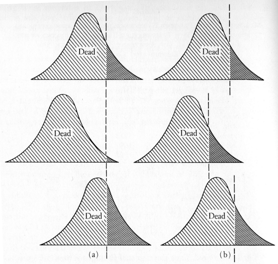


FIGURE 24-2. Two types of selective forces acting on populations. "Hard" selection (*a*) eliminates all individuals except those that meet rigid requirements (such as not being homozygous for a lethal mutation); "soft" selection (*b*) permits a certain, relatively constant, proportion of the population to survive and reproduce.

(c) [Wallace, 1968, p. 428]

In-between and beyond

- Density dependence,
- Non global pooling,
- Multiple dispersal steps.

[Wallace, 1968, Wallace, 1975, Débarre and Gandon, 2011]

Outline

Model ingredients

- Two habitats, 1 and 2, in equal proportions;

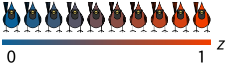
$$\frac{\partial N_j(z,t)}{\partial t} = \Big[\qquad\qquad\qquad\qquad\qquad\qquad \Big] N_j(z,t)$$

.

[Débarre et al., 2013]

Model ingredients

- Two habitats, 1 and 2, in equal proportions;
- Continuous trait determines adaptation to local habitat



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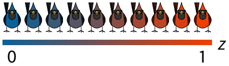

- Logistic growth

$$\frac{\partial N_j(z,t)}{\partial t} = \left[\left(1 - \int N_j(y,t)dy \right) \qquad\qquad \right] N_j(z,t)$$

.

[Débarre et al., 2013]

Model ingredients

- Two habitats, 1 and 2, in equal proportions;
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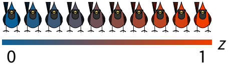


- Logistic growth
-  Additional mortality in habitat j of an individual with trait z is $g\left(1 - f_j(z)\right)$

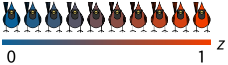
$$\frac{\partial N_j(z,t)}{\partial t} = \left[\left(1 - \int N_j(y,t)dy \right) - g\left(1 - f_j(z)\right) \right] N_j(z,t)$$

.

[Débarre et al., 2013]

Model ingredients

- Two habitats, 1 and 2, in equal proportions;
- Continuous trait determines adaptation to local habitat



- Logistic growth
-  Additional mortality in habitat j of an individual with trait z is $g\,(1 - f_j(z))$
- Dispersal in the other habitat at rate m

$$\frac{\partial N_j(z,t)}{\partial t} = \left[\left(1 - \int N_j(y,t)dy \right) - g\,(1 - f_j(z)) \right] N_j(z,t) + m(N_l(z,t) - N_j(z,t))$$

.

[Débarre et al., 2013]

Model ingredients

- Two habitats, 1 and 2, in equal proportions;
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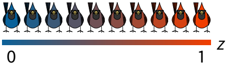

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-  Additional mortality in habitat j of an individual with trait z is $g\left(1 - f_j(z)\right)$
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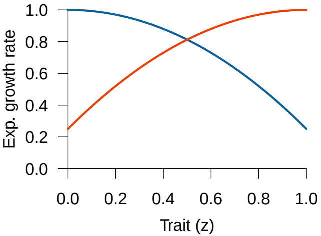
$$\frac{\partial N_j(z,t)}{\partial t} = \left[\left(1 - \int N_j(y,t)dy \right) - g\left(1 - f_j(z)\right) \right] N_j(z,t) \\ + m(N_l(z,t) - N_j(z,t)) \\ + \int \mu(y) N_j(z-y,t)dy - N_j(z,t).$$

[Débarre et al., 2013]

Model ingredients (2)

Adaptation to local conditions

$$1 - g(1 - f_j(z))$$



$$f_1(z) = 1 - z^2$$
$$f_2(z) = 1 - (1 - z)^2$$

Model ingredients (2)

Adaptation to local conditions

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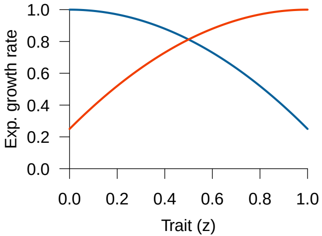
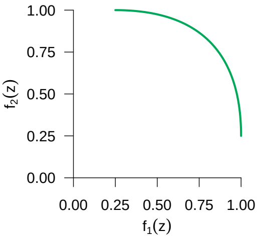


$$f_1(z) = 1 - z^2$$
$$f_2(z) = 1 - (1 - z)^2$$

$$f_2(z) = u\left(f_1(z)\right)$$



Trade-off

Model ingredients (2)

Adaptation to local conditions

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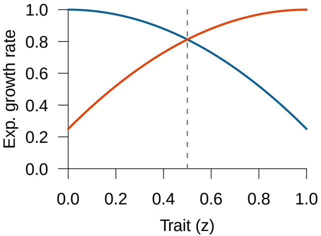

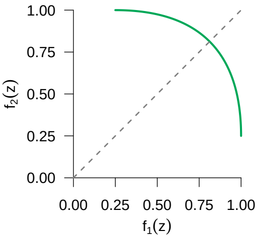

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Trade-off

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Adaptation to local conditions

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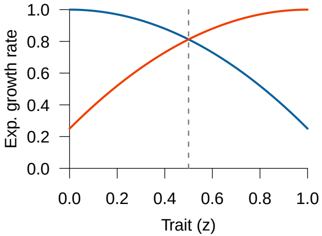

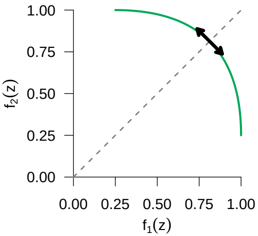

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Trade-off

Adaptive dynamics

[Meszéna et al., 1997]

Resident only

$$\frac{dN_1}{dt} = \left[(1 - N_1) - g(1 - f_1(z_r))\right] N_1 + m(N_2 - N_1)$$

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▸ eigenvalues ▸ more on stability analysis

Adaptive dynamics

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Dynamics of a rare mutant

$$\frac{dN_1^m}{dt} = \left[\left(1 - \tilde{N}_1\right) - g(1 - f_1(z_m))\right] N_1^m + m(N_2^m - N_1^m)$$
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$\rightarrow$ invasion fitness $\lambda(z_m, z_r)$

Dominant eigenvalue of the Jacobian matrix obtained from the above system.

eigenvalues | more on stability analysis

Adaptive dynamics (2)

Selection gradient

$$D(z_r) = \left.\frac{\partial \lambda}{\partial z_m}\right|_{z_m=z_r} = g\left(1 - 2z_r + \frac{\tilde{N}_1 - \tilde{N}_2 - g(1-2z_r)}{\sqrt{4m^2 + (g(1-2z_r) - (\tilde{N}_1 - \tilde{N}_2))^2}}\right)$$

It vanishes when $z_r = z^* = \frac{1}{2}$: by symmetry indeed, $\tilde{N}_1 = \tilde{N}_2$ at this point.

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$$\left.\frac{dD(z_r)}{dz_r}\right|_{z_r = z^*} = \frac{g}{m}\left(g - 2m + \frac{d\tilde{N}_1}{dz_r}(z^*)\right)$$

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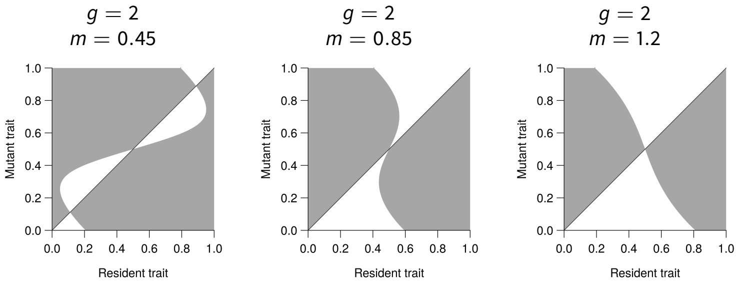
Invadability

$$\left.\frac{\partial^2 \lambda}{\partial z_m^2}\right|_{z_m=z_r=z^*} = \frac{g\,(g-2m)}{m}.$$

Pairwise invasibility plots (PIPs)

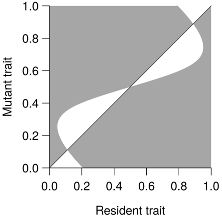


z^* not CS, not ES | z^* CS, not ES | z^* CS and ES

Bistability | Branching point | ESS

Pairwise invasibility plots (PIPs)

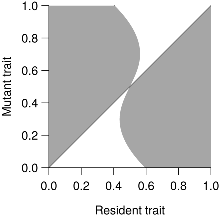
$g = 2$
$m = 0.45$



z^* not CS, not ES

Bistability

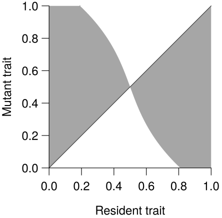
$g = 2$
$m = 0.85$



z^* CS, not ES

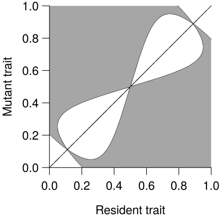
Branching point

$g = 2$
$m = 1.2$



z^* CS and ES

ESS



Mutual invasibility

Identify polymorphic equilibria

There are now 2 resident types, with traits z_r and z_r'; because of symmetry in the model, $z_r' = 1 - z_r$.

- System of 2×2 equations for the dynamics of the residents; identify the equilibrium $(\tilde{N}_1, \tilde{N}_2, \tilde{N}_1' = \tilde{N}_2\ , \tilde{N}_2' = \tilde{N}_1)$.

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- Mutant dynamics

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- Determine invasion condition $\lambda(z_m, z_r, z_r')$, selection gradients $\frac{\partial \lambda}{\partial z_m}$, and identify singular strategies:

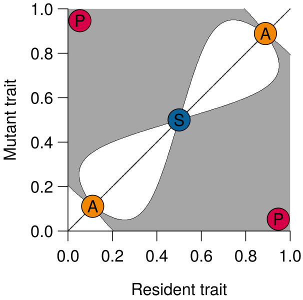
$$z_r = \frac{1}{2} - \frac{\sqrt{1 - 4(m/g)^2}}{2}; \qquad z_r' = 1 - z_r.$$

Local vs. global equilibria

“Strict” adaptive dynamics

Asymmetric equilibrium

adaptation to one habitat only



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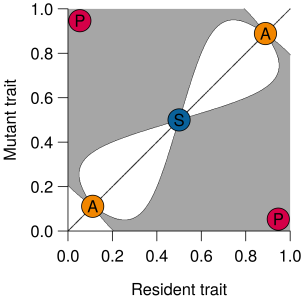
Asymmetric equilibrium
adaptation to one habitat only

PDE model / larger mutations

Polymorphic equilibrium
adaptation to both habitats



Local vs. global equilibria

"Strict" adaptive dynamics

Asymmetric equilibrium

adaptation to one habitat only

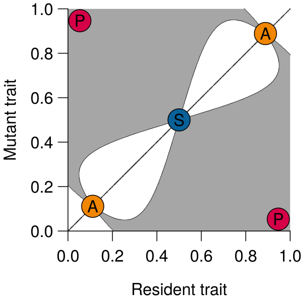
Local stability

PDE model / larger mutations

Polymorphic equilibrium

adaptation to both habitats

Global stability



[Mirrahimi, 2016]

A few take-home messages

- Question the tools you are using, the assumptions that you are making;

  Potential issues of generality and robustness

- Symmetry makes analyses easier. But it isn't realistic!

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Appendix

Interlude – How to find the leading eigenvalue

$$\frac{dN_1^m}{dt} = h_1(N_1^m, N_2^m)$$
$$\frac{dN_2^m}{dt} = h_2(N_1^m, N_2^m)$$

▸ back ▸ more

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Jacobian matrix

$$J = \begin{pmatrix} \frac{\partial h_1}{\partial N_1^m} & \frac{\partial h_1}{\partial N_2^m} \\ \frac{\partial h_2}{\partial N_1^m} & \frac{\partial h_2}{\partial N_2^m} \end{pmatrix} \Bigg|_{N_1^m = N_2^m = 0} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

back more

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Characteristic polynomial

$$P(x) = x^2 - (a + d)\,x + (a\,d - b\,c)$$

▸ back ▸ more

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Leading eigenvalue

$$\lambda = \frac{1}{2}\left(a + d + \sqrt{a^2 + d^2 - 2ad + 4bc}\right)$$

back more

Stability analysis – Continuous time

Model

$$\frac{dN_1}{dt} = f_1(N_1, N_2, \ldots, N_k)$$
$$\frac{dN_2}{dt} = f_2(N_1, N_2, \ldots, N_k)$$
$$\ldots$$
$$\frac{dN_k}{dt} = f_k(N_1, N_2, \ldots, N_k)$$

Stability analysis – Continuous time

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$$\ldots$$
$$\frac{dN_k}{dt} = f_k(N_1, N_2, \ldots, N_k)$$

Equilibria

$(N_1^*, N_2^*, \ldots, N_k^*)$ is such that

$$f_1(N_1^*, N_2^*, \ldots, N_k^*) = 0$$
$$f_2(N_1^*, N_2^*, \ldots, N_k^*) = 0$$
$$\ldots$$
$$f_k(N_1^*, N_2^*, \ldots, N_k^*) = 0$$

Stability analysis – Continuous time

1. Write system of equations for the change over time of a small derivation from the equilibrium

For variable i and an equilibrium $\mathbf{N}^* = (N_1^*, \ldots, N_k^*)$, let's define

$$\delta_i = N_i - N_i^*.$$

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Stability analysis – Continuous time

2. Get a linear approximation of this system (Taylor series)

First-order approximation of the dynamics of δ_i:

$$\frac{d\delta_i}{dt} = f_i(\delta_1 + N_1^*, \ldots, \delta_k + N_k^*)$$

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$$\approx f_i(N_1^*, \dots, N_k^*) + \sum_{j=1}^{k} (N_j - N_j^*) \left.\frac{\partial f_i}{\partial N_j}\right|_{\mathbf{N}=\mathbf{N}^*}$$

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In matrix form:

$$\begin{pmatrix} \frac{d\delta_1}{dt} \\ \vdots \\ \frac{d\delta_k}{dt} \end{pmatrix} = \left.\begin{pmatrix} \frac{\partial f_1}{\partial N_1} & \cdots & \frac{\partial f_1}{\partial N_k} \\ \vdots & \cdots & \vdots \\ \frac{\partial f_k}{\partial N_1} & \cdots & \frac{\partial f_k}{\partial N_k} \end{pmatrix}\right|_{\mathbf{N}=\mathbf{N}^*} \cdot \begin{pmatrix} \delta_1 \\ \vdots \\ \delta_k \end{pmatrix}$$

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Stability analysis – Continuous time

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with the c_i constants determined by the initial conditions, and $\boldsymbol{\delta}_{(i)}$ an eigenvector associated to the eigenvalue λ_i, i.e., $\mathbf{J} \cdot \boldsymbol{\delta}_{(i)} = \lambda_i \, \boldsymbol{\delta}_{(i)}$.

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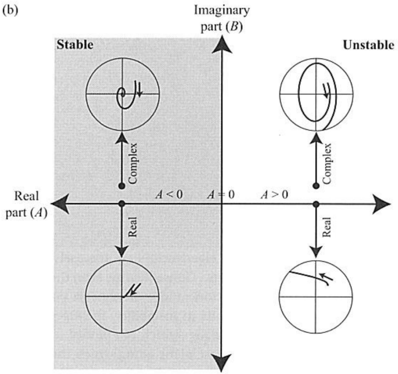

(c) [Otto and Day, 2007]

$$\lambda = A + B\imath$$

back

Stability analysis – Continuous time

And how do I find these eigenvalues?

Theory

$$\mathbf{M} \cdot \boldsymbol{u} = \lambda \boldsymbol{u} \iff (\mathbf{M} - \lambda \mathbf{I}) \cdot \boldsymbol{u} = \mathbf{0}.$$

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$\boldsymbol{u} \neq \mathbf{0}$, so we have to solve the *characteristic polynomial*

$$\text{Det} \, (\mathbf{M} - \lambda \, \mathbf{I}) = 0,$$

whose roots $(\lambda_1, \ldots, \lambda_k)$ are the eigenvalues of $\mathbf{M}$.

Stability analysis – Continuous time

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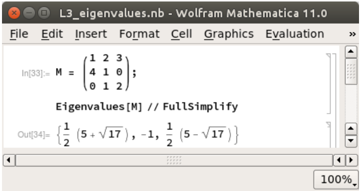
Practice



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