Lecture II: The evolution of dispersal

January 2017

Terminology

Dispersal “Any movement of individuals or propagules with potential consequences for gene flow across space” [Ronce, 2007]

(c) Wikimedia

Terminology

Dispersal “Any movement of individuals or propagules with potential consequences for gene flow across space” [Ronce, 2007]

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Migration “Mass directional movements of large numbers of a species from one location to another.” [Begon et al., 1996]

But in population genetics, often used as a synonym of dispersal.

(c) Wikimedia

Why disperse?

Why disperse?

- Avoid kin competition

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- Avoid kin competition
- Avoid inbreeding

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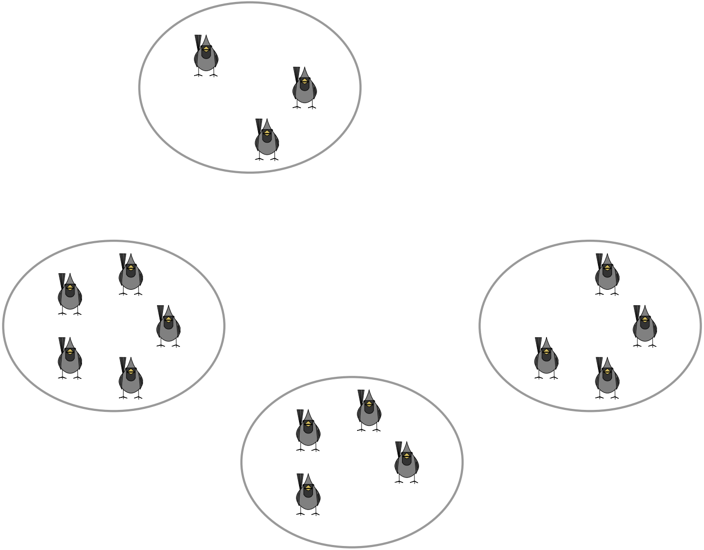
- Avoid kin competition
- Avoid inbreeding
- Explore new territories

Why disperse?

- Avoid kin competition
- Avoid inbreeding
- Explore new territories
- Find better conditions.

Dispersal stages



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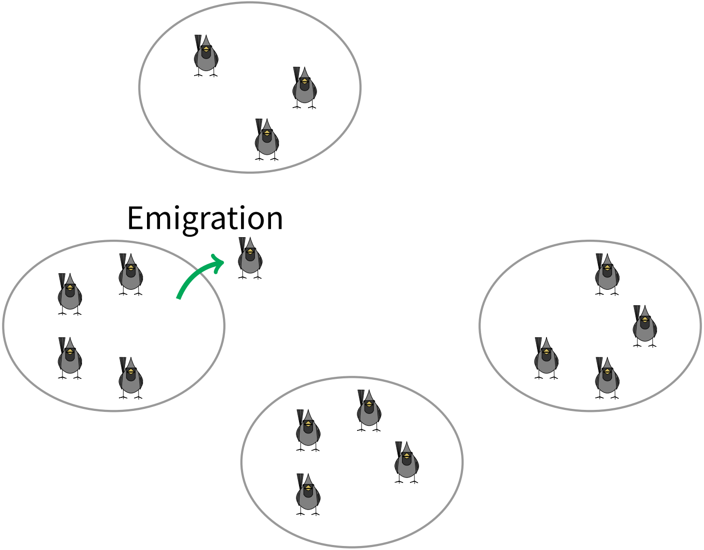

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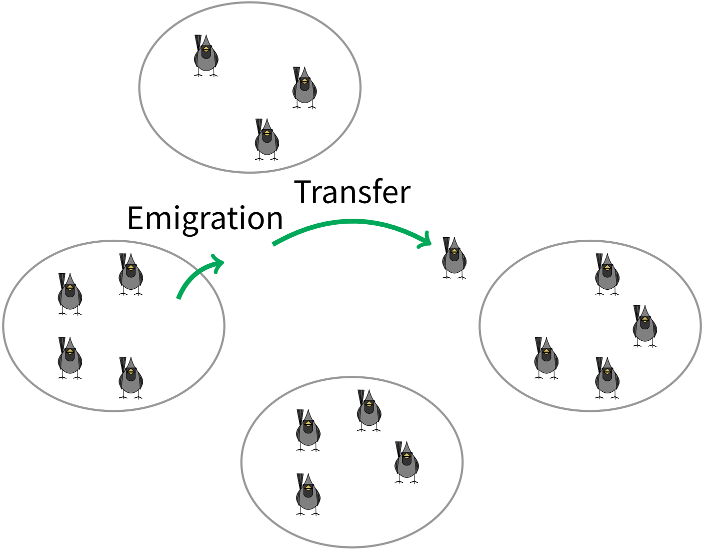

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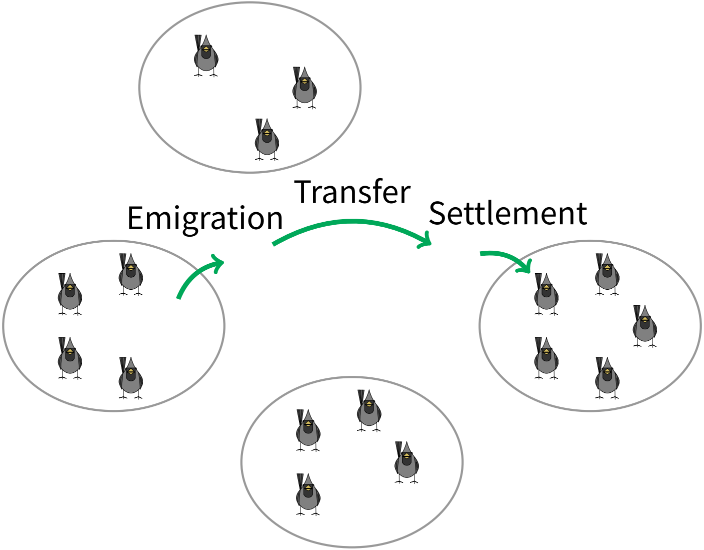

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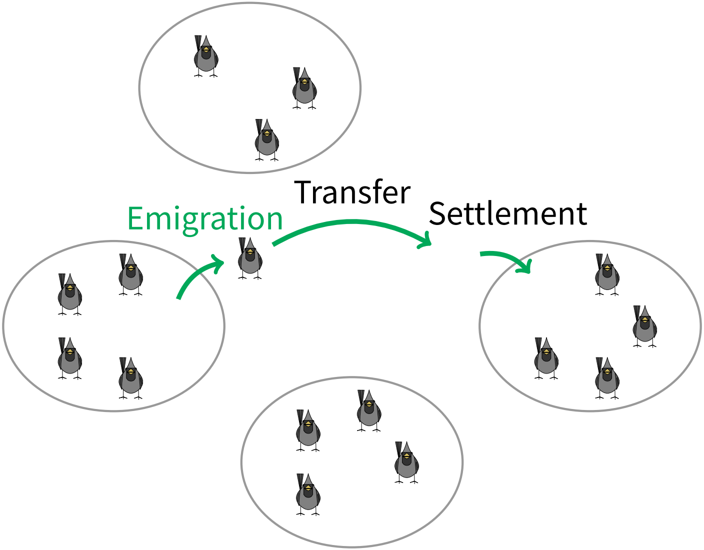


Outline

Introduction

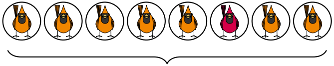
Dispersal and kin competition

- Hamilton & May 1977
- Island model

In spatially heterogeneous environments

An iconic example: [Hamilton and May, 1977]

Model



N saturated sites,
$N \to \infty$

An iconic example: [Hamilton and May, 1977]

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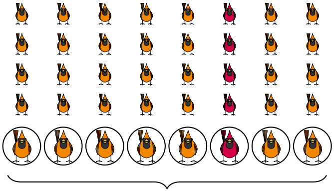

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Offspring production

An iconic example: [Hamilton and May, 1977]

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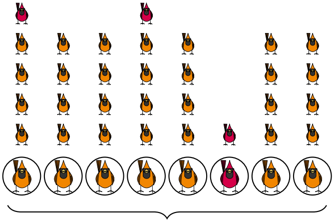

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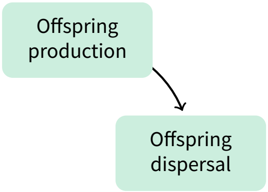

Emigration probabilities: $x = 0$, $y > 0$

Cost of emigration $c = 1 - p$.

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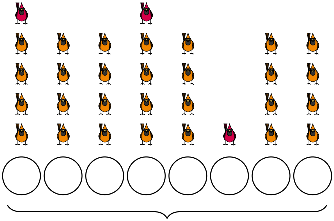

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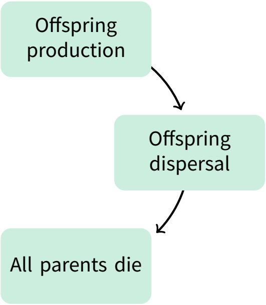

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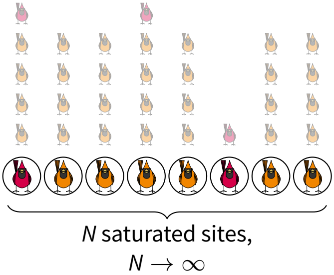

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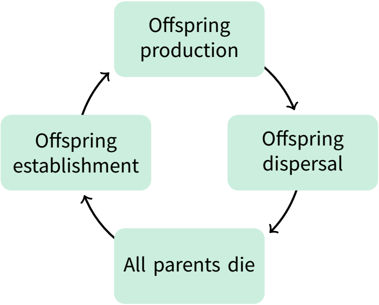

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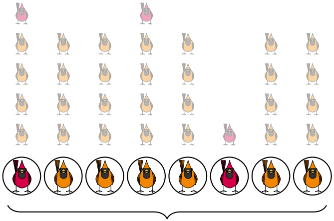

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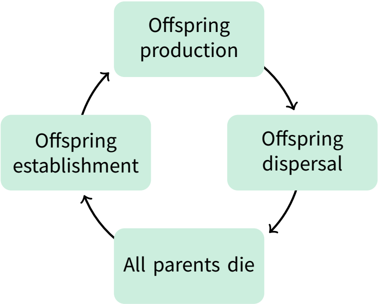

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Invasion fitness

$$w(y,x) = \frac{1-y}{1-y+(1-c)\,x} + \frac{(1-c)\,y}{1-x+(1-c)\,x}$$

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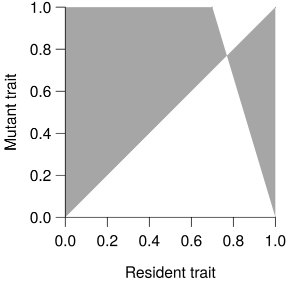
- Selection gradient

$$D(x) = \left.\frac{\partial w(y,x)}{\partial y}\right|_{y=x} = \frac{(1-c)(1-x(1+c))}{(1-cx)^2}$$

PIP



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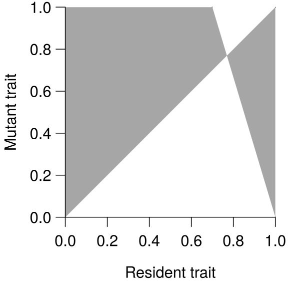

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$$\frac{dD(x)}{dx} = -\frac{(1-c)(1-c+(c+1)cx)}{(1-cx)^3} \leq 0$$

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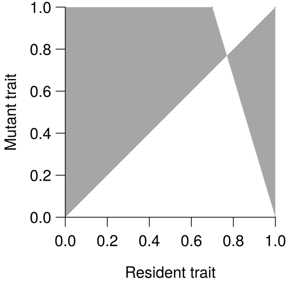

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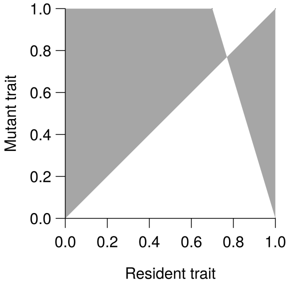
$$\frac{dD(x)}{dx} = -\frac{(1-c)(1-c+(c+1)cx)}{(1-cx)^3} \leq 0$$

- Uninvadability

$$\left.\frac{\partial^2 w(y,x)}{\partial y^2}\right|_{y=x=x^*} = -2(1-c)(c+1)^2 \leq 0$$

PIP



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We acknowledge that this simple model probably has few close parallels in the real world. Nevertheless it may usefully force a re-examination of some widely held ideas about migration.

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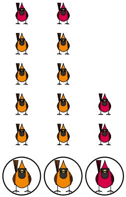
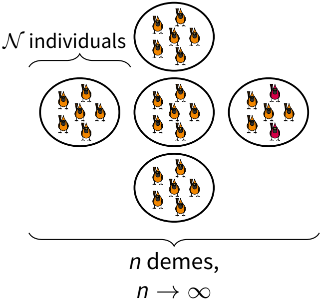
Kin competition Competition between related individuals.



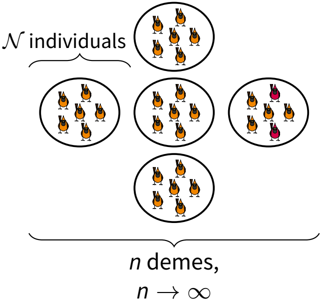
Dispersal evolution in a subdivided population



z_r	Emigration probability of residents
z_m	Emigration probability of mutants
c	Cost of dispersal
μ	Mutation probability ($\mu \to 0$).

[Gandon and Rousset, 1999]

Dispersal evolution in a subdivided population



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$q_0(z_m, z_r)$: Average frequency of mutants in demes that contain mutants.

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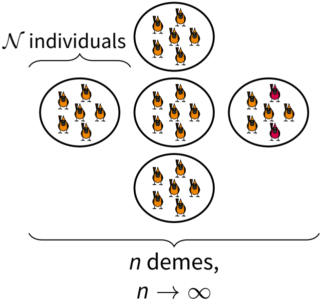

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Invasion fitness

$$w(z_m, z_r) = \frac{1 - z_m}{1 - (q_0\, z_m + (1 - q_0) z_r) + (1 - c)\, z_r} + \frac{(1 - c)\, z_m}{1 - z_r + (1 - c) z_r}$$

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Selection gradient

$$D(z) = \left. \frac{\partial w(z_m, z_r)}{\partial z_m} \right|_{z_m = z_r = z} = \frac{q - c - z\left(q - c^2\right)}{(1 - c\, z)^2},$$

with $q = q_0(z, z)$.

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Computing q, recursively

▸ More on q

$$q_{t+1} = \frac{1}{\mathcal{N}} + \frac{\mathcal{N} - 1}{\mathcal{N}} \left(1 - \frac{(1 - c) z}{1 - c z}\right)^2 q_t$$

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$$q = \frac{1}{1 + \left(\left(2 - \frac{(1-c)z}{1-cz}\right) \frac{(1-c)z}{1-cz}(\mathcal{N} - 1\right)}$$

Dispersal evolution in a subdivided population (3)

Singular strategy

$$z^* = \frac{1 + 2c\,\mathcal{N} - \sqrt{1 + 4\,c^2\,(\mathcal{N} - 1)\,\mathcal{N}}}{2\,c\,(1+c)\,\mathcal{N}}.$$

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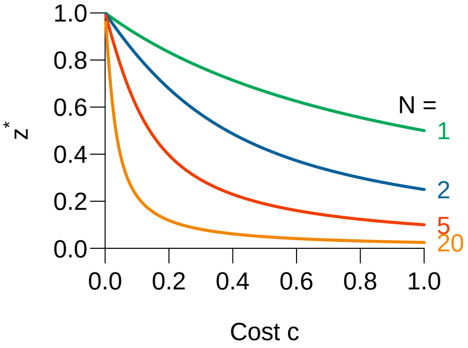

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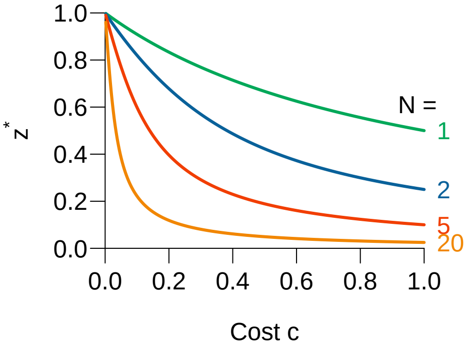

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Dispersal evolution in a subdivided population (4)

Invadability

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

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with $q^* = q_0(z^*, z^*)$

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- In this model, always z^* is always uninvadable [Ajar, 2003].

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- But with heterogeneity in deme sizes, diversification can occur [Massol et al., 2011]

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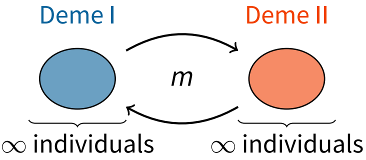
Dispersal and kin competition

In spatially heterogeneous environments

Another classic: [Balkau and Feldman, 1973]



Life-cycle Selection then dispersal.

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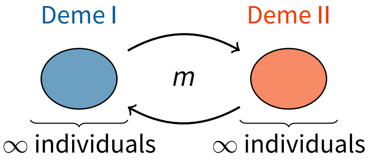

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Genotypes AB, Ab, aB, ab.

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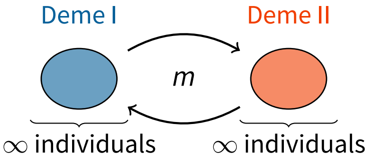

- Locus A: local adaptation
  Fitness:

	in I	in II
A	$1+s$	1
a	1	$1+s$

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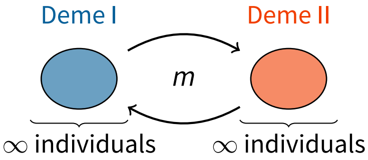

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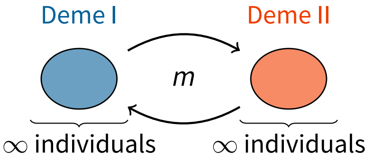

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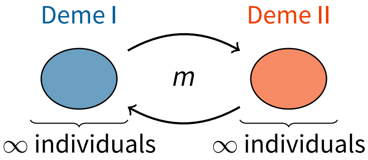

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$$x' = (1-z)\frac{(1+s)\,x}{(1+s)\,x + 1 - x} + z\frac{y}{y + (1+s)(1-y)}$$

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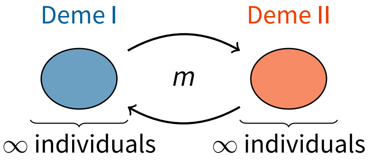

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$$x' = (1-z)\frac{(1+s)\,x}{(1+s)\,x+1-x} + z\frac{y}{y+(1+s)(1-y)}$$
$$y' = z\frac{(1+s)\,x}{(1+s)\,x+1-x} + (1-z)\frac{y}{y+(1+s)(1-y)}.$$

$\rightarrow$ Equilibrium $(\hat{x},\hat{y}) = (\hat{x}, 1-\hat{x})$.

Another classic: [Balkau and Feldman, 1973] (2)

Dynamics with the four genotypes

		AB	Ab	aB	ab
Frequencies:	in deme I	x_1	x_2	x_3	x_4
	in deme II	y_1	y_2	y_3	y_4

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Frequencies:	in deme I	x_1	x_2	x_3	x_4
	in deme II	y_1	y_2	y_3	y_4

$$x_1' = (1-z)\frac{(1+s)x_1}{(1+s)(x_1+x_2)+(x_3+x_4)} + z\frac{y1}{(y_1+y_2)+(1+s)(y_3+y_4)}$$

$$x_2' = (1-z_m)\frac{(1+s)x_2}{(1+s)(x_1+x_2)+(x_3+x_4)} + z_m\frac{y2}{(y_1+y_2)+(1+s)(y_3+y_4)}$$

$$x_3' = \dots$$

Another classic: [Balkau and Feldman, 1973] (2)

Dynamics with the four genotypes

		AB	Ab	aB	ab
Frequencies:	in deme I	x_1	x_2	x_3	x_4
	in deme II	y_1	y_2	y_3	y_4

$$x_1' = (1-z)\frac{(1+s)x_1}{(1+s)(x_1+x_2)+(x_3+x_4)} + z\frac{y1}{(y_1+y_2)+(1+s)(y_3+y_4)}$$

$$x_2' = (1-z_m)\frac{(1+s)x_2}{(1+s)(x_1+x_2)+(x_3+x_4)} + z_m\frac{y2}{(y_1+y_2)+(1+s)(y_3+y_4)}$$

$$x_3' = \dots$$

Invasion analysis

Local stability of the equilibrium without b,
$(\hat{x}, 0, 1-\hat{x}, 0, \hat{y}, 0, 1-\hat{y}, 0)$

▸ More on stability analysis

Another classic: [Balkau and Feldman, 1973] (3)

```
ev = Eigenvalues[Jac] // FullSimplify
```

$$
\Bigg\{\frac{4\,(1+s)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)^2},\ -\frac{4\,(1+s)\,(-1+2z)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)^2},\ -\frac{4\,(1+s)\,(-1+2z)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)^2},
$$

$$
1,\ \Bigg(4+2\sqrt{s^2-2s^2z+(2+s)^2z^2}+s^2(-1+z)(-1+zm)+4z(-1+zm)-s\left(4-4z+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)(-1+zm)-
$$

$$
2\left(2+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)zm-\sqrt{2}\sqrt{\Bigg(\Bigg(s^2(-1+z)^2+2\left(1+2z^2+\sqrt{s^2-2s^2z+(2+s)^2z^2}-z\left(2+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)\right)+}
$$

$$
\overline{s\left(2+4z^2+\sqrt{s^2-2s^2z+(2+s)^2z^2}-z\left(4+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)\right)\Bigg)\left(s^2-2s^2zm+(2+s)^2zm^2\right)\Bigg)}\Bigg)\Bigg/
$$

$$
\left(2+s-2z-sz+\sqrt{4sz+(s(-1+z)+2z)^2}\right)^2,\ \Bigg(4+2\sqrt{s^2-2s^2z+(2+s)^2z^2}+s^2(-1+z)(-1+zm)+4z(-1+zm)-
$$

$$
s\left(4-4z+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)(-1+zm)-2\left(2+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)zm+
$$

$$
\sqrt{2}\sqrt{\Bigg(\Bigg(s^2(-1+z)^2+2\left(1+2z^2+\sqrt{s^2-2s^2z+(2+s)^2z^2}-z\left(2+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)\right)+s\Bigg(2+4z^2+\sqrt{s^2-2s^2z+(2+s)^2z^2}-}
$$

$$
\overline{z\left(4+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)\Bigg)\Bigg)\left(s^2-2s^2zm+(2+s)^2zm^2\right)\Bigg)}\Bigg)\Bigg/\left(2+s-2z-sz+\sqrt{4sz+(s(-1+z)+2z)^2}\right)^2\Bigg\}
$$

Another classic: [Balkau and Feldman, 1973] (3)

```
ev = Eigenvalues[Jac] // FullSimplify
```

$$\Bigg\{\frac{4\,(1+s)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)^2},\; -\frac{4\,(1+s)\,(-1+2z)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)^2},\; -\frac{4\,(1+s)\,(-1+2z)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)^2},$$

$$1,\; \Bigg(4+2\sqrt{s^2-2s^2 z+(2+s)^2 z^2}+s^2(-1+z)(-1+zm)+4z(-1+zm)-s\left(4-4z+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)(-1+zm)-$$

$$2\left(2+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)zm-\sqrt{2}\,\sqrt{\Bigg(\bigg(s^2(-1+z)^2+2\left(1+2z^2+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}-z\left(2+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)\right)+}$$

$$\overline{s\left(2+4z^2+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}-z\left(4+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)\right)\bigg)\left(s^2-2s^2 zm+(2+s)^2 zm^2\right)\Bigg)}\Bigg)\Bigg/$$

$$\left(2+s-2z-sz+\sqrt{4sz+(s(-1+z)+2z)^2}\right)^2,\; \Bigg(4+2\sqrt{s^2-2s^2 z+(2+s)^2 z^2}+s^2(-1+z)(-1+zm)+4z(-1+zm)-$$

$$s\left(4-4z+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)(-1+zm)-2\left(2+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)zm+$$

$$\sqrt{2}\,\sqrt{\Bigg(\bigg(s^2(-1+z)^2+2\left(1+2z^2+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}-z\left(2+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)\right)+s\bigg(2+4z^2+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}-}$$

$$\overline{z\left(4+\sqrt{s^2-2s^2 z+(2+s)^2 z^2}\right)\bigg)\bigg)\left(s^2-2s^2 zm+(2+s)^2 zm^2\right)\Bigg)}\Bigg)\Bigg/\left(2+s-2z-sz+\sqrt{4sz+(s(-1+z)+2z)^2}\right)^2\Bigg\}$$

→ All eigenvalues ρ_i such that $|\rho_i| \leq 1$ when $z_m > z$

Another classic: [Balkau and Feldman, 1973] (3)

```
ev = Eigenvalues[Jac] // FullSimplify
```

$$\left\{\frac{4(1+s)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)^2},\ -\frac{4(1+s)(-1+2z)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)^2},\ -\frac{4(1+s)(-1+2z)}{\left(2+s-2z-sz+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)^2},\right.$$

$$1,\ \Big(4+2\sqrt{s^2-2s^2z+(2+s)^2z^2}+s^2(-1+z)(-1+zm)+4z(-1+zm)-s\left(4-4z+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)(-1+zm)-$$

$$2\left(2+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)zm-\sqrt{2}\sqrt{\Big(\Big(s^2(-1+z)^2+2\Big(1+2z^2+\sqrt{s^2-2s^2z+(2+s)^2z^2}-z\left(2+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)\Big)+}$$

$$s\Big(2+4z^2+\sqrt{s^2-2s^2z+(2+s)^2z^2}-z\left(4+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)\Big)\Big)\left(s^2-2s^2zm+(2+s)^2zm^2\right)\Big)}\Big)\Big/$$

$$\left(2+s-2z-sz+\sqrt{4sz+(s(-1+z)+2z)^2}\right)^2,\ \Big(4+2\sqrt{s^2-2s^2z+(2+s)^2z^2}+s^2(-1+z)(-1+zm)+4z(-1+zm)-$$

$$s\left(4-4z+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)(-1+zm)-2\left(2+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)zm+$$

$$\sqrt{2}\sqrt{\Big(\Big(s^2(-1+z)^2+2\Big(1+2z^2+\sqrt{s^2-2s^2z+(2+s)^2z^2}-z\left(2+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)\Big)+s\Big(2+4z^2+\sqrt{s^2-2s^2z+(2+s)^2z^2}-}$$

$$\left.z\left(4+\sqrt{s^2-2s^2z+(2+s)^2z^2}\right)\Big)\Big)\left(s^2-2s^2zm+(2+s)^2zm^2\right)\Big)}\Big)\Big/\left(2+s-2z-sz+\sqrt{4sz+(s(-1+z)+2z)^2}\right)^2\right\}$$

$\rightarrow$ All eigenvalues ρ_i such that $|\rho_i| \leq 1$ when $z_m > z$

Reduced emigration probabilities are favored.

A few take-home messages

- Kin competition favors the evolution of emigration

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A few take-home messages

- Kin competition favors the evolution of emigration
- Spatial heterogeneity only does not...
  but dispersal can evolve when local conditions change with time and space.
- Dispersal is a complicated trait to study, because it affects spatial structure ($\rightarrow$ Lecture 4).

References

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Appendix

Outline

More on q

Stability analysis

More on q

New parameters:

n	Number of demes
μ	Mutation probability (infinite allele model)

[Cockerham and Weir, 1987]

Back

More on q

New parameters:

- n Number of demes
- μ Mutation probability (infinite allele model)
- $m = \dfrac{1-z}{1-c\,z}$ Backward dispersal probability

[Cockerham and Weir, 1987]

Back

More on q

New parameters:

n	Number of demes	
μ	Mutation probability (infinite allele model)	
m	$= \dfrac{1-z}{1-cz}$	Backward dispersal probability

Probability that two individuals came from the same deme and

- are in the same deme: $a = (1-m)^2 + \frac{m^2}{n-1}$,

[Cockerham and Weir, 1987]

Back

More on q

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- are in different demes: $b = \frac{1-(1-m)^2}{n-1} - \frac{m^2}{(n-1)^2}$.

[Cockerham and Weir, 1987]

Back

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Probabilities of identity by descent, with replacement:

- In the same deme: $q_{0,t+1} = \frac{1}{\mathcal{N}} + \frac{\mathcal{N}-1}{\mathcal{N}}(1-\mu)^2\left(a\,q_{0,t} + (1-a)\,q_{1,t}\right)$,

[Cockerham and Weir, 1987]

Back

More on q

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- In different demes: $q_{1,t+1} = (1-\mu)^2\left(b\,q_{0,t} + (1-b)\,q_{1,t}\right)$,

[Cockerham and Weir, 1987]

Back

More on q (2)

$$q_{0,t+1} = \frac{1}{\mathcal{N}} + \frac{\mathcal{N}-1}{\mathcal{N}}(1-\mu)^2 \left(a\, q_{0,t} + (1-a)\, q_{1,t}\right),$$
$$q_{1,t+1} = (1-\mu)^2 \left(b\, q_{0,t} + (1-b)\, q_{1,t}\right),$$

Order of limits

[Cockerham and Weir, 1987]

Back

More on q (2)

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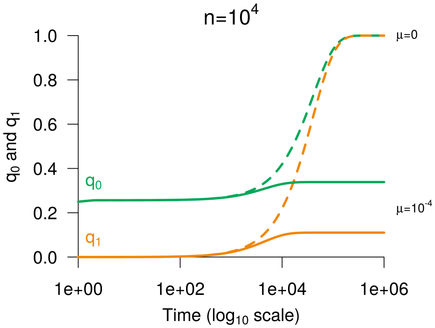
$$q_{1,t+1} = (1-\mu)^2 \left(b\, q_{0,t} + (1-b)\, q_{1,t}\right),$$

Order of limits

- When $\mu = 0$,
  $q_{0,\infty} = q_{1,\infty} = 1$.



[Cockerham and Weir, 1987]

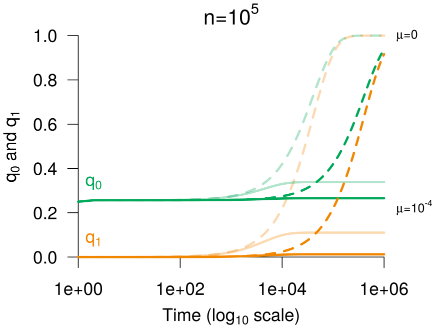
Back

More on q (2)

$$q_{0,t+1} = \frac{1}{\mathcal{N}} + \frac{\mathcal{N}-1}{\mathcal{N}}(1-\mu)^2\left(a\, q_{0,t} + (1-a)\, q_{1,t}\right),$$
$$q_{1,t+1} = (1-\mu)^2\left(b\, q_{0,t} + (1-b)\, q_{1,t}\right),$$

Order of limits

- When $\mu = 0$,
  $q_{0,\infty} = q_{1,\infty} = 1$.
- When $n \to \infty$, $q_{1,\infty} = 0$
  and $q_{0,\infty} =$
  $\frac{1}{\mathcal{N}} + \frac{\mathcal{N}-1}{\mathcal{N}}(1-\mu)^2\left(a\, q_{0,\infty}\right).$



[Cockerham and Weir, 1987]

Back

Outline

More on q

Stability analysis

Stability analysis for discrete-time models

Model

$$
\begin{aligned}
N_1(t+1) &= G_1(N_1(t), N_2(t), \ldots, N_k(t)) \\
N_2(t+1) &= G_2(N_1(t), N_2(t), \ldots, N_k(t)) \\
&\vdots \\
N_k(t+1) &= G_k(N_1(t), N_2(t), \ldots, N_k(t))
\end{aligned}
$$

Stability analysis for discrete-time models

Model

$$
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N_1(t+1) &= G_1(N_1(t), N_2(t), \dots, N_k(t)) \\
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&\vdots \\
N_k(t+1) &= G_k(N_1(t), N_2(t), \dots, N_k(t))
\end{aligned}
$$

Equilibrium

$\tilde{\mathbf{N}} = (\tilde{N}_1, \dots, \tilde{N}_k)$, such that

$$
\begin{aligned}
G_1(\tilde{N}_1, \dots, \tilde{N}_k) &= \tilde{N}_1 \\
&\vdots \\
G_k(\tilde{N}_1, \dots, \tilde{N}_k) &= \tilde{N}_k
\end{aligned}
$$

Stability analysis for discrete-time models

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

Deviations from equilibrium

Define $n_i(t) = N_i(t) - \tilde{N}_i$.

Stability analysis for discrete-time models

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

Deviations from equilibrium

Define $n_i(t) = N_i(t) - \tilde{N}_i$.

$$n_i(t+1) = G_i(N_1(t), \ldots, N_k(t)) - \tilde{N}_i$$

Stability analysis for discrete-time models

2. Write system of equations for the change over time of a small derivation from the equilibrium, and get a linear approximation of this system (Taylor series)

Deviations from equilibrium

Define $n_i(t) = N_i(t) - \tilde{N}_i$.

$$\begin{aligned} n_i(t+1) &= G_i(N_1(t), \ldots, N_k(t)) - \tilde{N}_i \\ &\approx 0 + \left.\frac{\partial G_i}{\partial N_1}\right|_{\mathbf{N}(t)=\tilde{\mathbf{N}}} (N_1(t) - \tilde{N}_1) + \cdots + \left.\frac{\partial G_i}{\partial N_k}\right|_{\mathbf{N}(t)=\tilde{\mathbf{N}}} (N_k(t) - \tilde{N}_k). \end{aligned}$$

Stability analysis for discrete-time models

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Deviations from equilibrium

Define $n_i(t) = N_i(t) - \tilde{N}_i$.

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In matrix form:

$$\begin{pmatrix} n_1 \\ \vdots \\ n_k \end{pmatrix}(t+1) = \left.\begin{pmatrix} \frac{\partial G_1}{\partial N_1} & \dots & \frac{\partial G_1}{\partial N_k} \\ \vdots & \dots & \vdots \\ \frac{\partial G_k}{\partial N_1} & \dots & \frac{\partial G_k}{\partial N_k} \end{pmatrix}\right|_{\mathbf{N}=\tilde{\mathbf{N}}} \cdot \begin{pmatrix} n_1 \\ \vdots \\ n_k \end{pmatrix}(t)$$

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Deviations from equilibrium

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In matrix form:

$$\underbrace{\begin{pmatrix} n_1 \\ \vdots \\ n_k \end{pmatrix}(t+1)}_{\mathbf{n}(t+1)} = \underbrace{\left.\begin{pmatrix} \frac{\partial G_1}{\partial N_1} & \dots & \frac{\partial G_1}{\partial N_k} \\ \vdots & \dots & \vdots \\ \frac{\partial G_k}{\partial N_1} & \dots & \frac{\partial G_k}{\partial N_k} \end{pmatrix}\right|_{\mathbf{N}=\tilde{\mathbf{N}}}}_{\mathbf{J}} \cdot \underbrace{\begin{pmatrix} n_1 \\ \vdots \\ n_k \end{pmatrix}(t)}_{\mathbf{n}(t)}$$

Stability analysis for discrete-time models (3)

3. Identify solutions of $\mathbf{n}(t+1) = \mathbf{J} \cdot \mathbf{n}(t)$

[Case, 2000]

Stability analysis for discrete-time models (3)

3. Identify solutions of $\mathbf{n}(t+1) = \mathbf{J} \cdot \mathbf{n}(t)$

Solution:

$$\mathbf{n}(t) = c_1 \boldsymbol{\nu}_1 \lambda_1^t + c_2 \boldsymbol{\nu}_2 \lambda_2^t + \cdots + c_k \boldsymbol{\nu}_k \lambda_k^t,$$

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

[Case, 2000]

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Leading eigenvalue: eigenvalue with the largest modulus

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Leading eigenvalue: eigenvalue with the largest modulus

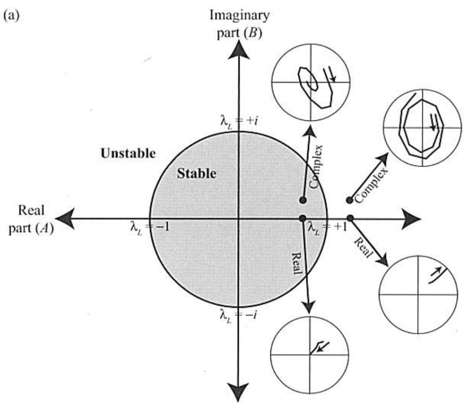
Modulus: for a complex number $\lambda = A + \imath B$,

$$|\lambda| = \sqrt{A^2 + B^2}.$$

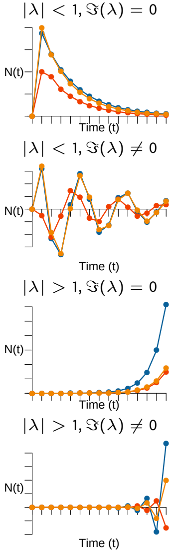
[Case, 2000]

Stability analysis for discrete-time models (4)

4 Inspect the eigenvalues of **J**



(c) [Otto and Day, 2007]



Back