

Topics in evolutionary dynamics

Lecture 3: Evolution in metapopulations

François Massol

3rd summer school on Mathematical Biology

São Paulo, February 2014

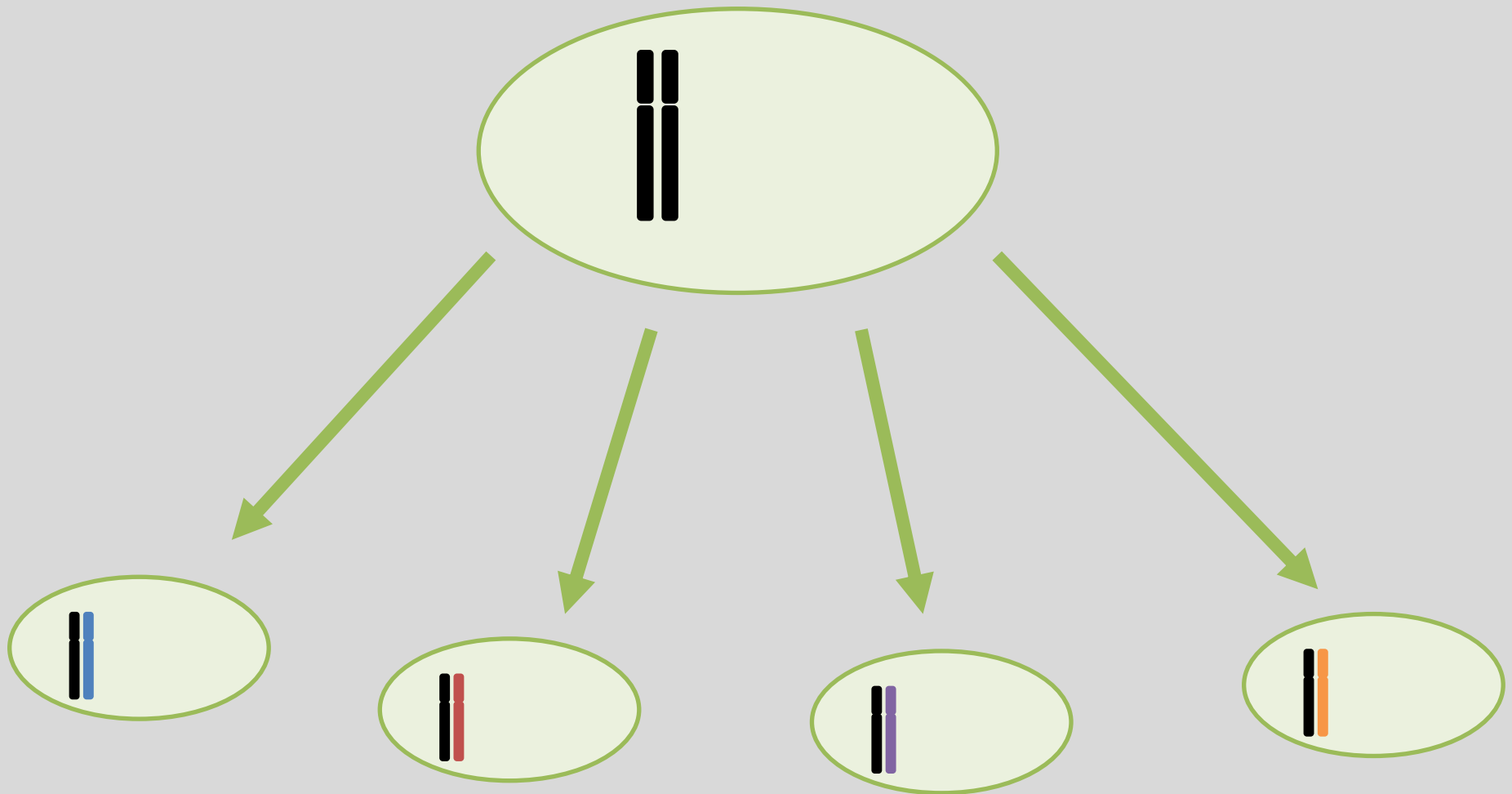
Lecture outline

1. Kin selection & group selection
2. Fitness in metapopulations
3. Case study: the evolution of dispersal

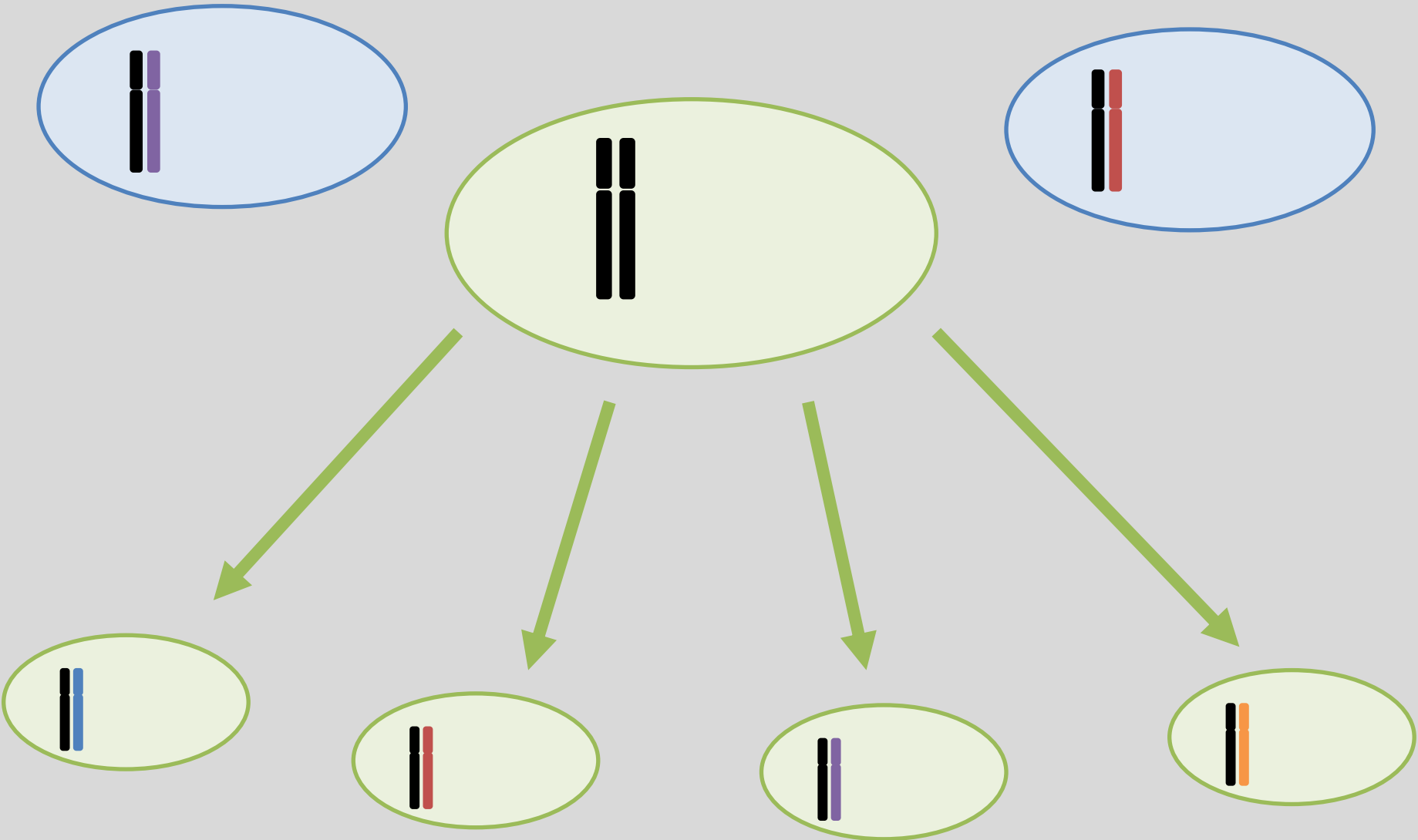


KIN SELECTION & GROUP SELECTION

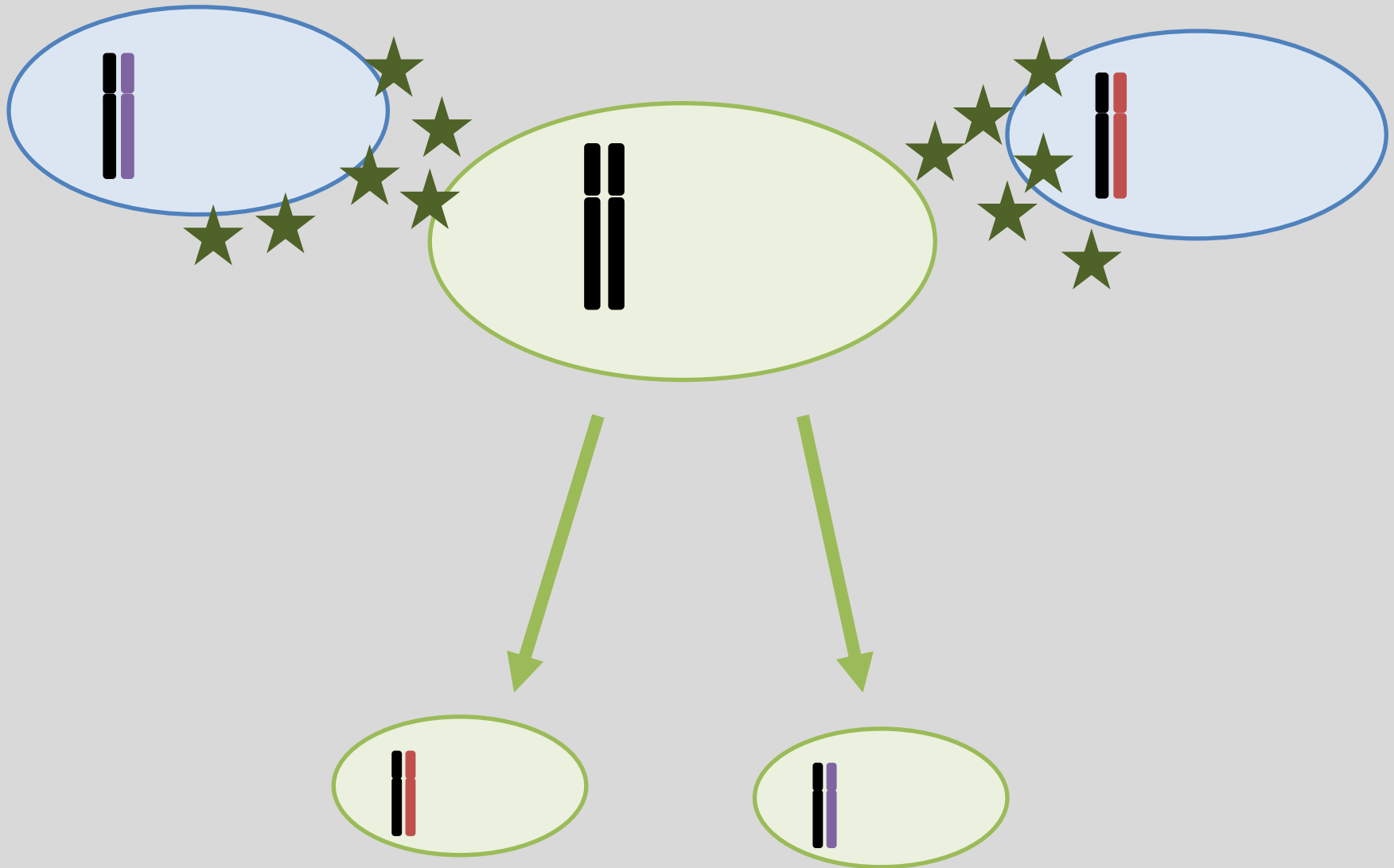
Kin selection



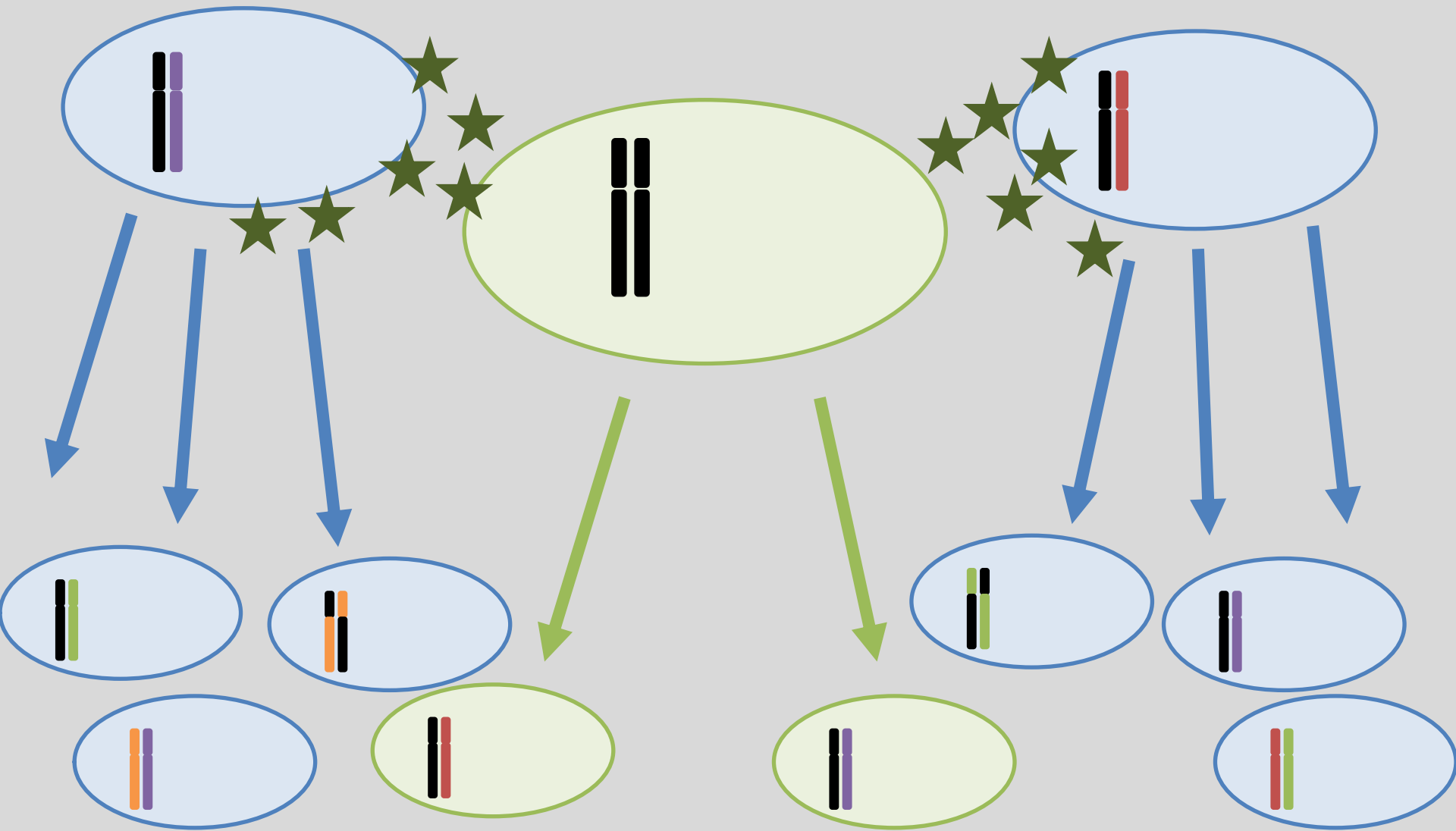
Kin selection



Kin selection



Kin selection



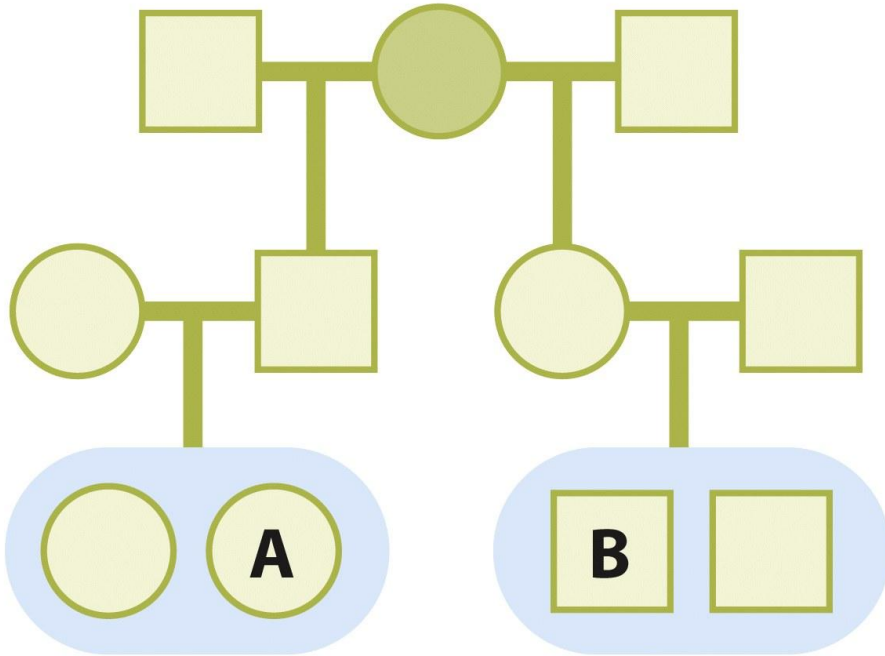
Kin selection



Overall effect = relatedness × benefit to helped – cost to helper

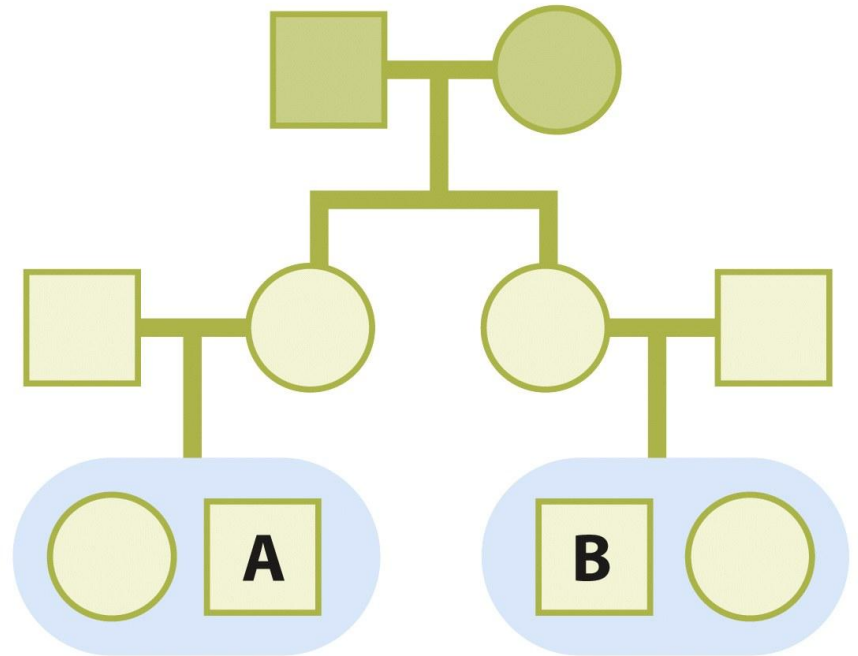


Relatedness



$$r = 0.5^4 = 0.0625$$

Evolution, 1/e Figure 18.2a
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$$r = 0.5^4 + 0.5^4 = 0.125$$

Evolution, 1/e Figure 18.2b
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Relatedness

In a population, relatedness depends on:

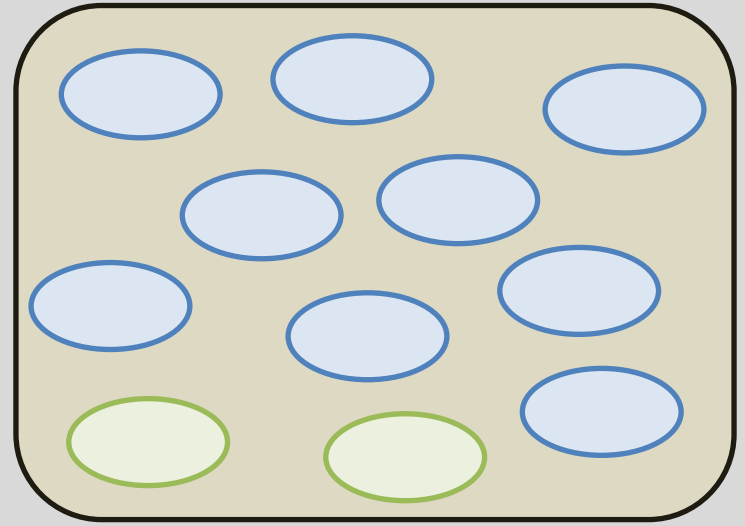
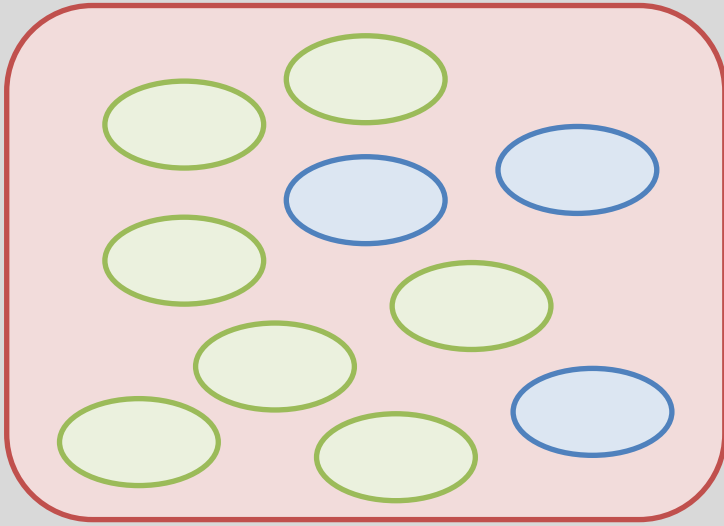
- immigration rate
- population size

Also called “identity by descent” (i.e. whether two alleles at the same locus, carried by two random individuals, come from the same ancestor)

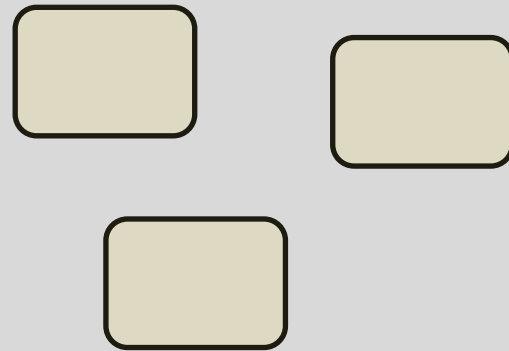
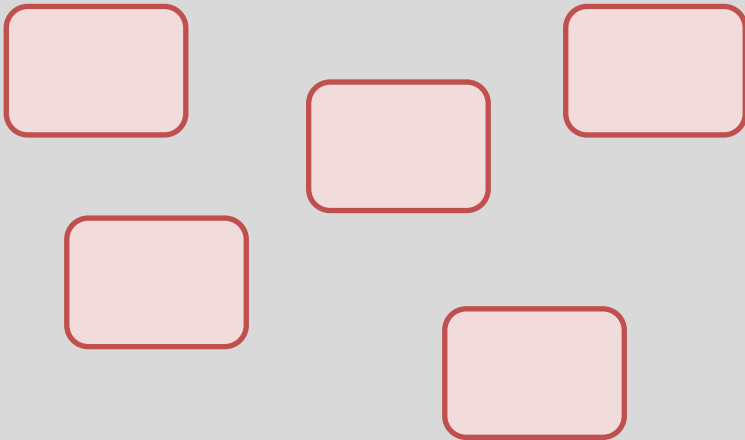
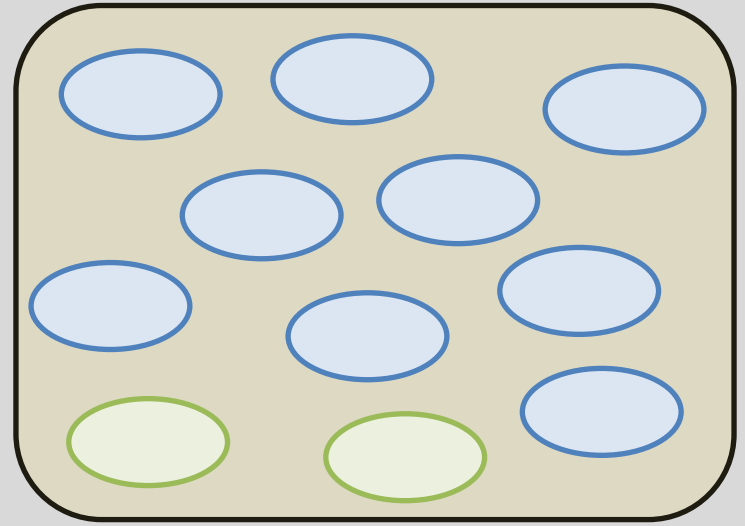
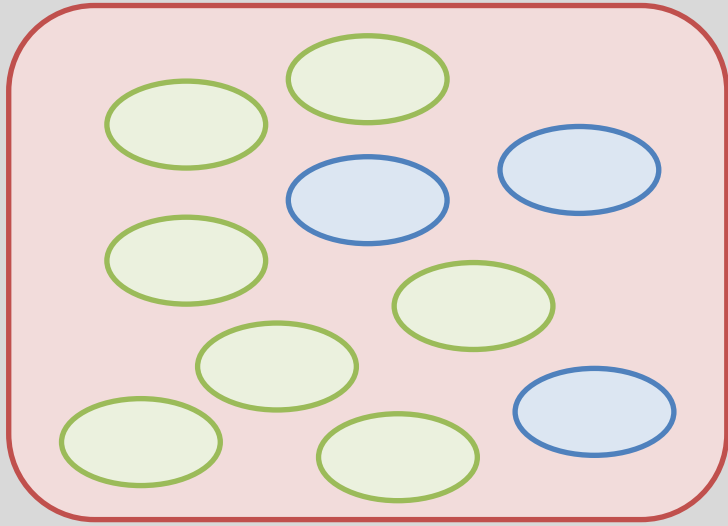
e.g. discrete-time model with constant N individuals and migration m

$$r = 1 / \left[N - (N - 1)(1 - m)^2 \right]$$

Group selection



Group selection



Group selection

“The reputation of group selection comes not from mathematical models, nor from deliberate discussion of group selection, but from a certain naivety practised by laymen and many biologists alike in their day-to-day thinking about the adaptedness of animals to their environments.

(...) adaptations arise only by natural selection, and natural selection does not normally promote adaptations for the good of any unit larger than the organism.”

A. Grafen, *in* Krebs & Davies 1984

Problems with group selection

- Groups do not carry genes, individuals do
- “for the benefit of the group” = very Panglossian way of thinking about evolution
- Even with group benefits, separation of time scales might advantage groups containing genotypes impeding the creation of new groups

Further reading on group selection



doi:10.1111/j.1558-5646.2012.01835.x

TOWARDS A GENERAL THEORY OF GROUP SELECTION

Burton Simon,^{1,2} Jeffrey A. Fletcher,³ and Michael Doebeli⁴

$$\frac{\partial \theta}{\partial t} + \sum_i \frac{\partial (\alpha_i \theta)}{\partial x_i} = g(\vec{x})$$

$\theta(\vec{x}, t)$ Density of groups made of x_1, x_2, \dots individuals of genotypes 1, 2, ...

$$\alpha_i(\vec{x}) = b_i(\vec{x}) + i_i(\vec{x}) - d_i(\vec{x}) - e_i(\vec{x})$$

Birth rate

Immigration rate

Death rate

Emigration rate

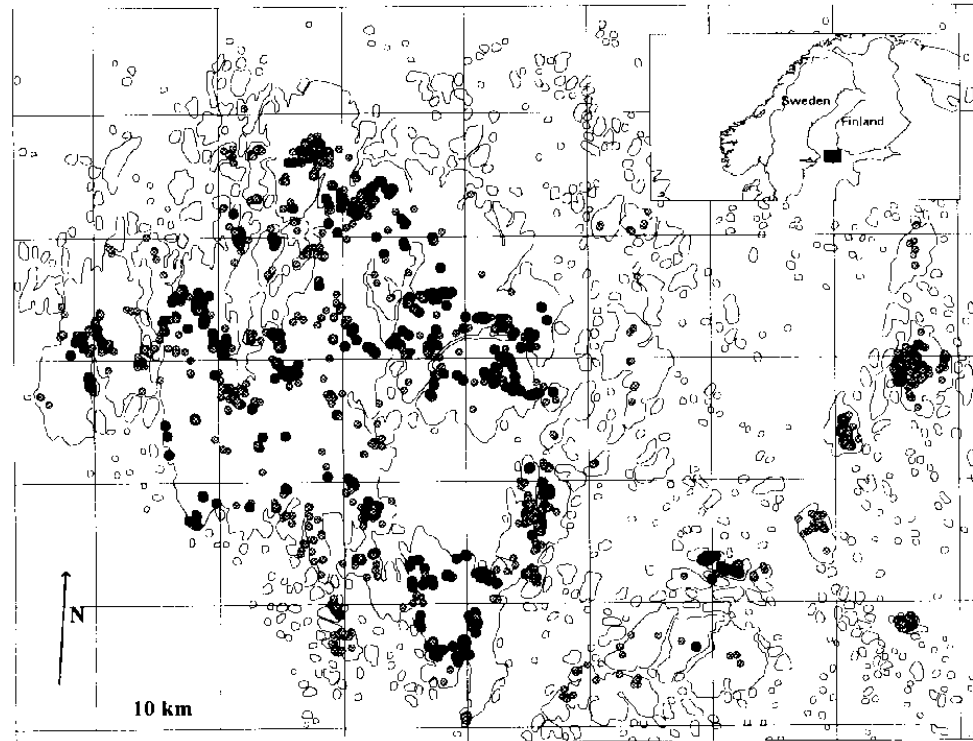


FIGURE 1 Map of Åland islands in southwestern Finland, showing the locations of the habitat patches (dry meadows) suitable for the Glanville fritillary *Melitaea cinxia* (dots). Patches that were occupied in late summer 1993 are shown by black dots. The size of the grid is 100 km² (modified from Hanski *et al.*, 1995a).

FITNESS IN METAPOPOPULATIONS

Spatially structured fitness?

Main issue:

How to compute fitness when...

- interactions occur at a small scale (patch)
- individuals disperse among patches
- patches harbor finite populations

Spatially structured fitness?

Main issue:

How to compute fitness when...

- interactions occur at a small scale (patch)
- individuals disperse among patches
- patches harbor finite populations

Crux of the problem!

Otherwise, simple models
would do the trick

Spatially structured fitness?

Main issue:

How to compute fitness when...

- interactions occur at a small scale (patch)
- individuals disperse among patches
- patches harbor finite populations

Specific issue:

what is typical scarcity in this context?

How can this issue be solved?

Inclusive fitness & Direct fitness

Both methods allow for the computation of selection gradients

$$\frac{dW}{dx} \approx \frac{\partial W}{\partial y} \text{Cov}[x, y] + \frac{\partial W}{\partial z} \text{Cov}[x, z]$$

when W is the ‘individual fitness’ of focal (genotype x , phenotype y) with patch mates having average phenotype z

$\text{Cov}(x, z) / \text{Cov}(x, y) =$ relatedness among patch mates

How can this issue be solved?

Inclusive fitness & Direct fitness

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when W is the ‘individual fitness’ of focal (genotype x , phenotype y) with patch mates having average phenotype z

finite populations = non-zero relatedness

$\text{Cov}(x, z) / \text{Cov}(x, y) =$ relatedness among patch mates

How can this issue be solved?

Inclusive fitness & Direct fitness

BUT these methods could not sort out evolutionary stability

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Inclusive fitness & Direct fitness

BUT these methods could not sort out **evolutionary stability**

mutant trait resident trait

$$\underbrace{w(y, z)}_{\text{mutant fitness}} \approx w(z, z) + (y - z) \partial_y w(z, z) + \frac{1}{2} (y - z)^2 \partial_{y,y} w(z, z)$$

mutant fitness

How can this issue be solved?

Inclusive fitness & Direct fitness

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mutant trait resident trait

$$\underbrace{w(y,z)}_{\text{mutant fitness}} \approx w(z,z) + (y-z) \underbrace{\partial_y w(z,z)}_{\text{selection gradient}} + \frac{1}{2}(y-z)^2 \partial_{y,y} w(z,z)$$

mutant fitness

selection gradient

= what happens first

when	$\partial_y w(z,z) = 0$
$d_z [\partial_y w(z,z)] < 0$	means convergence

How can this issue be solved?

Inclusive fitness & Direct fitness

BUT these methods could not sort out **evolutionary stability**

mutant trait resident trait

$$\underbrace{w(y,z)}_{\text{mutant fitness}} \approx w(z,z) + (y-z) \underbrace{\partial_y w(z,z)}_{\text{selection gradient}} + \frac{1}{2}(y-z)^2 \underbrace{\partial_{y,y} w(z,z)}_{\text{ESS criterion}}$$

mutant fitness

selection gradient

ESS criterion

= what happens first

= what happens next

when $\partial_y w(z,z) = 0$
means
 $d_z [\partial_y w(z,z)] < 0$ convergence

$\partial_{y,y} w(z,z) < 0$ means ESS
no type can beat z
 $\partial_{y,y} w(z,z) > 0$ means branching

How can this issue be solved?

Inclusive fitness & Direct fitness

BUT these methods could not sort out **evolutionary stability**

NO INFORMATION!

mutant trait resident trait

$$\underbrace{w(y,z)}_{\text{mutant fitness}} \approx \underbrace{w(z,z)}_{\text{resident fitness}} + \underbrace{(y-z)\partial_y w(z,z)}_{\text{selection gradient}} + \underbrace{\frac{1}{2}(y-z)^2 \partial_{y,y} w(z,z)}_{\text{ESS criterion}}$$

mutant fitness

selection gradient

ESS criterion

= what happens first

= what happens next

when $\partial_y w(z,z) = 0$
 $d_z [\partial_y w(z,z)] < 0$ means convergence

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How can this issue be solved?

R_m method

Principle: account for demographic variability among patches through state vectors

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R_m method

Principle: account for demographic variability among patches through state vectors

patch state dynamics $\frac{d\mathbf{P}}{dt} = \mathbf{G}(\mathbf{P}) \cdot \mathbf{P}$ with $\mathbf{P} = \begin{pmatrix} p_{00} \\ p_{01} \\ \vdots \\ p_{K0} \end{pmatrix}$

How can this issue be solved?

R_m method

Principle: account for demographic variability among patches through state vectors

patch state dynamics $\frac{d\mathbf{P}}{dt} = \mathbf{G}(\mathbf{P}) \cdot \mathbf{P}$ with $\mathbf{P} = \begin{pmatrix} p_{00} \\ p_{01} \\ \vdots \\ p_{K0} \end{pmatrix}$

emigrant production

$R_m = \mathbf{A}^T \cdot (-\mathbf{G}^{-1}) \cdot \mathbf{Y}$ is a fitness criterion

inverse (transitions)
 \approx typical times in each state

initial pop. state

$R_m > 1$ invades !

$R_m < 1$ fails to invade

How can this issue be solved?

R_m method

Principle: account for demographic variability among patches through state vectors

Two separate proofs that the R_m is an instability criterion

discrete time

Persistence of a Markovian Population in a Patchy Environment

Peter L. Chesson*

Chesson (1984) ZWtG

continuous time

The metapopulation fitness criterion: Proof and perspectives

François Massol^{a,b,c,*}, Vincent Calcagno^d, Julien Massol^e

Massol et al. (2009)
TPB

How can this issue be solved?

R_m method

Principle: account for demographic variability among patches through state vectors

Benefit: we get a “true” metapopulation fitness function $R_m(y,z)$

→ convergence and evolutionary stability can be solved using the same tool

How can this issue be solved?

R_m and the inclusive fitness can be reconciled...

$$\frac{\partial R_m}{\partial y}(z, z) = \frac{1}{P_m} \left[\dot{k} \left(\frac{\partial}{\partial y} [jW_j] \right) + F \ddot{k} \left(\frac{\partial}{\partial y} [jW_j] \right) \right]$$

relatedness

probability of being an immigrant

Individual "fitness"

Selection gradient with R_m = inclusive fitness
(discrete-time, haploid, non-overlapping generations)

How can this issue be solved?

... and “inclusive fitness” can even get beyond the selection gradient!

probability that three different individuals
from the same patch descend from the same
immigrant

$$\frac{\partial^2 R_m}{\partial y^2}(z, z) = \frac{1}{P_m} \left[\begin{array}{l} \dot{\kappa} \left(\frac{\partial^2}{\partial y^2} [jW_j] \right) + F\ddot{\kappa} \left(\frac{\partial^2}{\partial y^2} [jW_j] \right) + K\ddot{\kappa} \left(\frac{\partial^2}{\partial y^2} [jW_j] \right) \\ + 4N^2(N-1)\pi_1 F \left(F\dot{\kappa} \left(\frac{\partial}{\partial y} [\pi_j] \right) + K\ddot{\kappa} \left(\frac{\partial}{\partial y} [\pi_j] \right) \right) \dot{\kappa} \left(\frac{\partial}{\partial y} [jW_j] \right) \end{array} \right]$$

Spatially structured fitness

Extensions / similar methods in spatially realistic models

SIAM J. APPLIED DYNAMICAL SYSTEMS
Vol. 11, No. 2, pp. 567–596

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R_0 Analysis of a Spatiotemporal Model for a Stream Population*

H. W. Mckenzie[†], Y. Jin[†], J. Jacobsen[‡], and M. A. Lewis^{†§}

ORIGINAL ARTICLE

doi:10.1111/j.1558-5646.2011.01254.x

EVOLUTIONARY RESPONSES OF DISPERSAL DISTANCE TO LANDSCAPE STRUCTURE AND HABITAT LOSS

Ace North,^{1,2,3} Stephen Cornell,⁴ and Otso Ovaskainen¹

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Proc. R. Soc. A
doi:10.1098/rspa.2011.0194
Published online

Pattern solutions of the Klausmeier model for banded vegetation in semi-arid environments II: patterns with the largest possible propagation speeds

BY JONATHAN A. SHERRATT*

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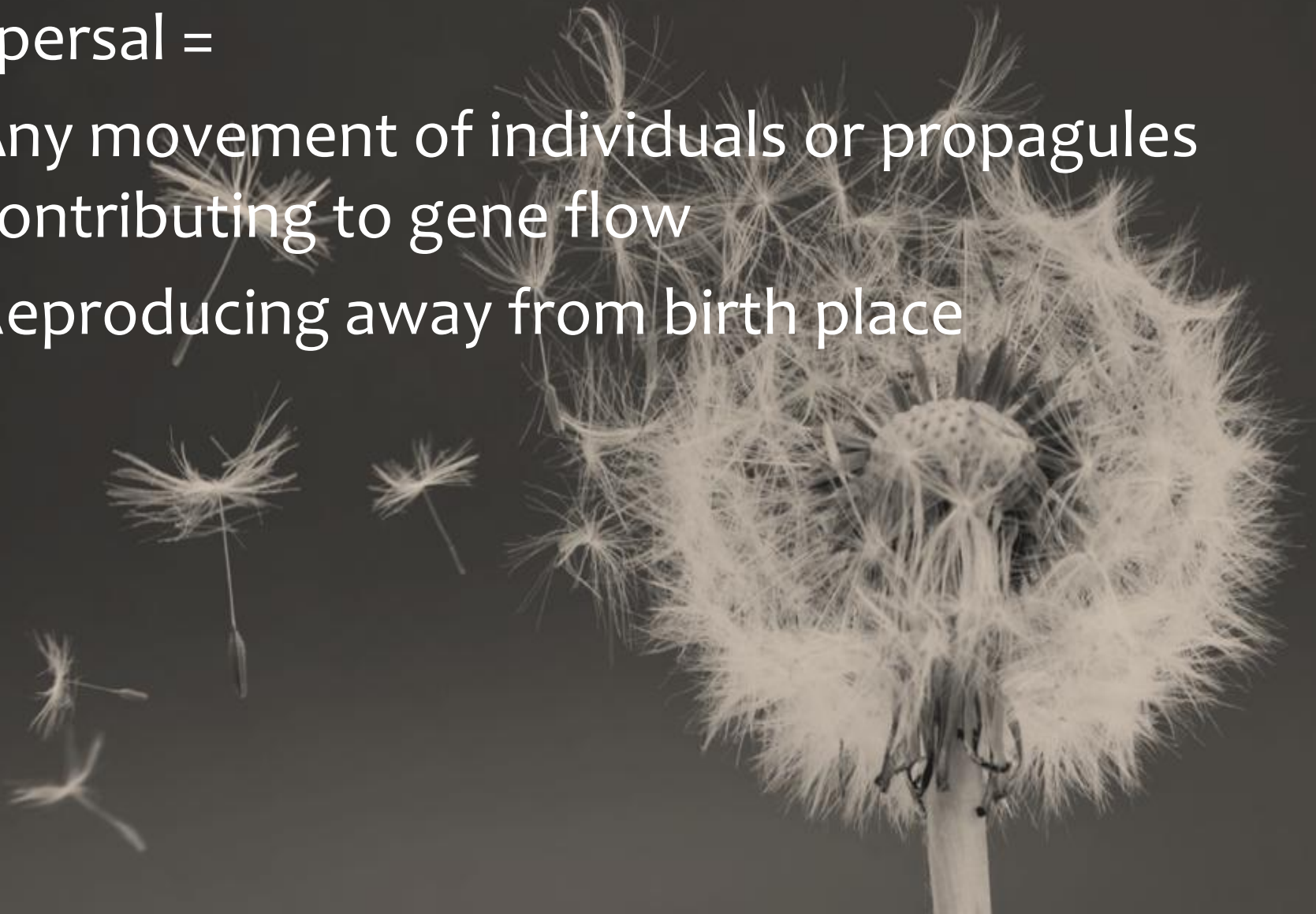


THE EVOLUTION OF DISPERSAL

What is dispersal?

Dispersal =

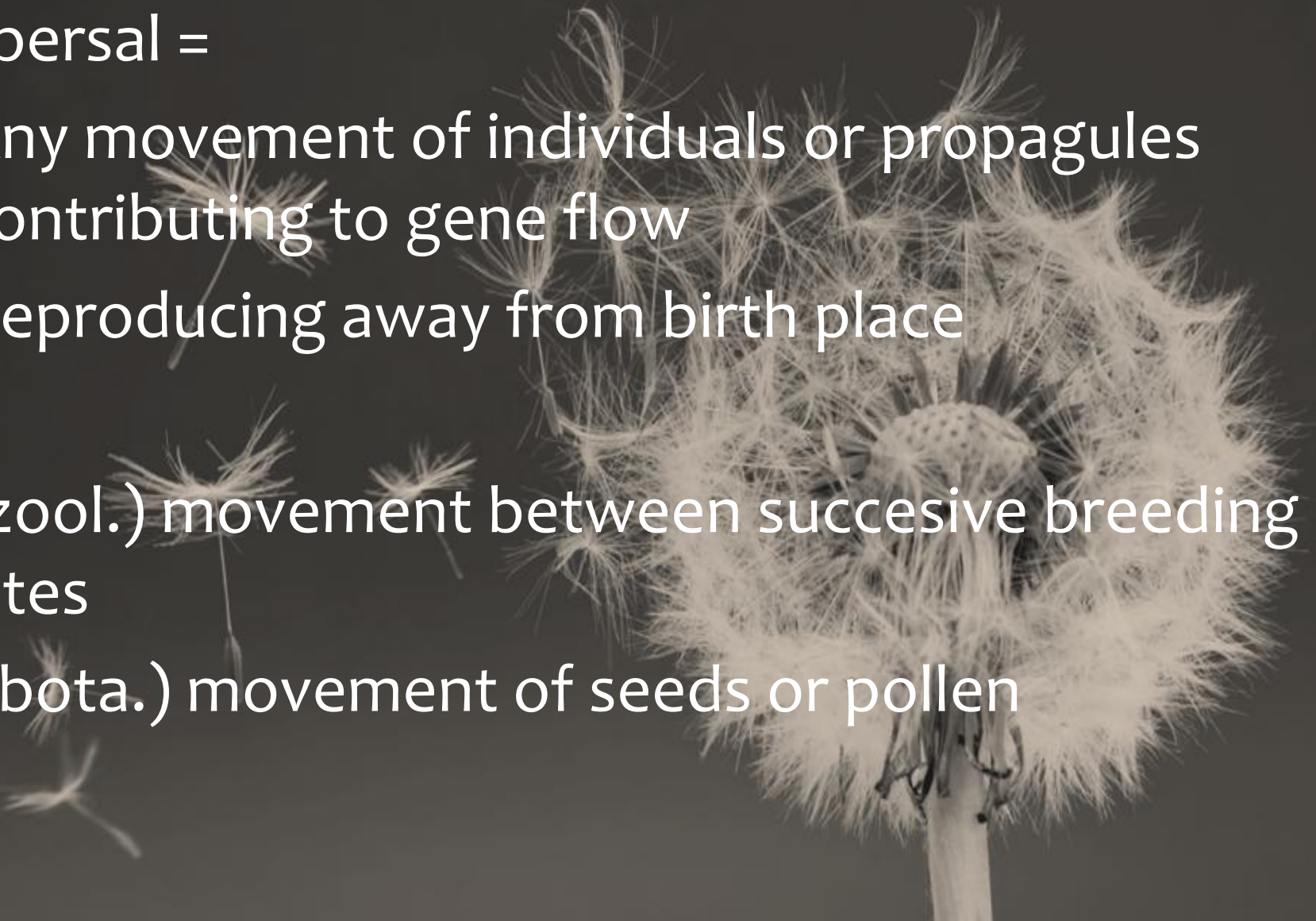
- Any movement of individuals or propagules contributing to gene flow
- Reproducing away from birth place



What is dispersal?

Dispersal =

- Any movement of individuals or propagules contributing to gene flow
- Reproducing away from birth place
- (zool.) movement between successive breeding sites
- (bota.) movement of seeds or pollen



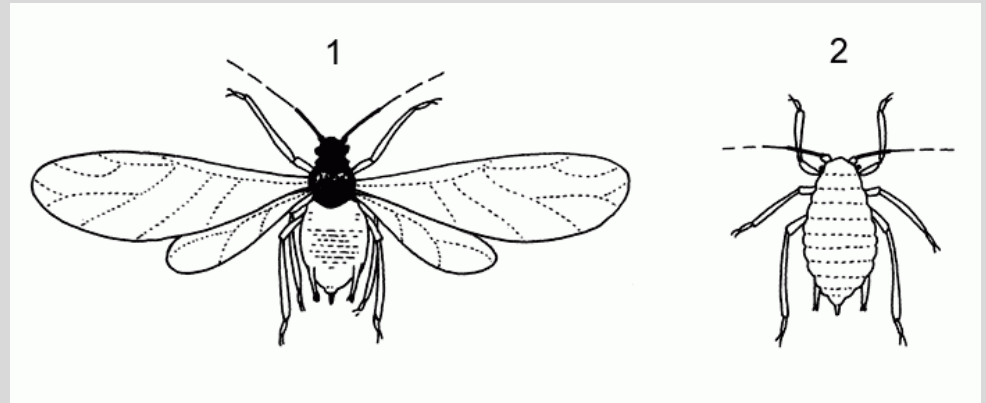
Motivations

- On ecological grounds
 - Coexistence of species mediated by environmental heterogeneity and dispersal
 - Biology of invasive species
 - Persistence in a metapopulation depends on dispersal

Motivations

- On ecological grounds
 - Coexistence of species mediated by environmental heterogeneity and dispersal
 - Biology of invasive species
 - Persistence in a metapopulation depends on dispersal
- On evolutionary grounds
 - Local adaptation evolves in response to dispersal level
 - Speciation depends on dispersal
 - Dispersal can co-evolve with other traits

Dispersal variability in natura



Koppert

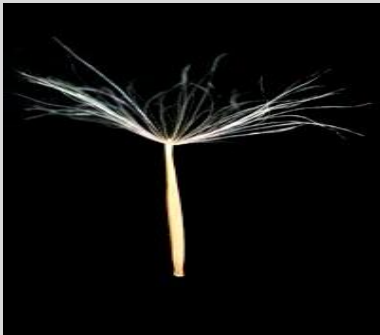


Photo : P. Goujon



Photo : S. Amn

Selective pressures

Pros

Avoid inbreeding

Kin competition

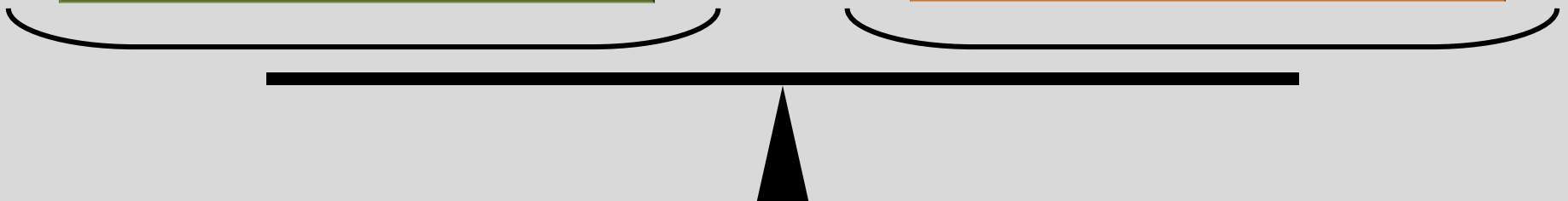
Oscillating / chaotic
population dynamics

Environmental
variability

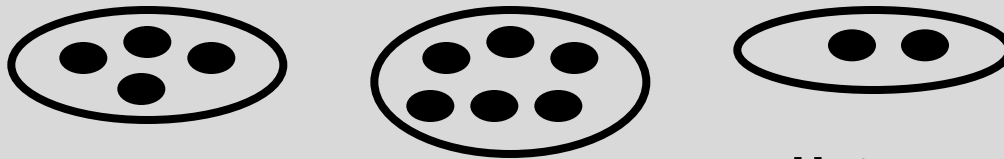
Cons

Environmental
heterogeneity

Cost of dispersal

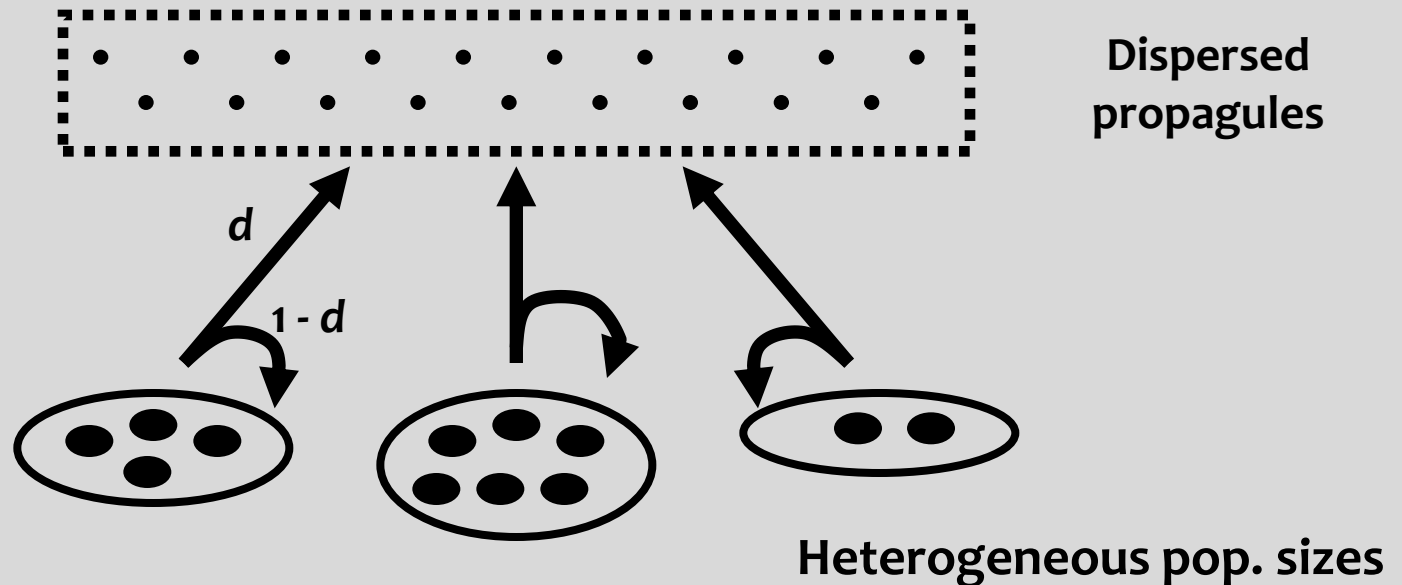


A metapopulation model

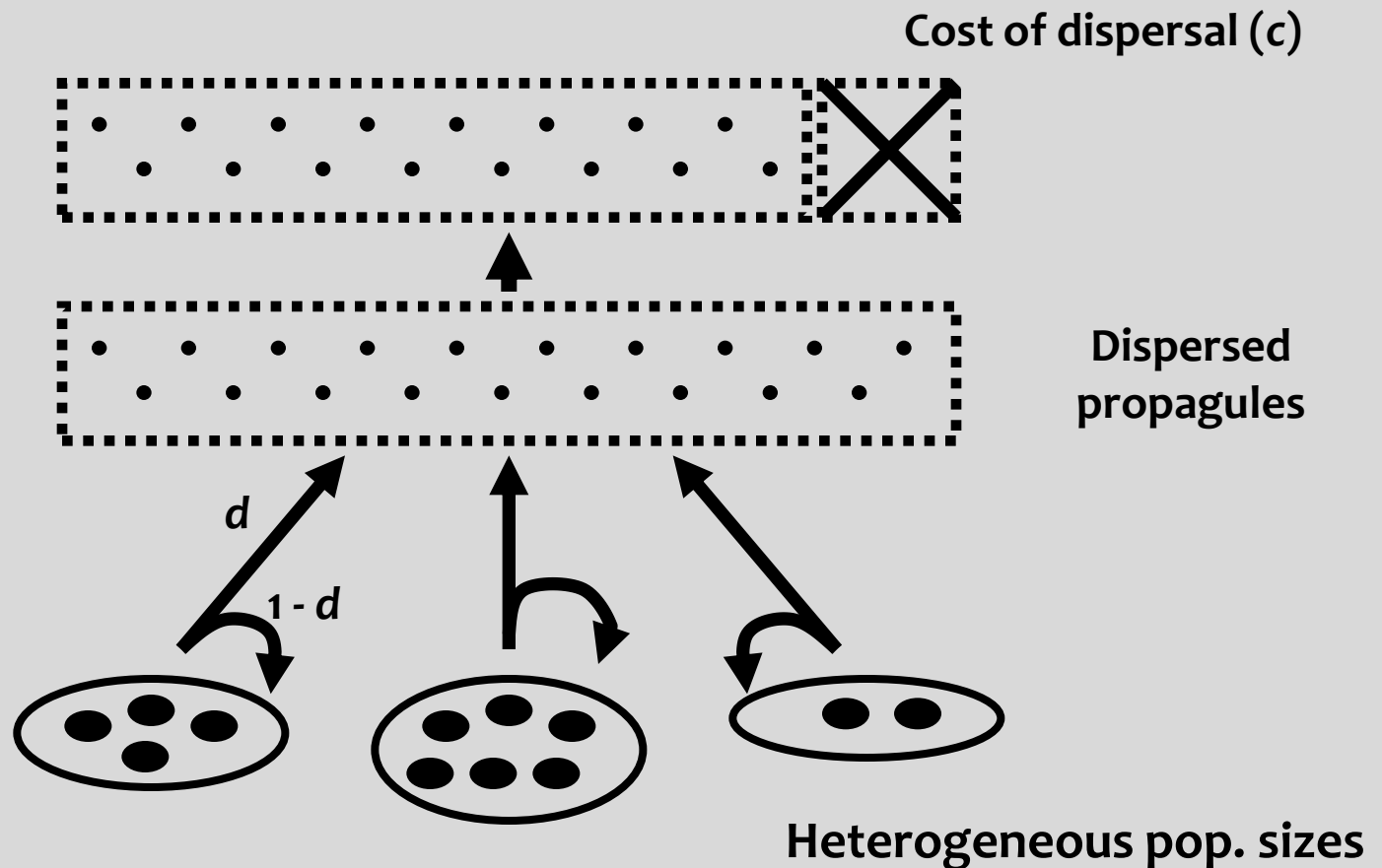


Heterogeneous pop. sizes

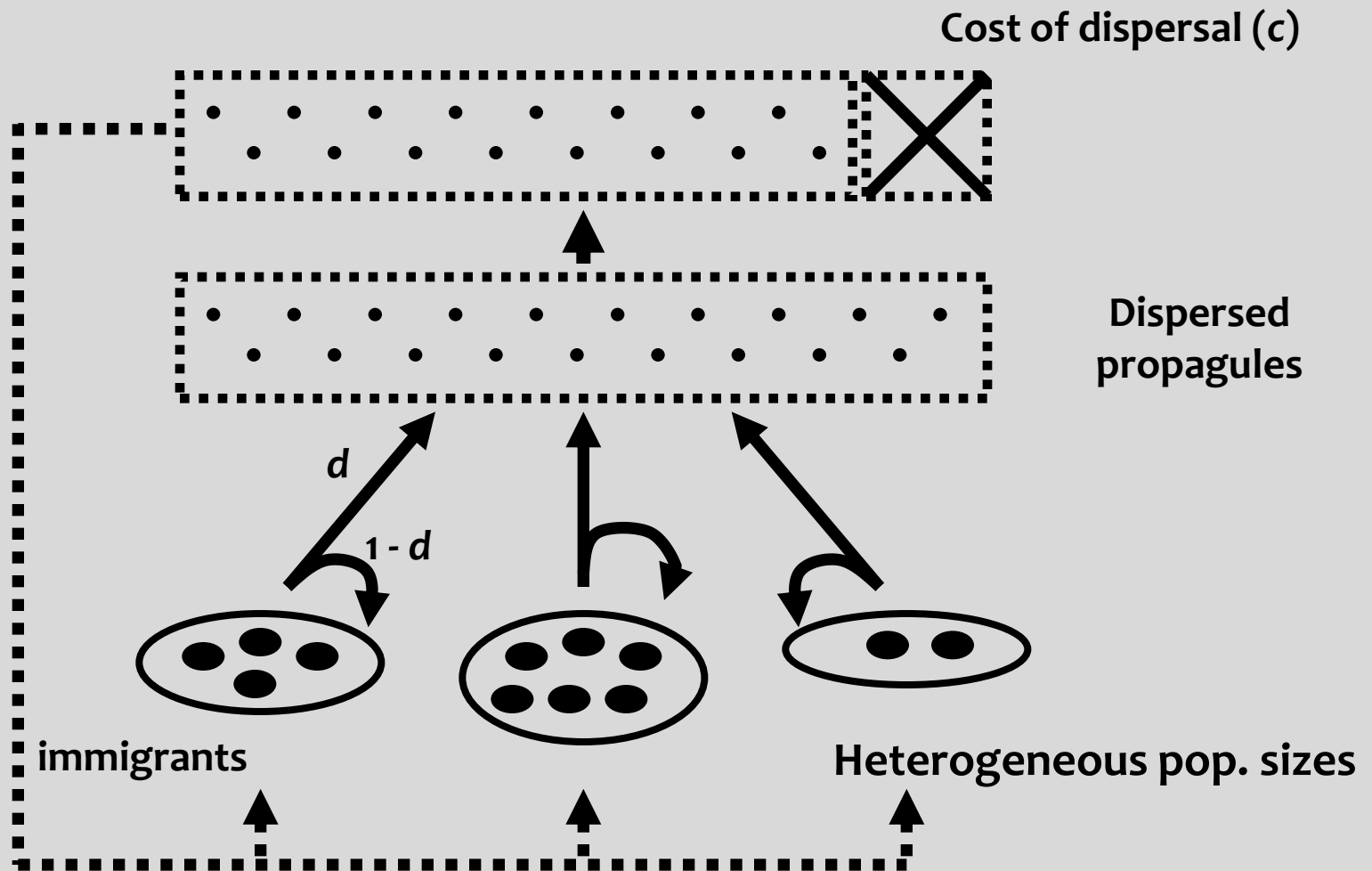
A metapopulation model



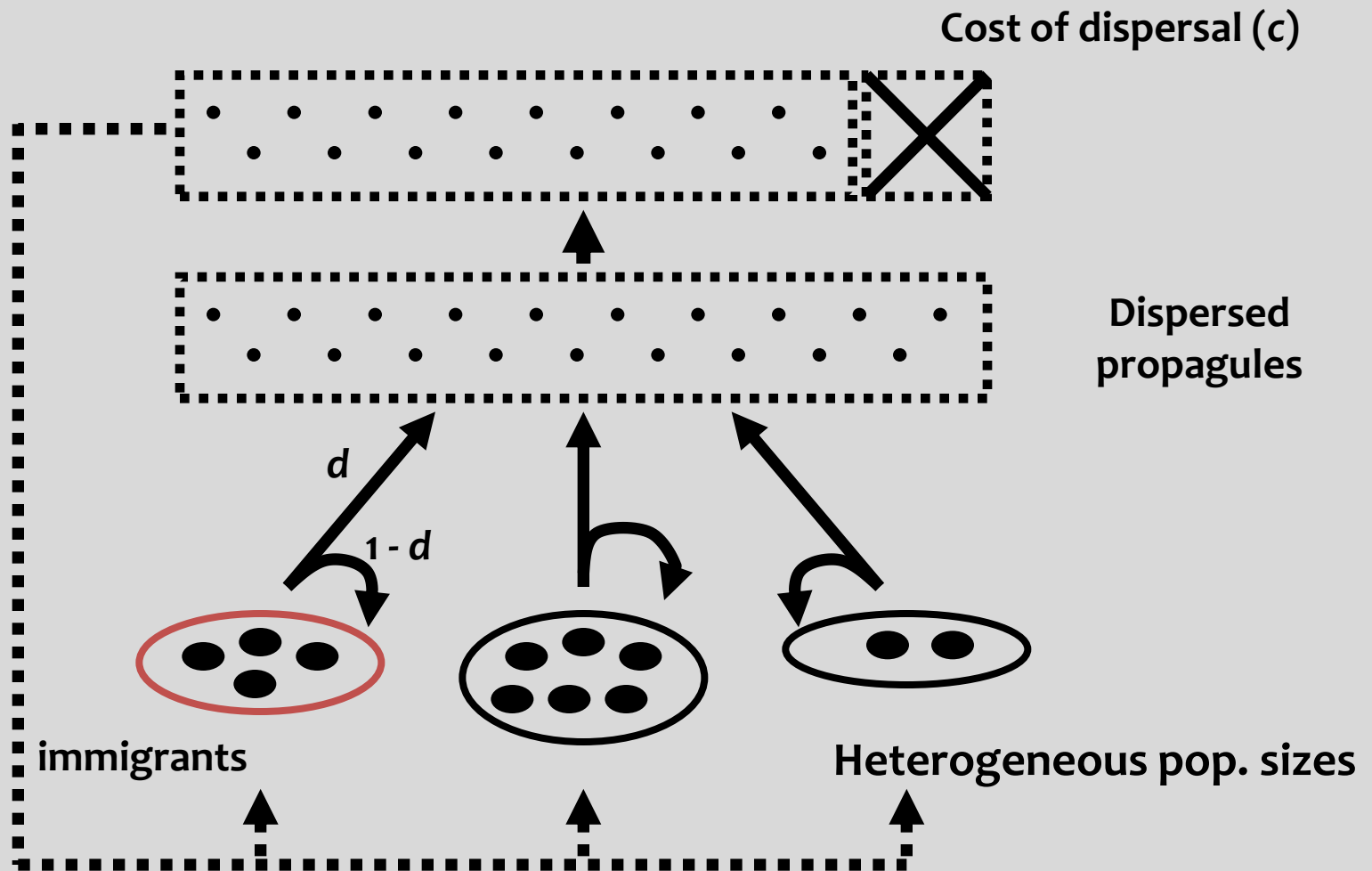
A metapopulation model



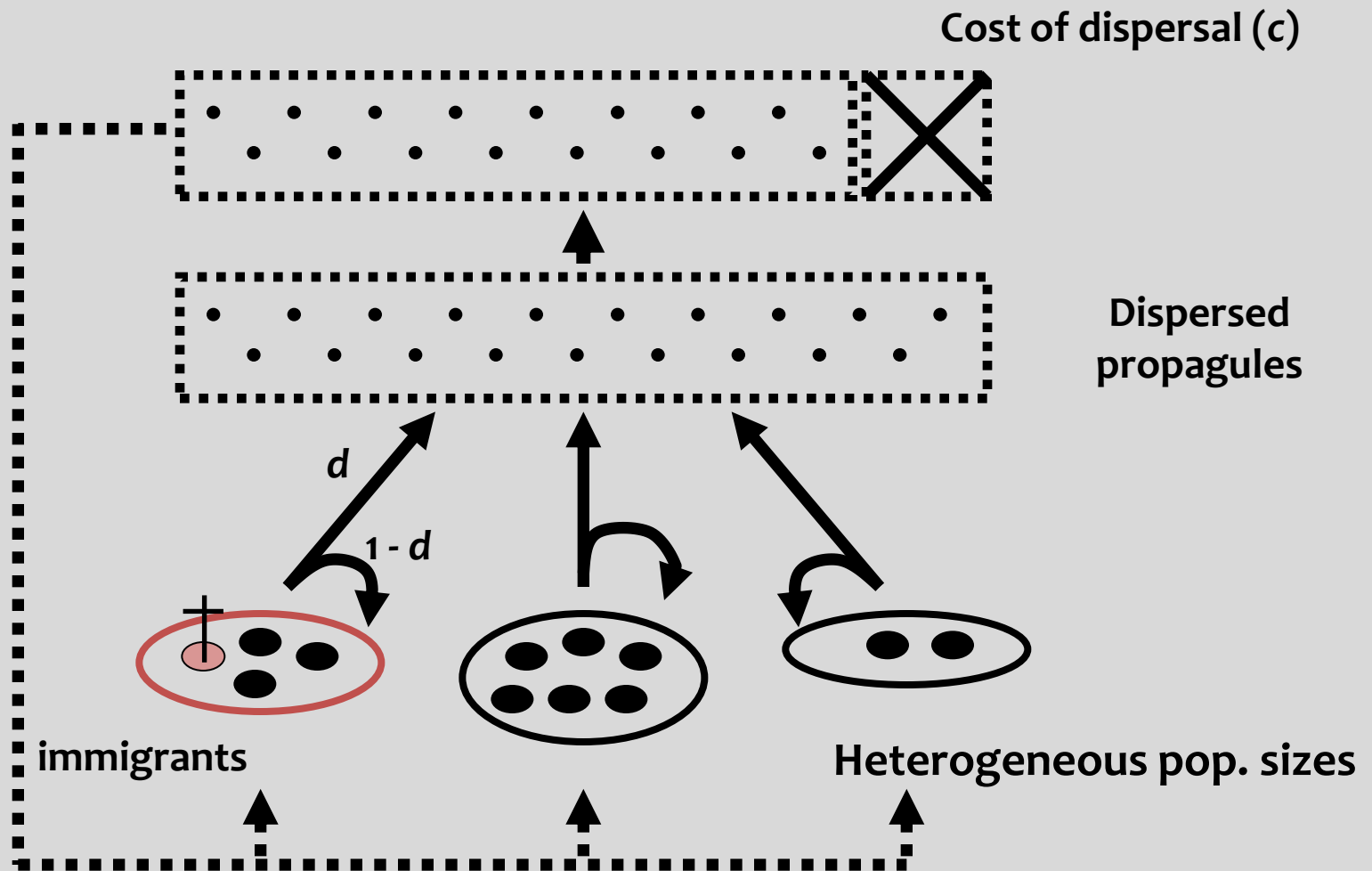
A metapopulation model



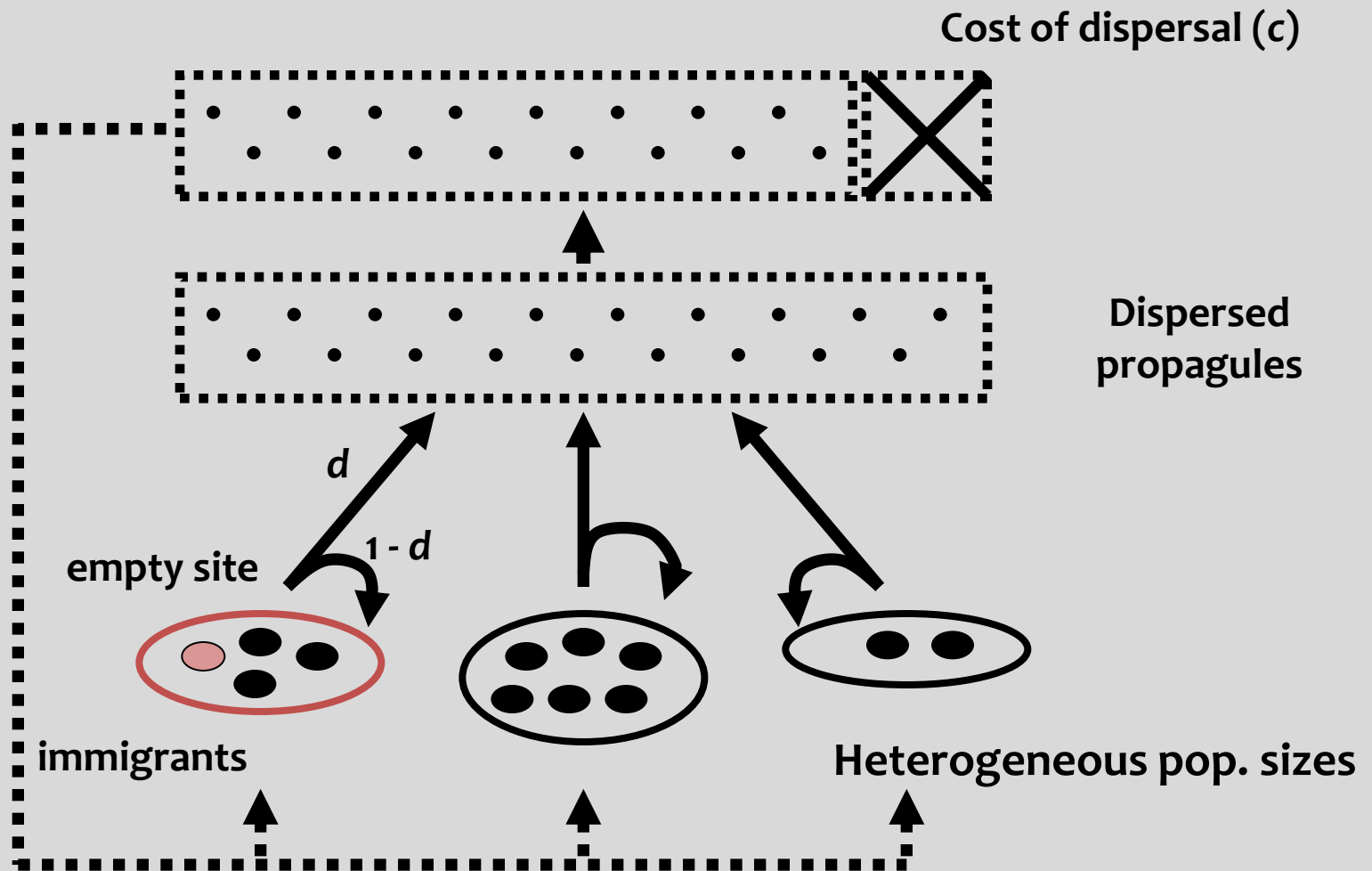
Births and Deaths



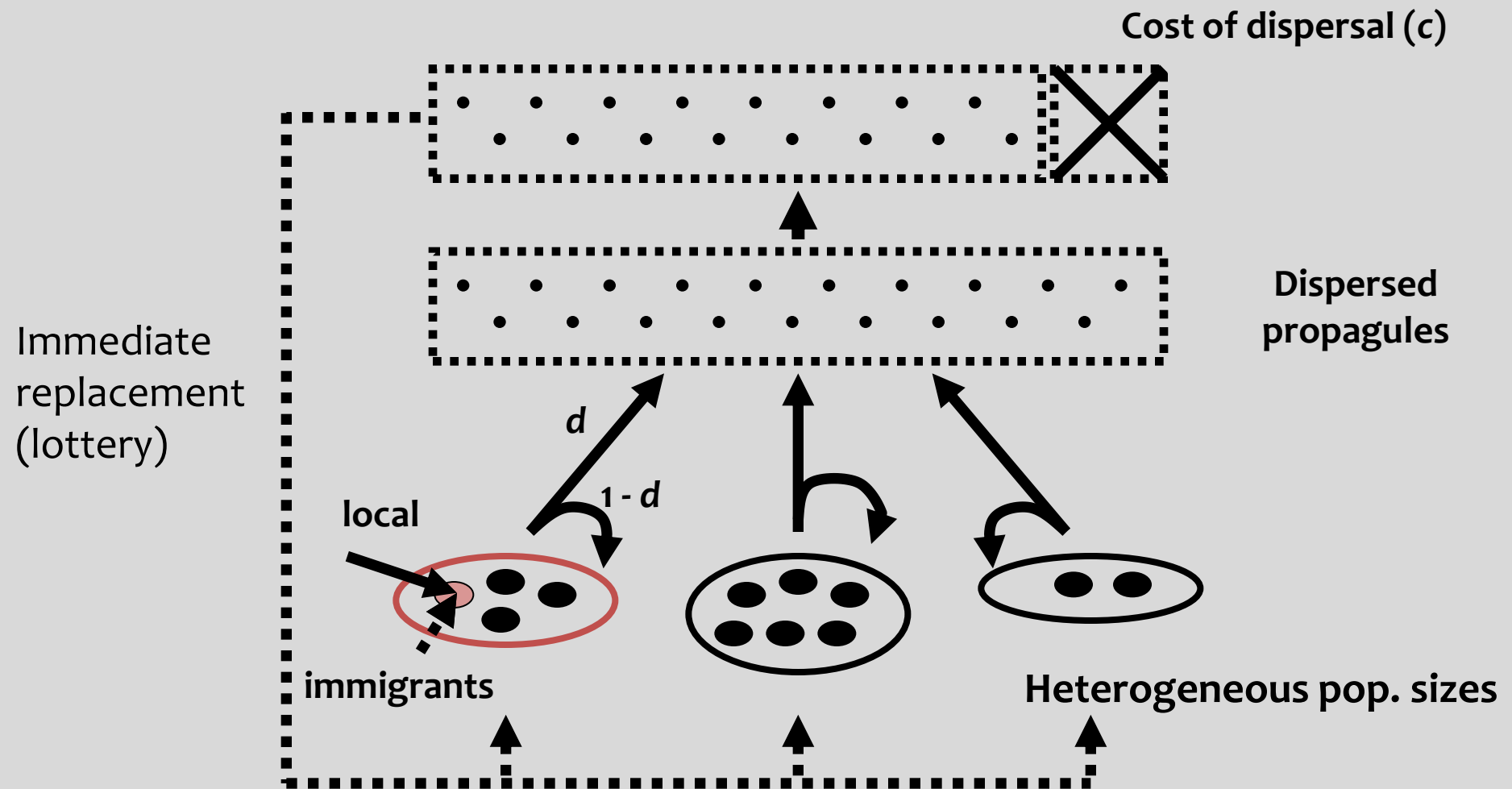
Births and Deaths



Births and Deaths



Births and Deaths



Methods

- Model analysis
 - Metapopulation fitness criterion (R_m , Metz & Gyllenberg 1992)
 - Adaptive dynamics assumptions (Hofbauer & Sigmund 1990)
- Confirmed with simulations
- Supplementary simulations: what if replacement is not immediate? (answer: nothing changes much)

Results: singular strategies

c cost of dispersal

\bar{K} average K

d dispersal

γ_2 CV^2 of K

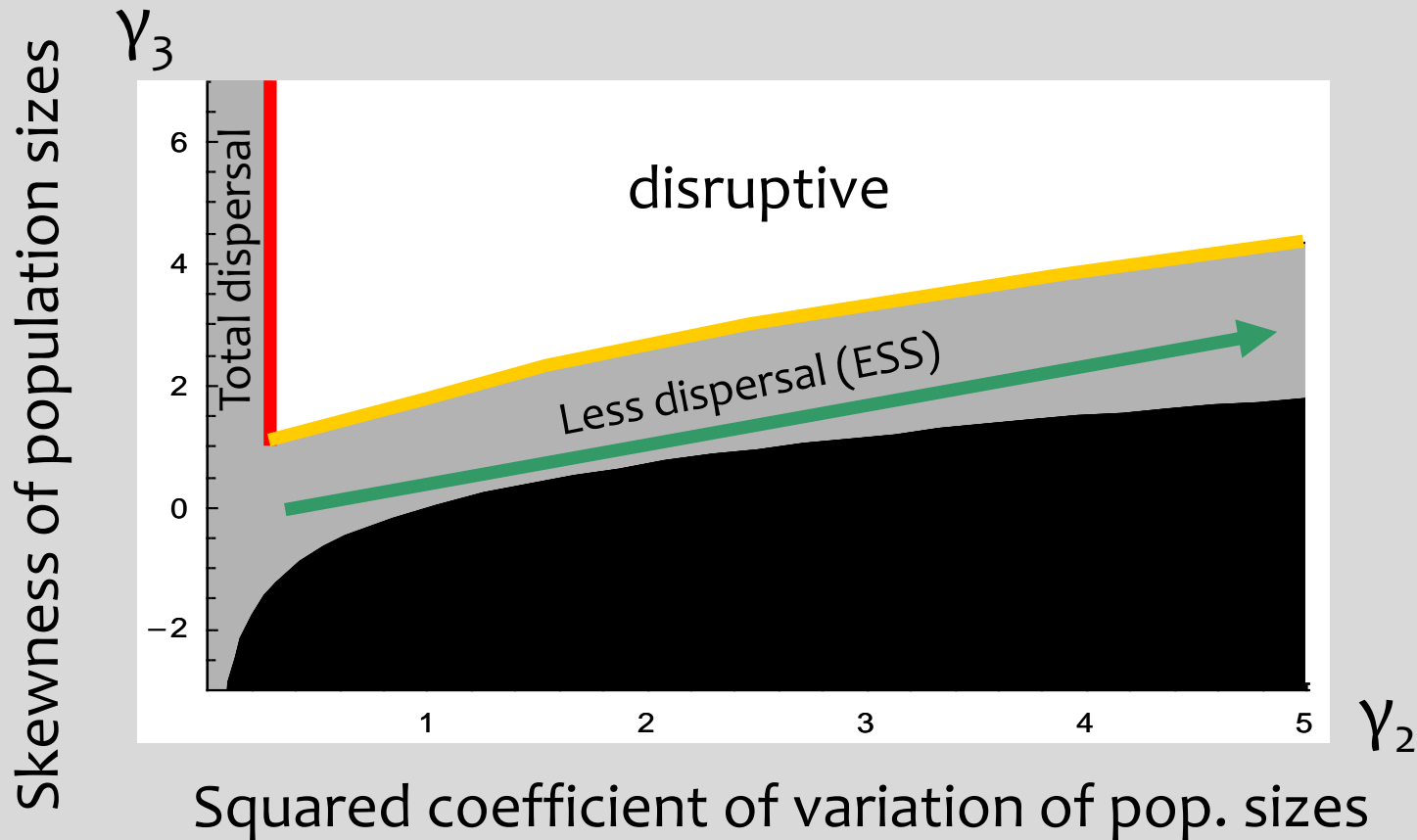
$$d^* = \text{Min} \left[\frac{1}{(c + \gamma_2) \bar{K}}, 1 \right]$$

Cost of dispersal

Heterogeneity

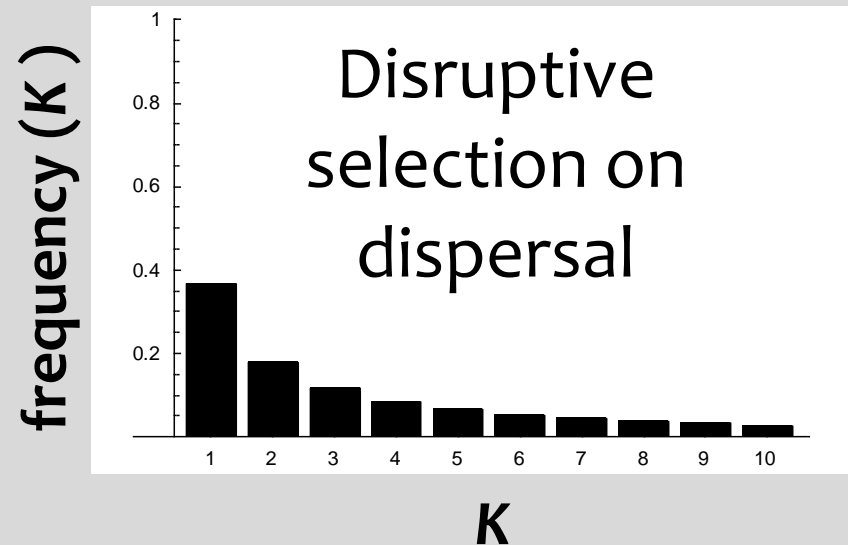
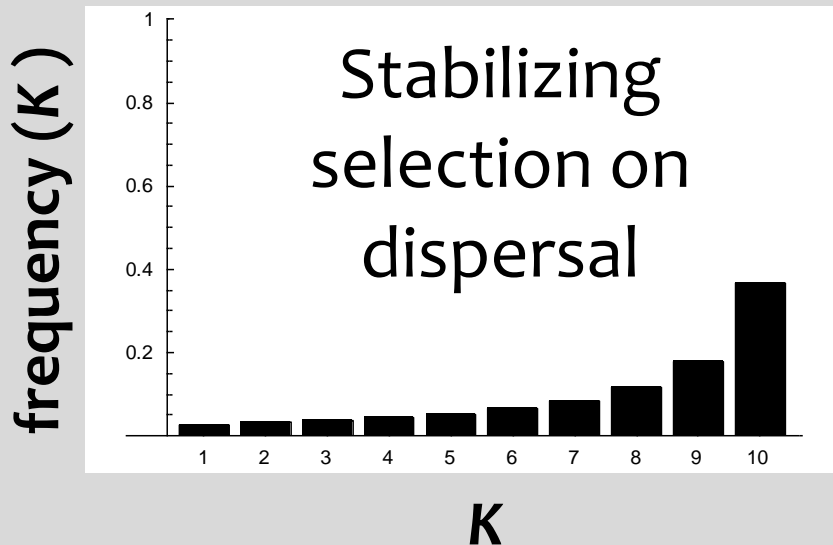
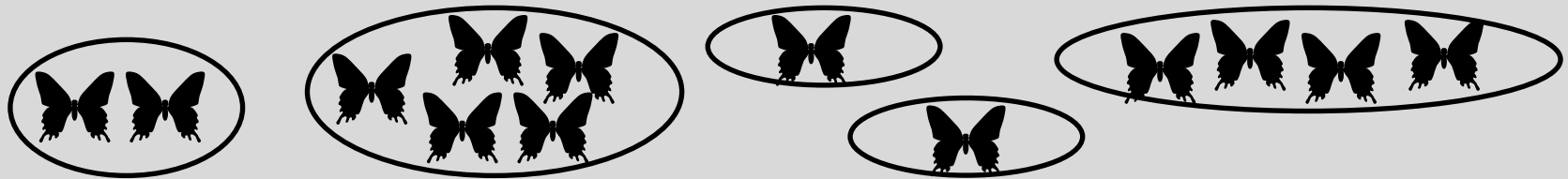
Kin competition

Results: evolutionary outcome



Results: predict polymorphism

Interpretation:



Results: what do data say?

Understanding what nature says

$$c_{max} = \frac{(\gamma_3 - 2\gamma_2^{1/2})\gamma_2^{3/2}}{1 + \gamma_2}$$

When $c_{max} > 1$, we're sure that our mechanism can create dispersal polymorphism

Results: what do data say?

Data set	# patches	γ_2	γ_3	c_{\max}	prediction
Ponds (Guadeloupe)	274	1.7	4.5	1.5	disruptive
Population in big cities (China)	664	1.5	6.7	3.2	disruptive
Dry meadows (Åland islands, Finland)	4,109	7.3	11.1	13.5	disruptive
Tuamotu archipelago (French Polynesia)	118	10.7	8.1	4.7	disruptive
Forest patches (Pennsylvania, USA)	252	44.7	12.0	-8.7	stabilising
Svalbard islands (Norway)	11	4.5	2.7	-2.7	stabilising
Coral reefs (Northern Florida Keys, USA)	1,034	1.3	3.8	1.0	disruptive

Results: what do data say?

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Conclusions

1. Steady state of dispersal = balance between direct cost, environmental heterogeneity and kin competition
2. Skewed population size distribution
→ disruptive selection on dispersal
3. Skewed distributions of proxies for pop. size are common in nature
4. Simplified criterion $c_{\max} > 1$ = test to validate the plausibility of our hypothesis
5. Few large and many small populations
= recipe for a better conservation of types that do and do not disperse

Thank you for your attention!

Further reading

Kin selection & group selection

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