Diversification of dispersal rates in variable environments

François Massol

Décembre 2016 – Journée Maths-Bio Dauphine

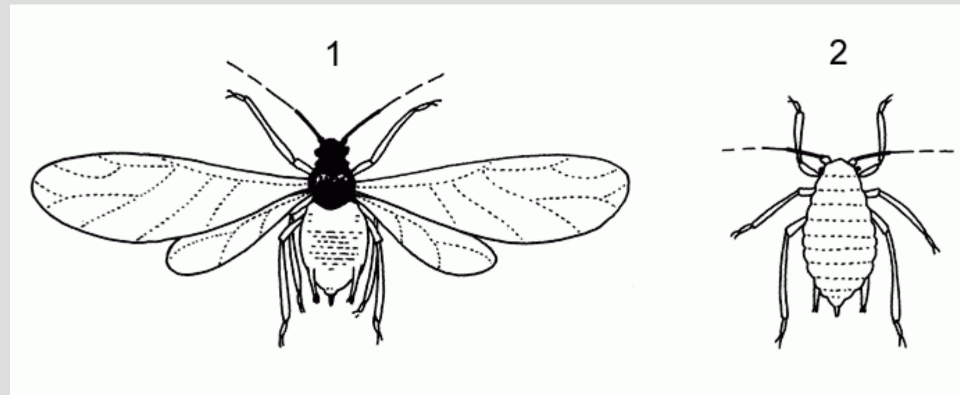
What is dispersal?

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

Variability of dispersal *in natura*



Koppert

Photo : P. Goujon

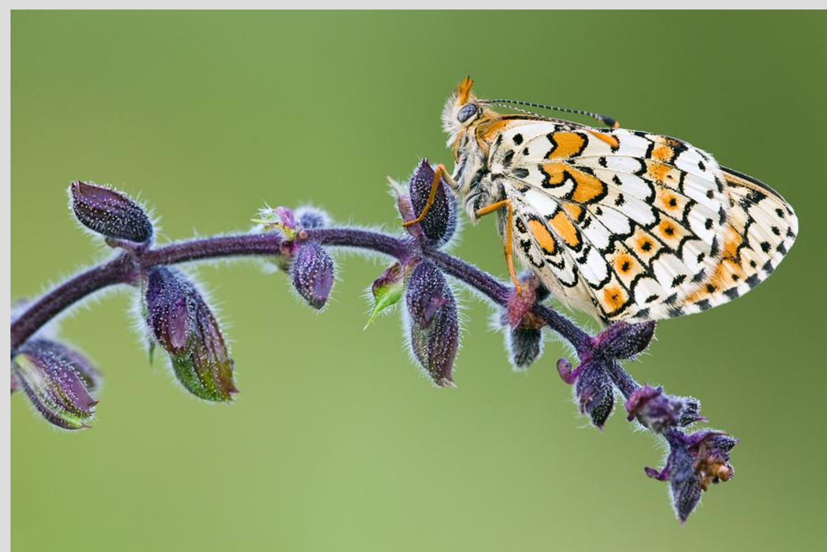


Photo : S. Amn

Heritability of dispersal

Heredity (2008) 100, 39–46

www.nature.com/hdy

ORIGINAL ARTICLE

Heritability of dispersal rate and other life history traits in the Glanville fritillary butterfly

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Department of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

JOURNAL OF Evolutionary Biology
eseb European Society for Evolutionary Biology
doi: 10.1111/j.1420-9101.2011.02281.x

Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross

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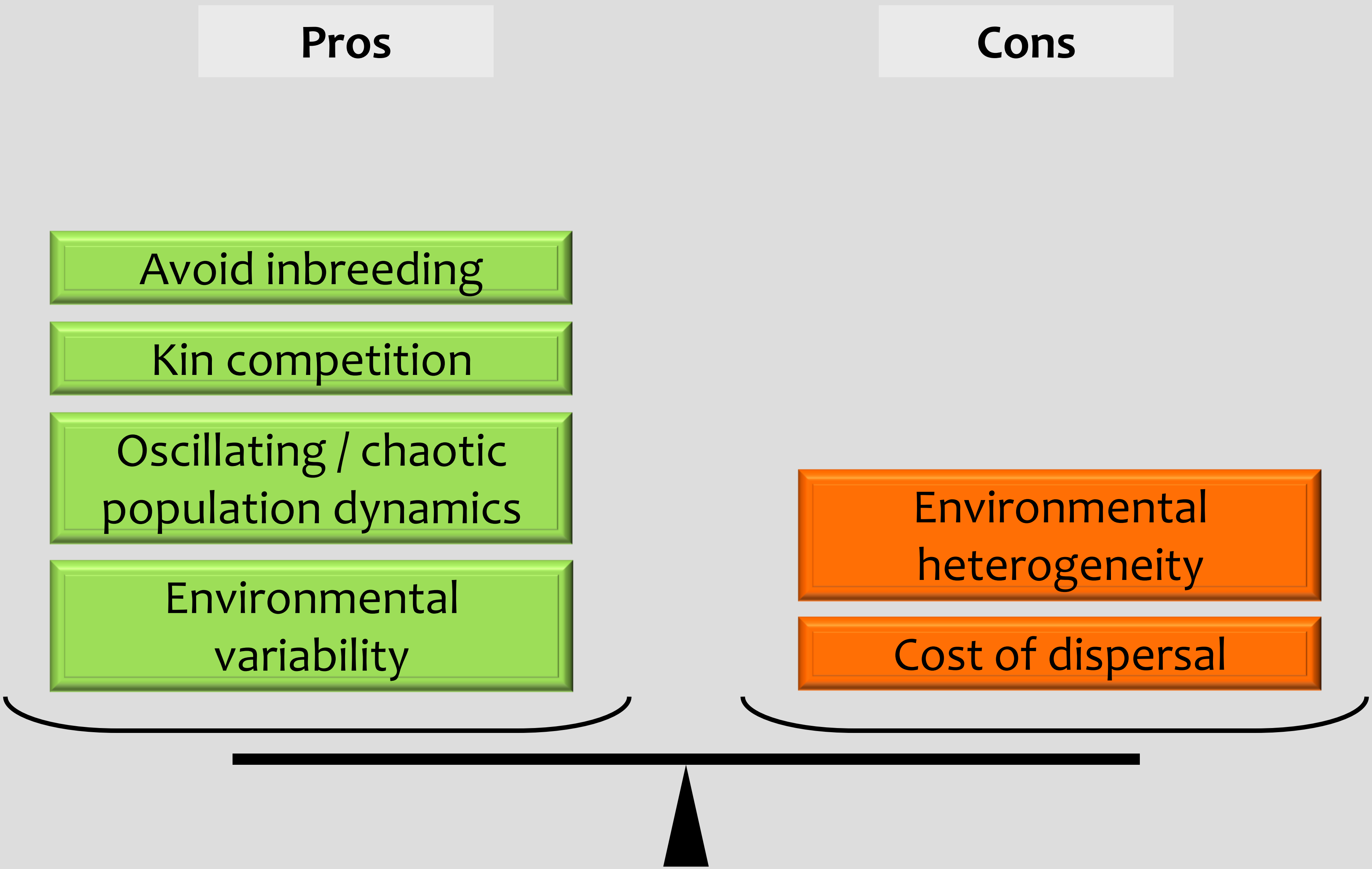
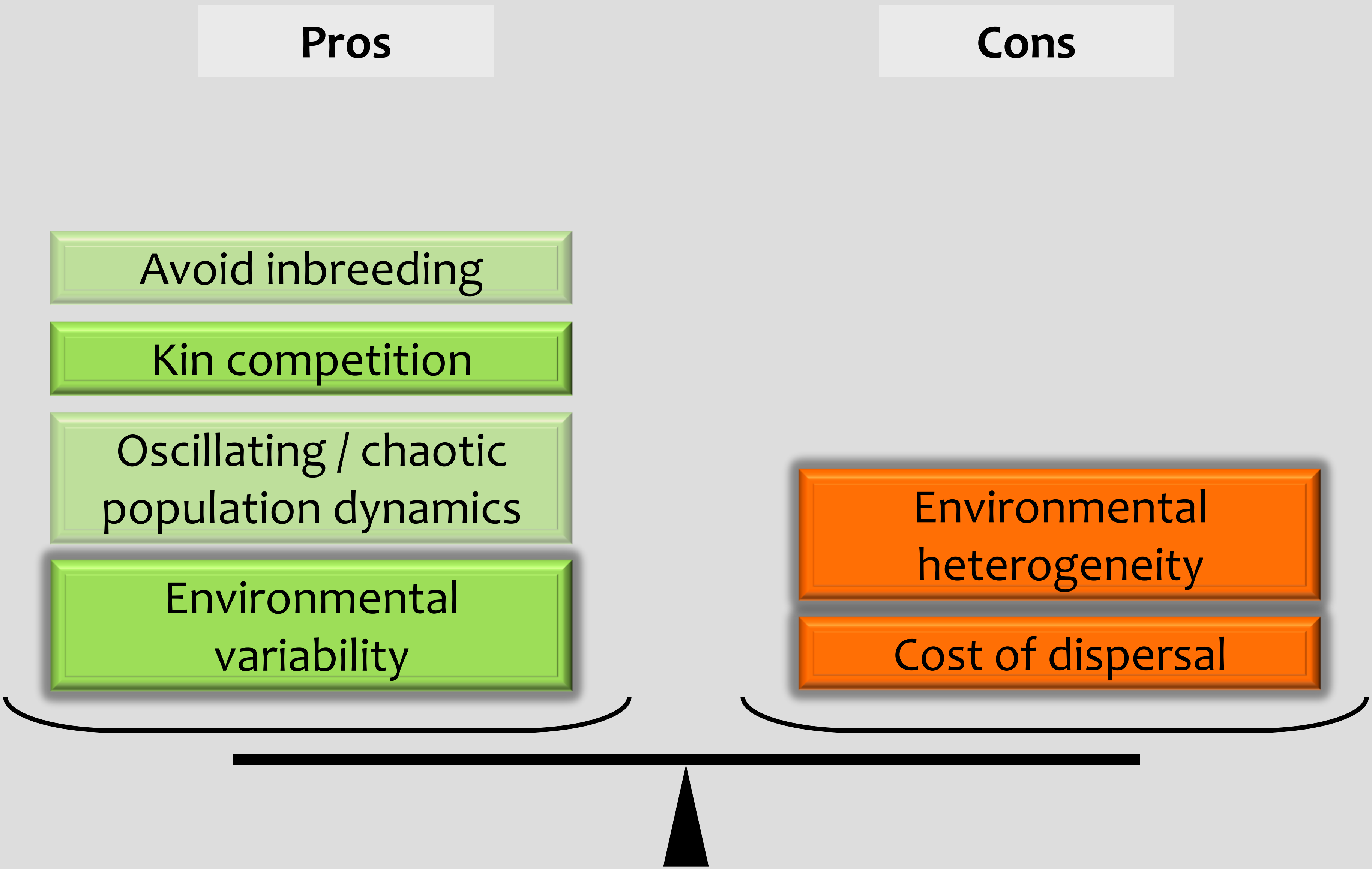
Selective pressures on dispersal



Selective pressures on dispersal



Kin competition

- Hamilton's rule (1964) :

Selection gradient = direct effect+ r * kin effect

where r is relatedness/kinship

- Theoretical predictions:

dispersal = prevents related offspring from competing with one another

- With some precisions:
  - Iteroparity or overlapping generations => higher relatedness => stronger selection for dispersal
  - Mother or offspring-controlled dispersal => different predictions (because relatedness is different)

Hamilton & May 1977; Frank 1986; Ronce *et al*. 2000

Cost(s) of dispersal

- Selects for less dispersal

- Direct costs: can intervene at different life stages / different times of the life cycle

- Different types of direct costs (energy, opportunity, time, risk)

Bonte *et al.* 2012

Heterogeneity and variability

- Environments are temporally variable

  organisms experience temporally variable habitats

  geometric average -> sensitivity to “lows”

  selects for more dispersal

- Environments are spatially heterogeneous

  dispersing allows for different habitats among siblings

  dispersal bias from good to bad habitats

  selects for less dispersal

Selection (on dispersal)

- Directional selection (= not at equilibrium)
- Stabilizing selection (= ESS)
- Disruptive selection (= branching point)

Questions / Outline

1. What is the effect of heterogeneity of population densities on the evolution of dispersal?

2. What is the effect of temporal changes in patch quality on the evolution of dispersal?

Common theme:

conditions of disruptive selection

Adaptive dynamics

Assumptions:

- phenotypic gambit

"The phenotypic gambit is to examine the evolutionary basis of a character as if the very simplest genetic system controlled it: as if there were a haploid locus at which each distinct strategy was represented by a distinct allele, as if the payoff rule gave the number of offspring for each allele, and as if enough mutation occurred to allow each strategy the chance to invade."

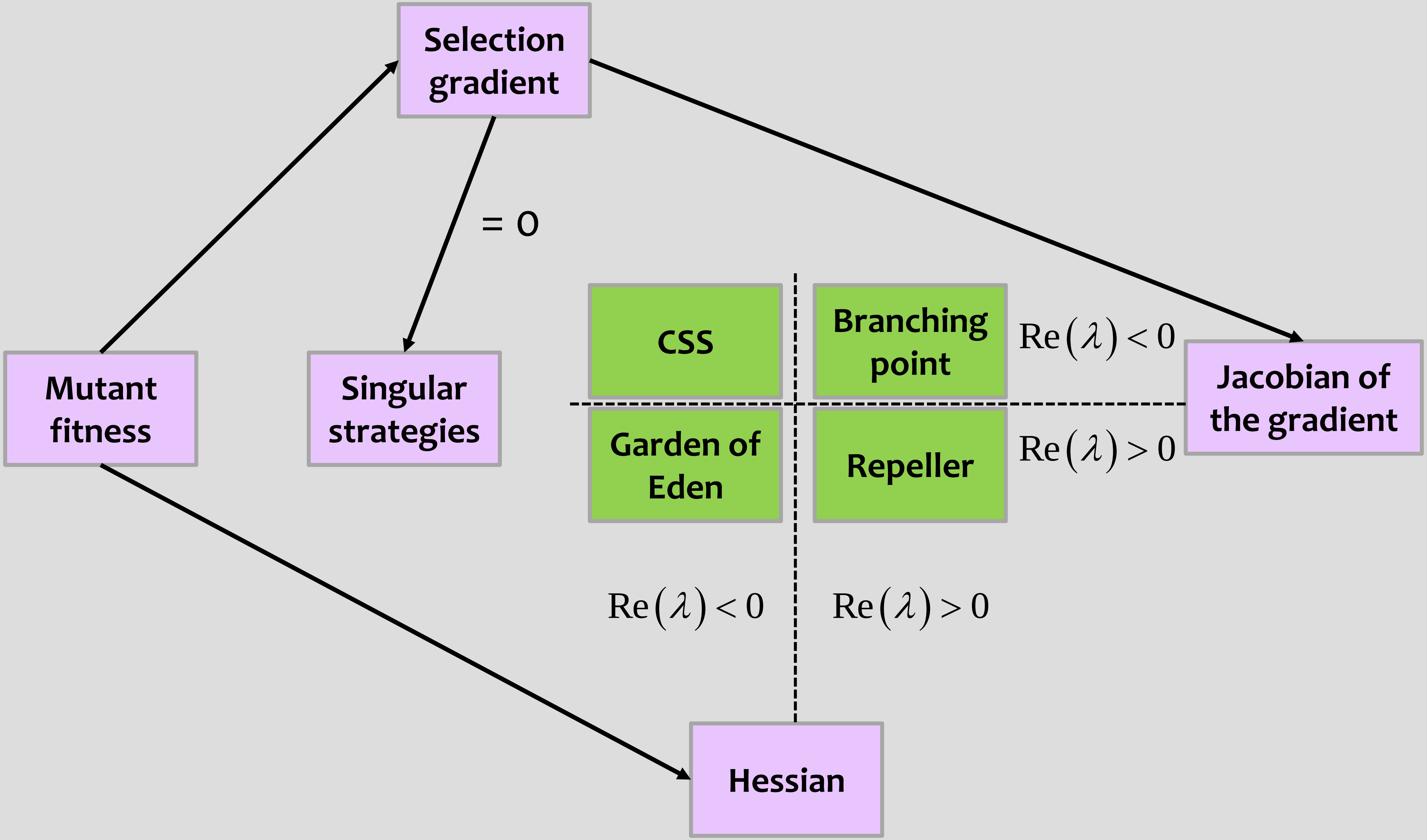
A. Grafen, *in* Krebs & Davies 1984

- rare mutations of small effects

Tools:

- expression for fitness (using matrices)
- selection gradient → convergence stability
- Hessian of mutant fitness → evolutionary stability

Methodology



ASYMMETRIC PATCH SIZE DISTRIBUTION LEADS TO DISRUPTIVE SELECTION ON DISPERSAL

François Massol[1,2,3,4,5], Anne Duputié[1,2,6], Patrice David[1,7], and Philippe Jarne[1,8]

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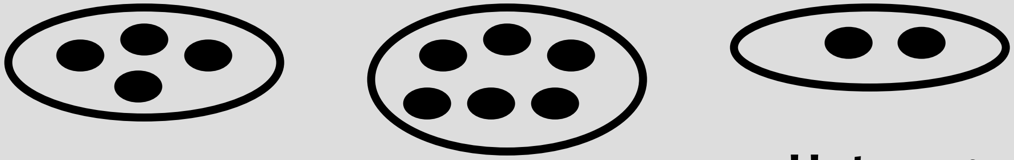
[4]*Centre Alpin de Recherche sur les Réseaux Trophiques des Écosystèmes Limniques (INRA), 75, avenue de Corzent-BP 511, 74203 Thonon-les-Bains Cedex, France*

DISPERSAL AMONG POPULATIONS OF DIFFERENT DENSITY

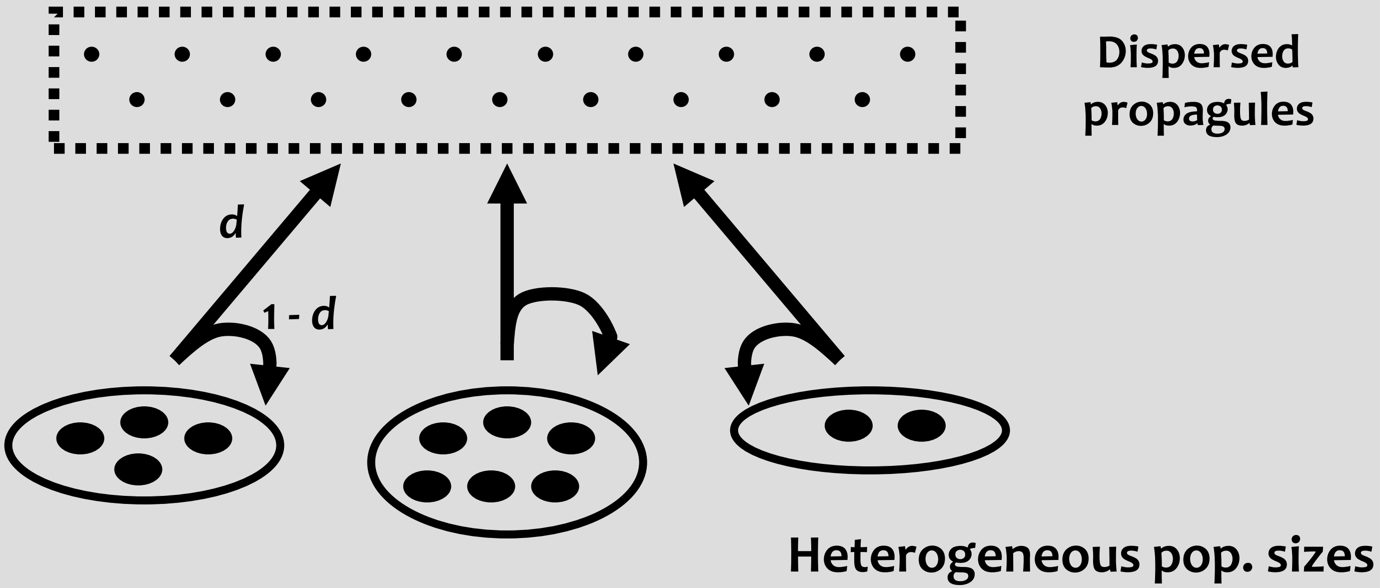
Massol *et al.* 2011 *Evolution*

A metapopulation model



Heterogeneous pop. sizes

A metapopulation model



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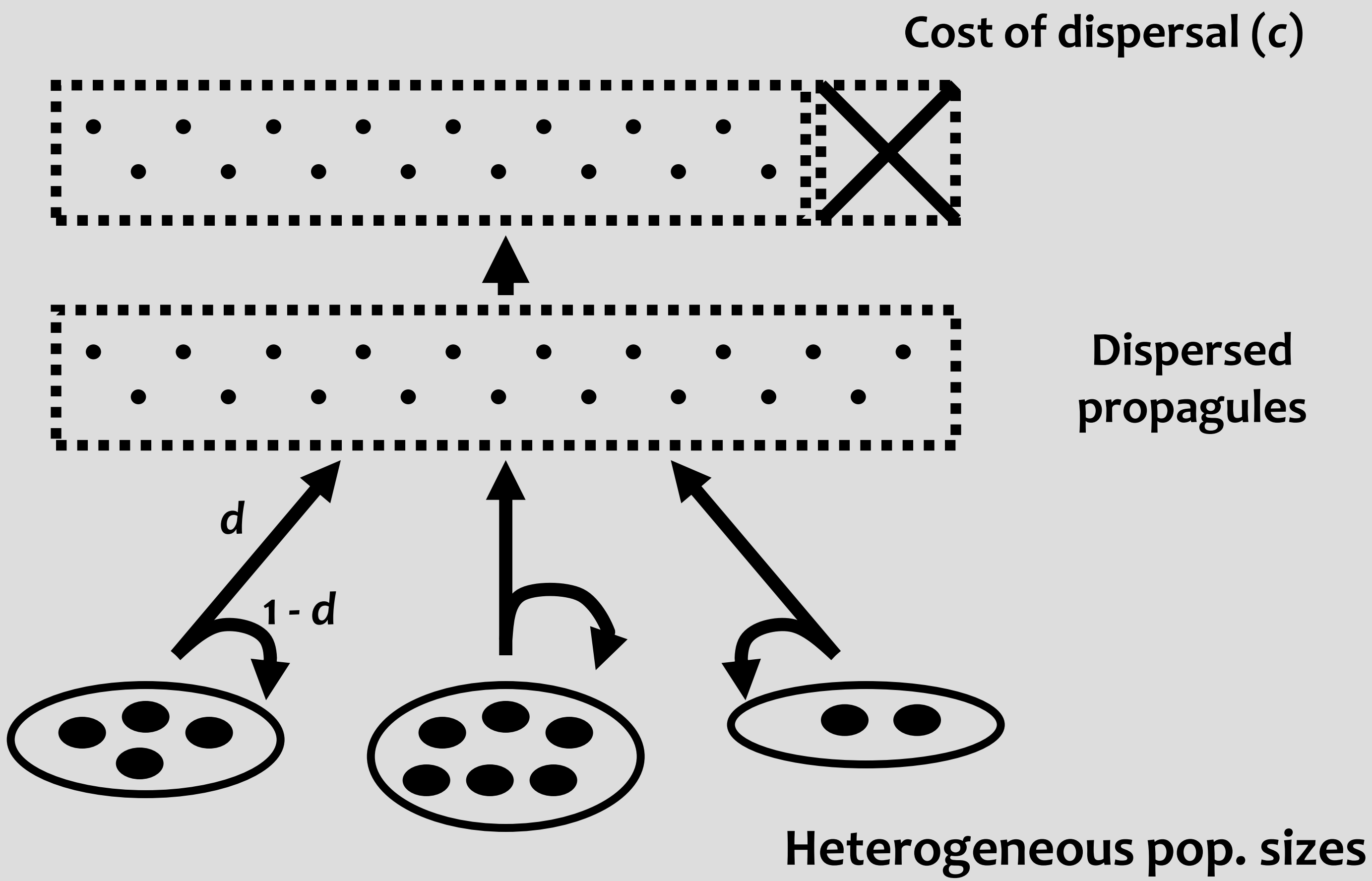

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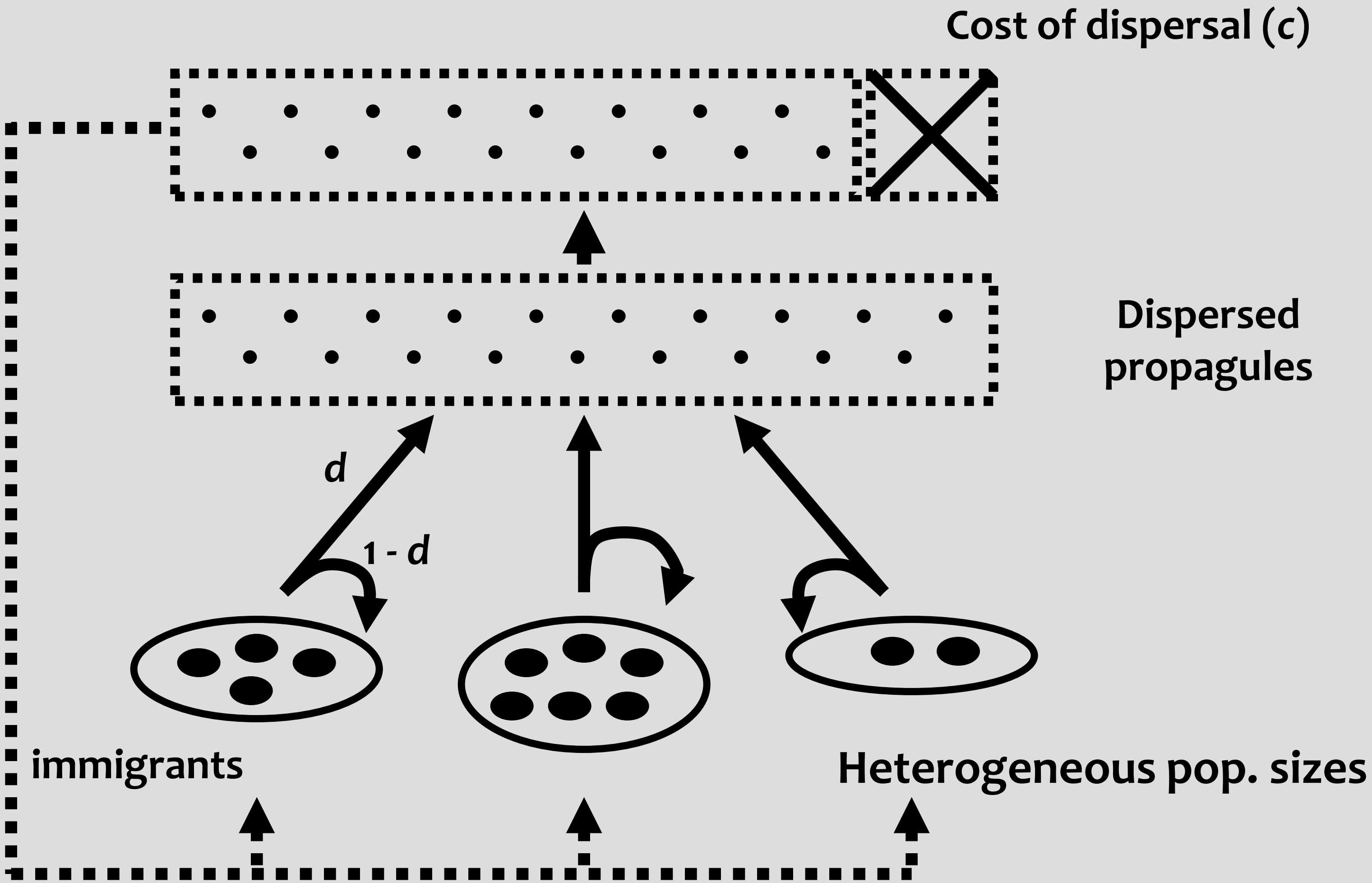
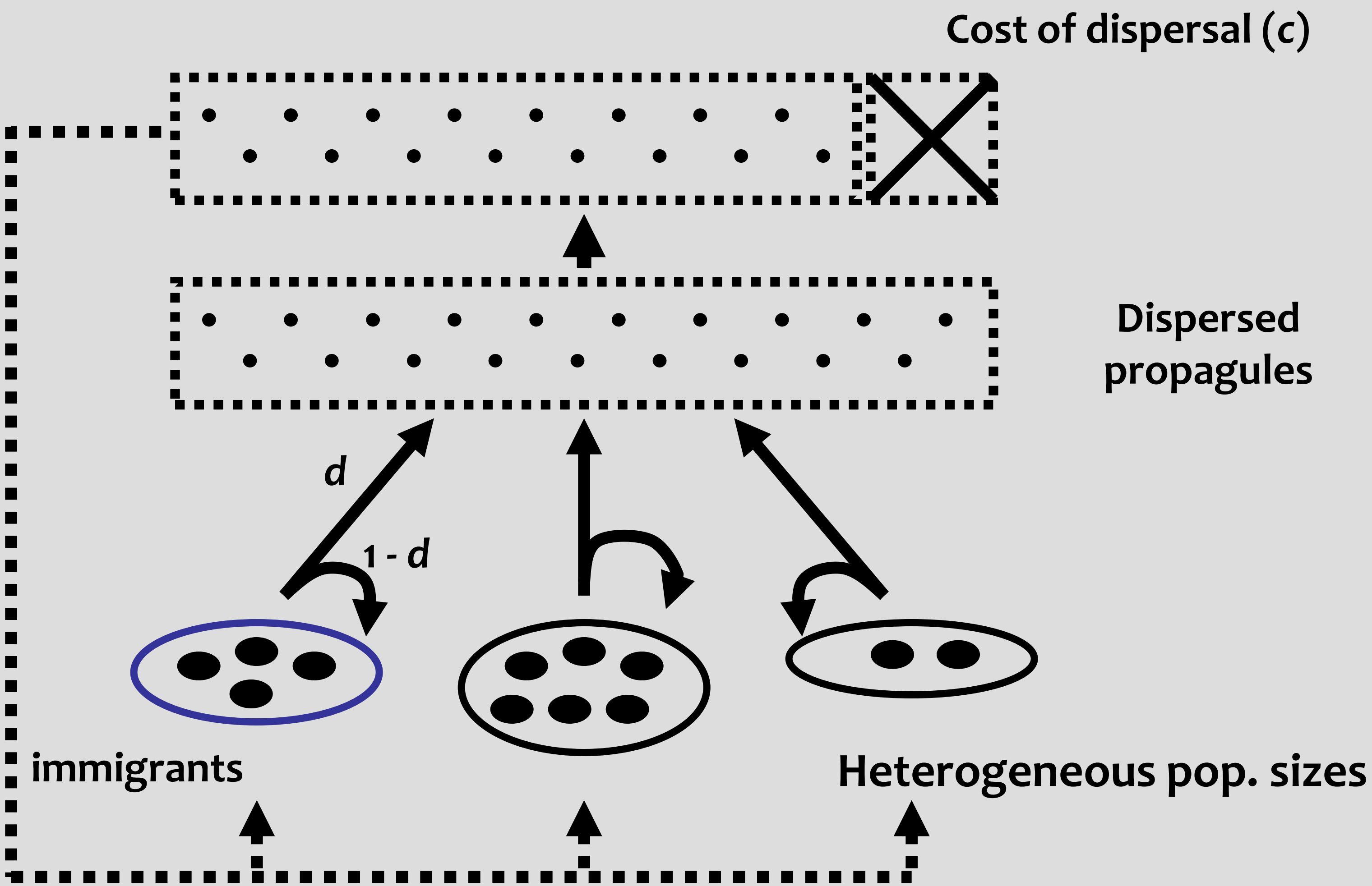


Births and Deaths



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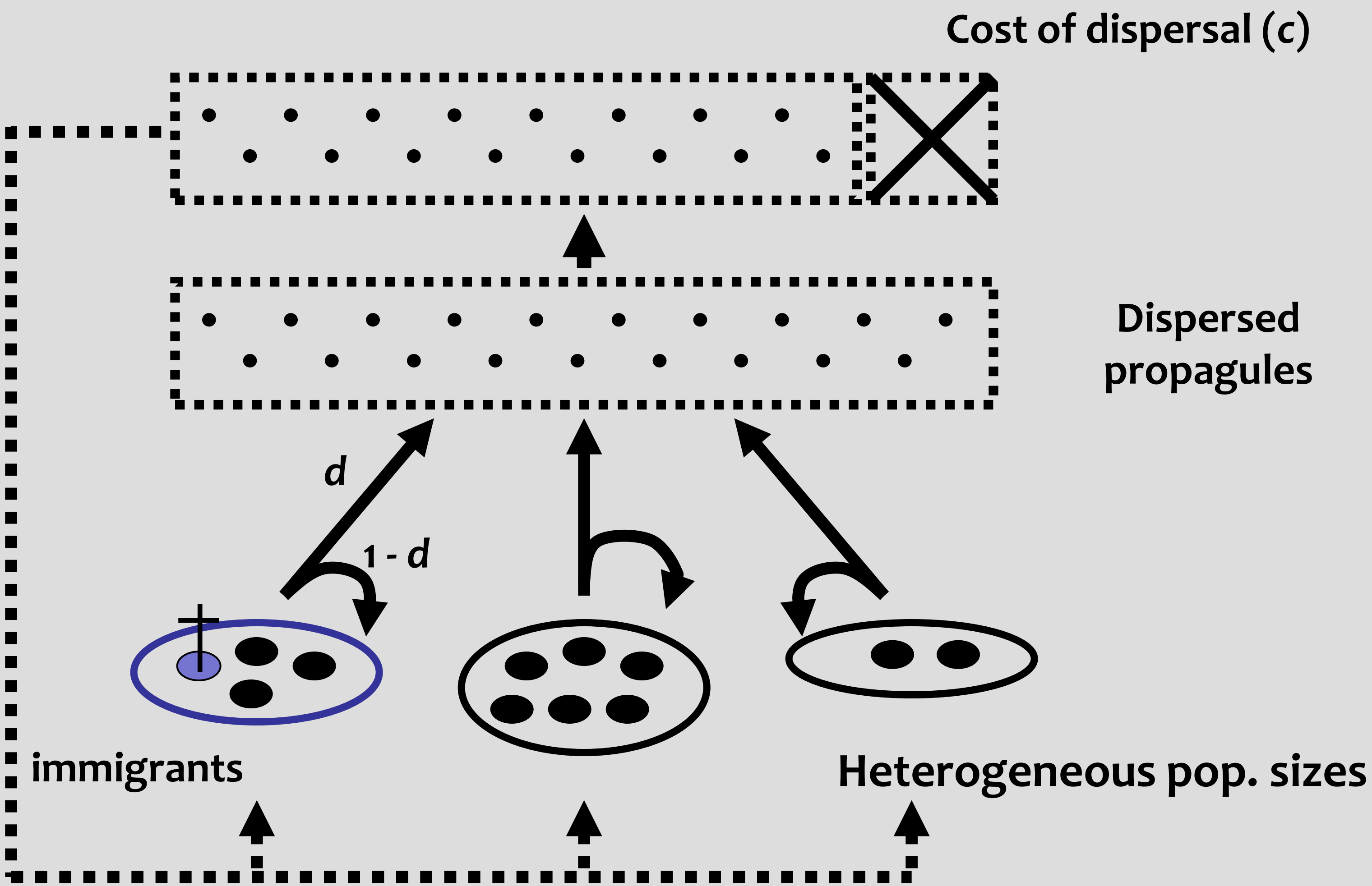

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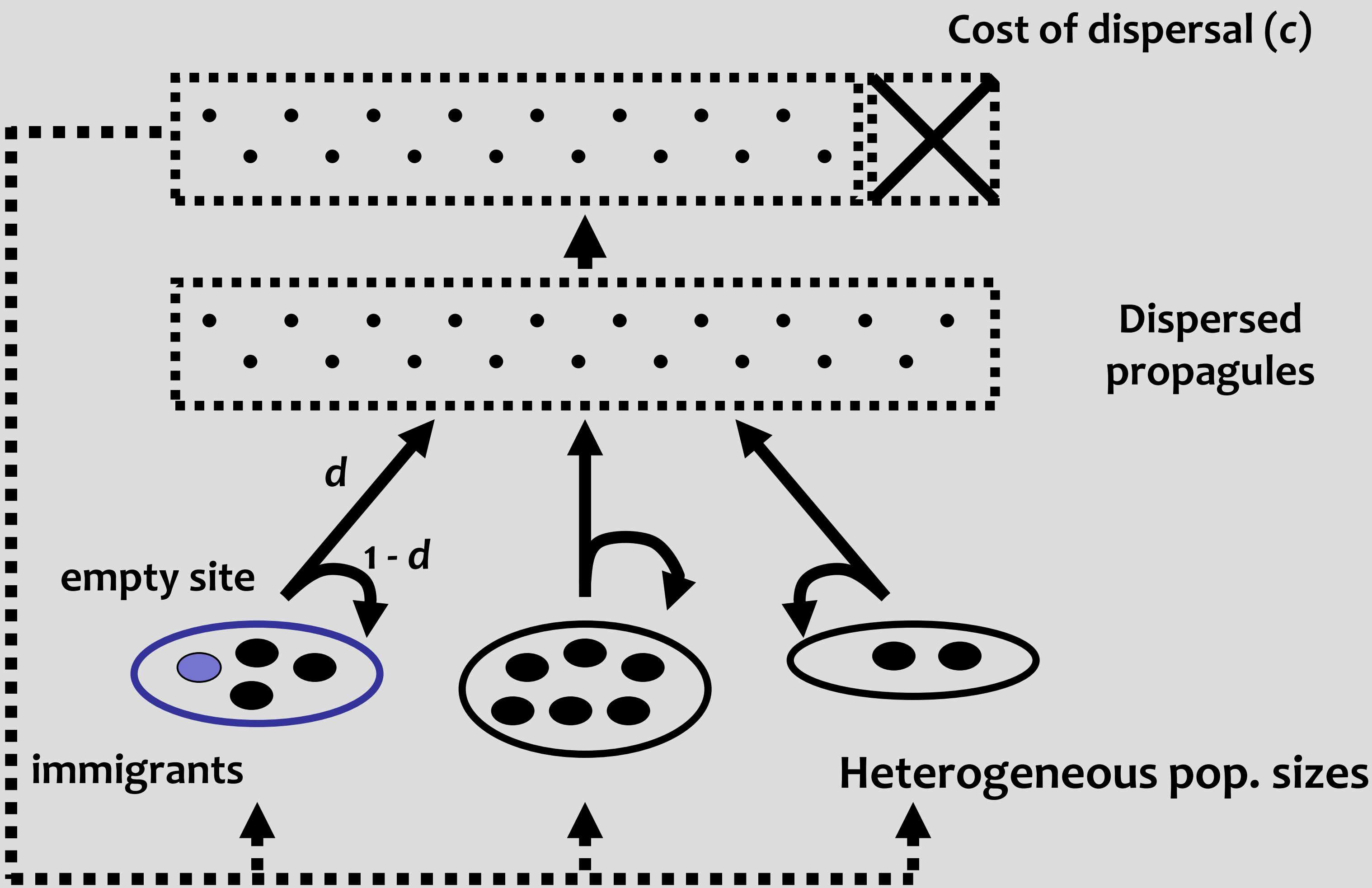

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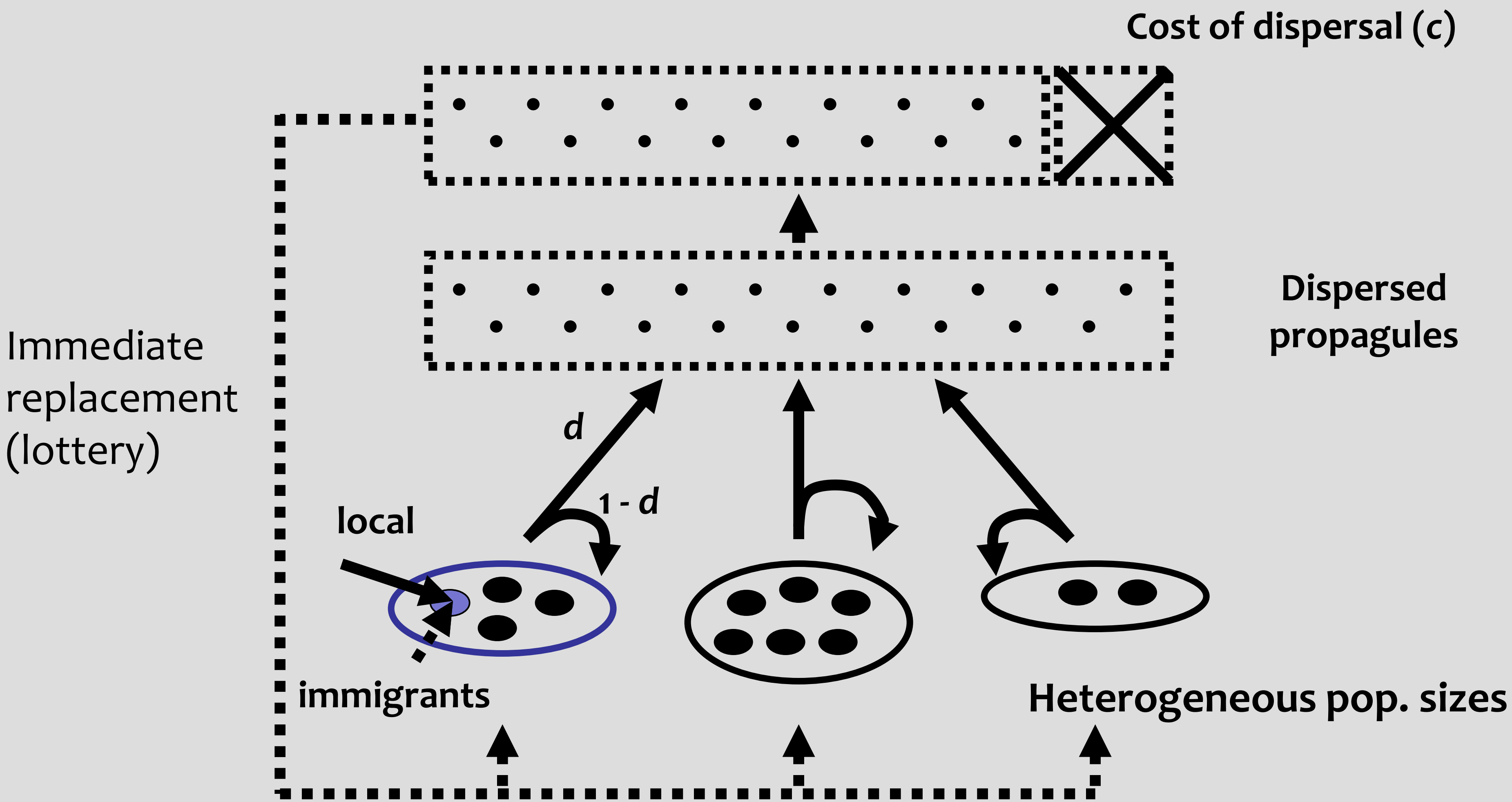


Methods

- 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

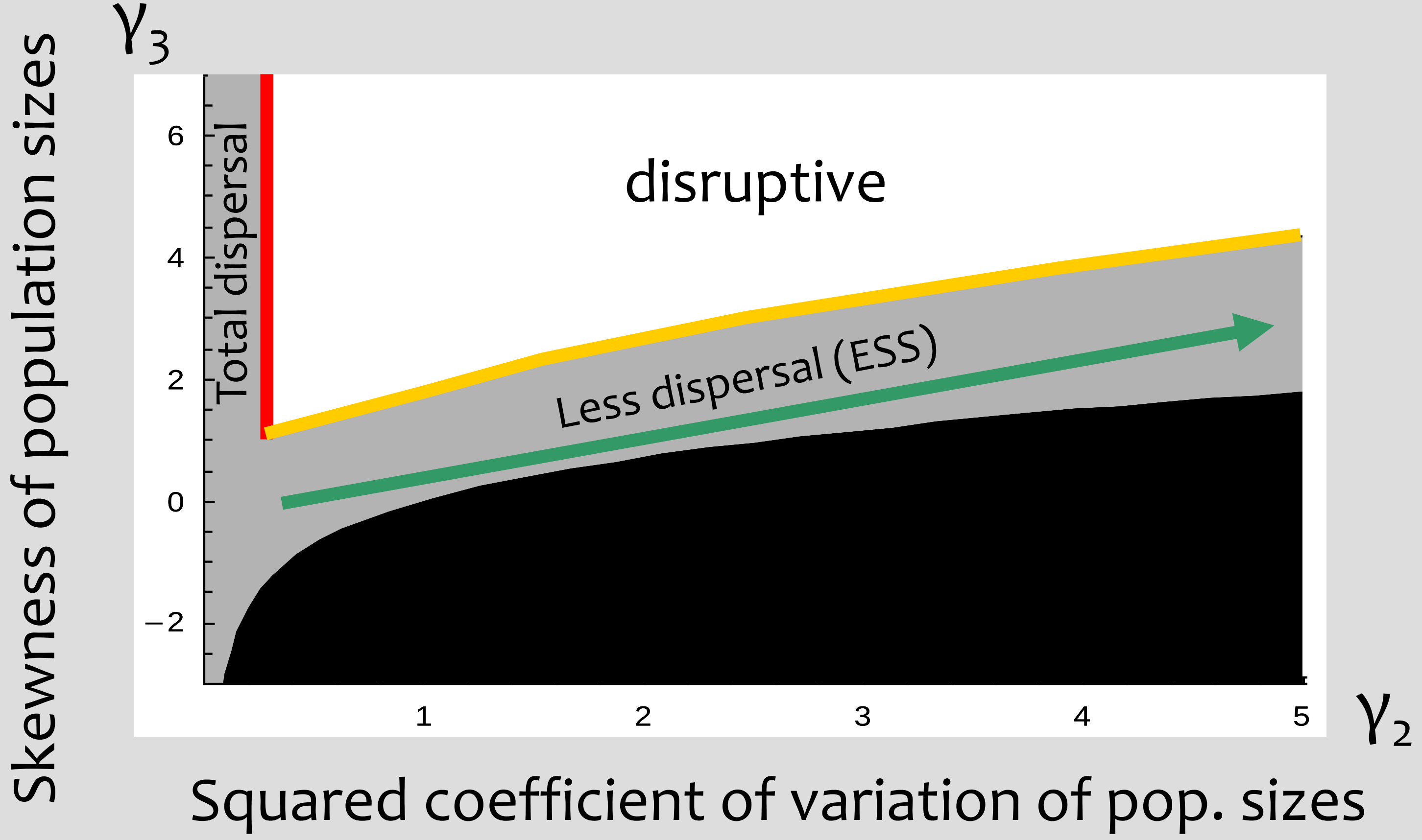
$$d^* = \mathrm{Min}\left[\frac{1}{(c+\gamma_2)\bar{K}}, 1\right]$$

Cost of dispersal

Heterogeneity **Kin competition**

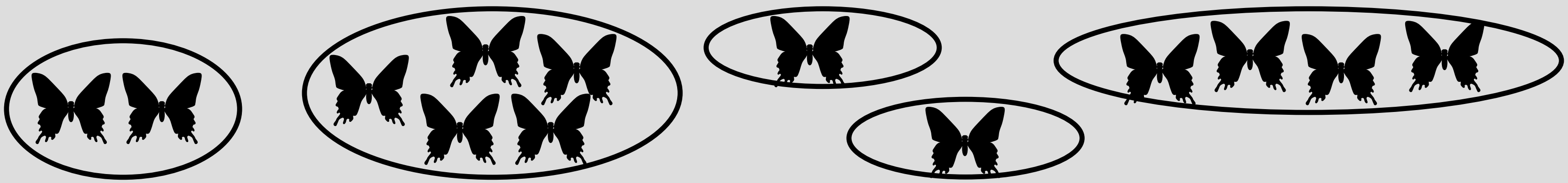
Results: evolutionary outcomes

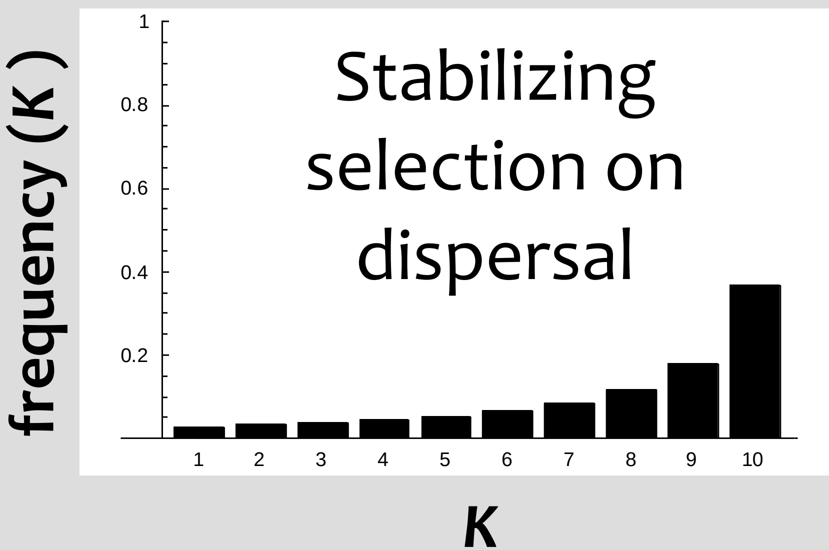
$$\gamma_3 > 2\gamma_2^{1/2} + \frac{c\bar{K}-1}{\bar{K}}\gamma_2^{-1/2} + \frac{c\left(\bar{K}-1\right)}{\bar{K}}\gamma_2^{-3/2}$$

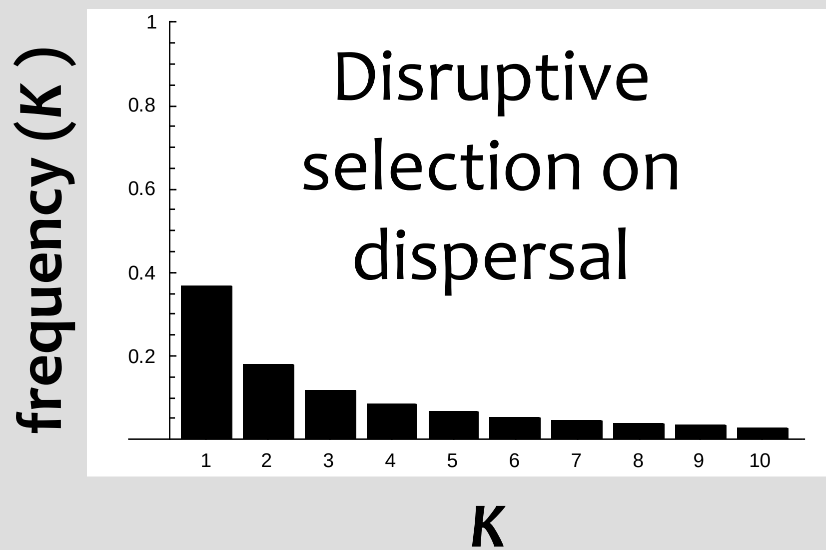


Results: predicting polymorphism

Interpretation:

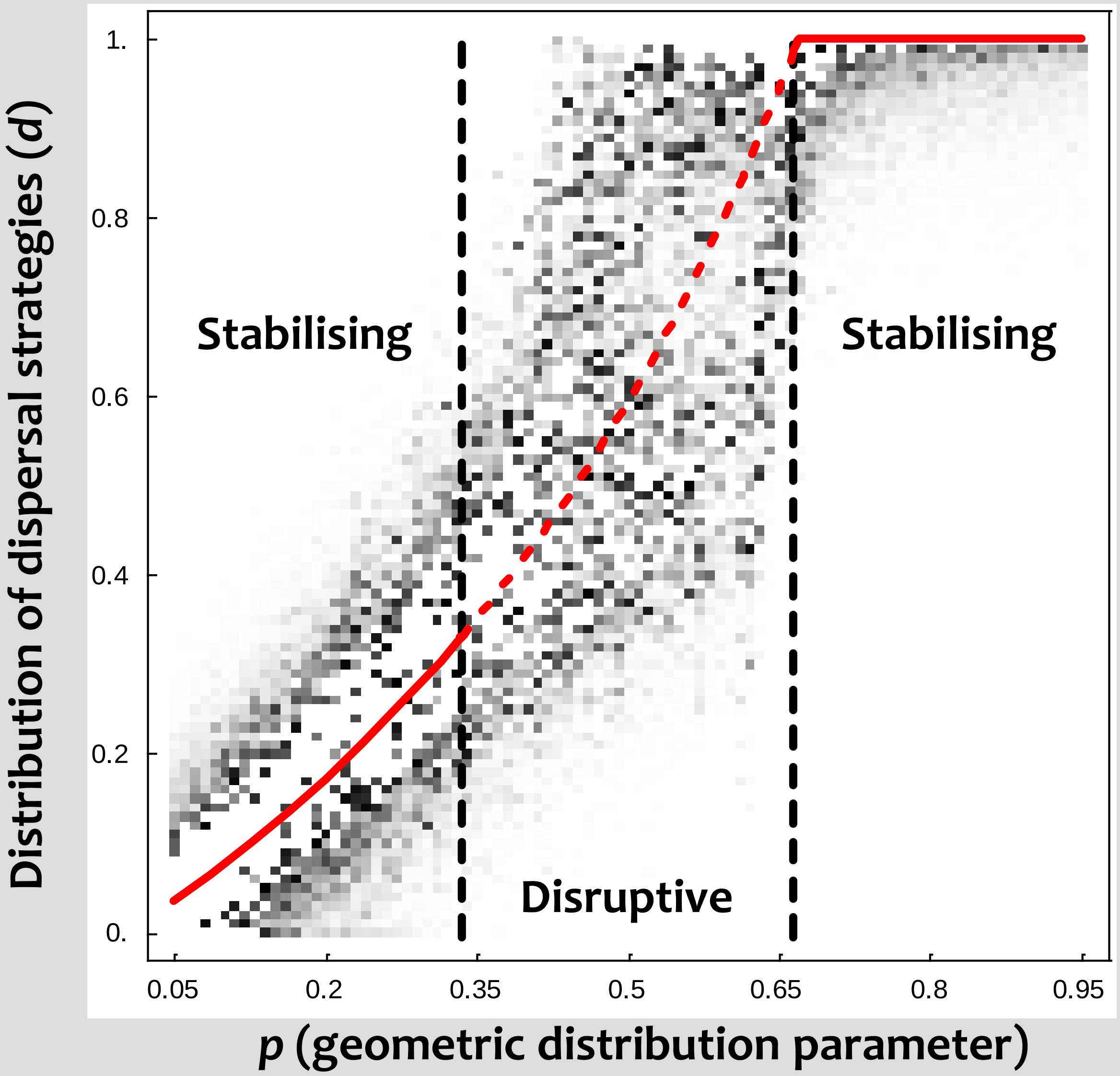






Results: simulations

without demographic stochasticity



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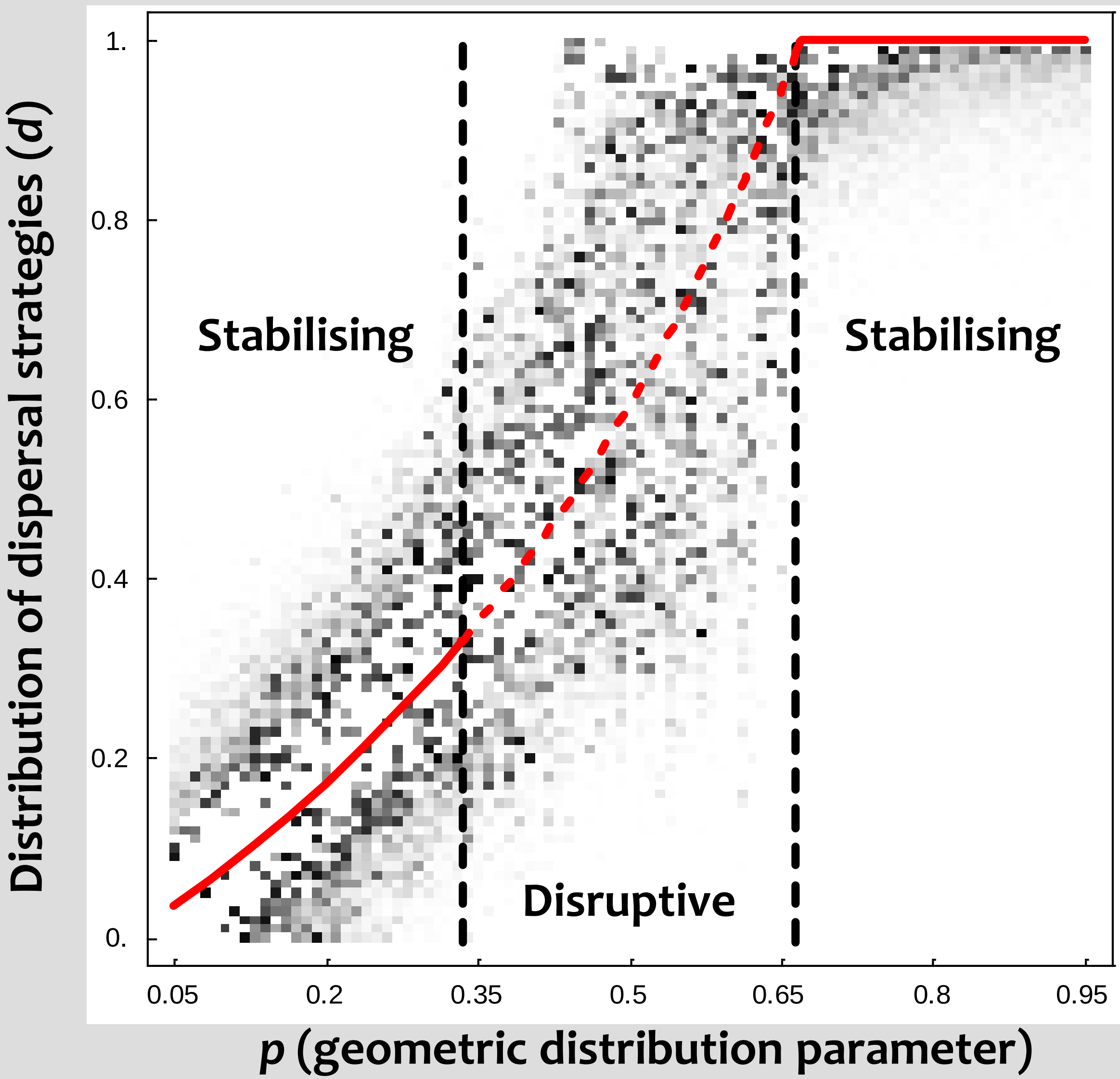

Results: what do data say?

Understanding what nature says

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

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

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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

doi:10.1111/evo.12699

Evolution of dispersal in spatially and temporally variable environments: The importance of life cycles

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DISPERSAL AMONG PATCHES OF UNCERTAIN QUALITY

Massol (2013) *Ecological Complexity*, 16, 9-19

Massol & Débarre (2015) *Evolution*, 69, 1925-1937

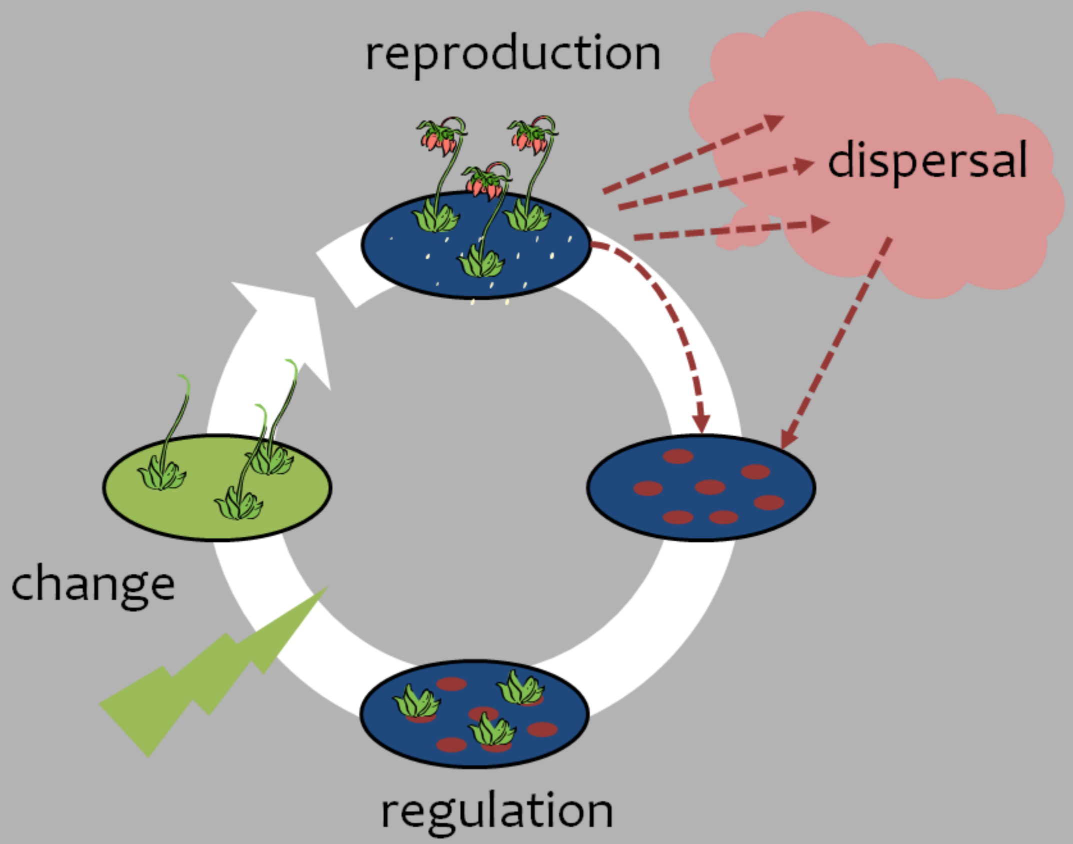
A general model

Massol (2013)

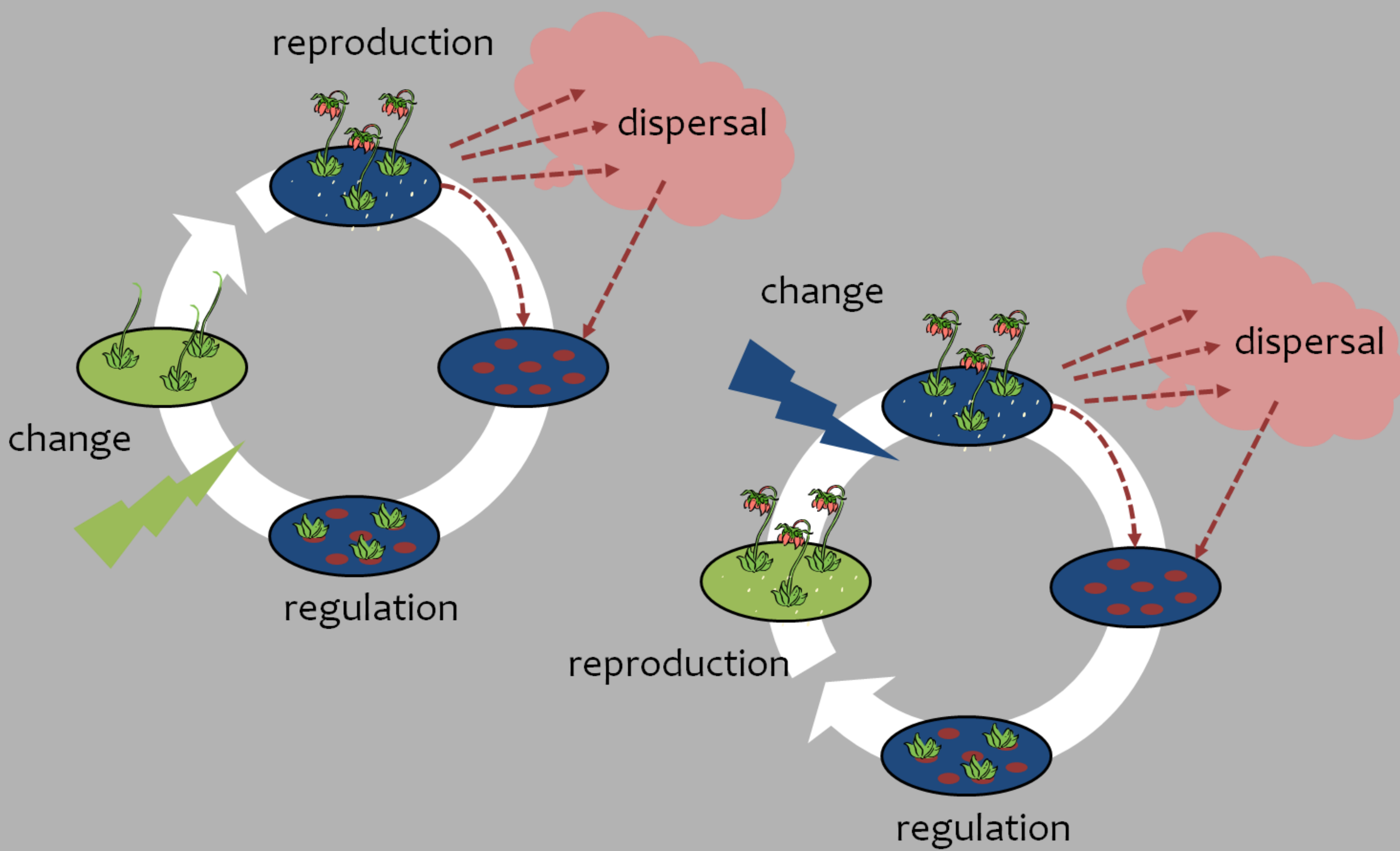
Ingredients:

- 2 patch types (1 & 2; affect fecundity through f_1 and f_2), infinity of patches
- 4 life cycle events: reproduction, dispersal, regulation & environmental change
- discrete, non-overlapping generations
- reproduction: result of local adaptation, not limiting
- regulation: local (but large populations)
- dispersal: global (no limitation by distance)

How does environmental state change?



How does environmental state change?



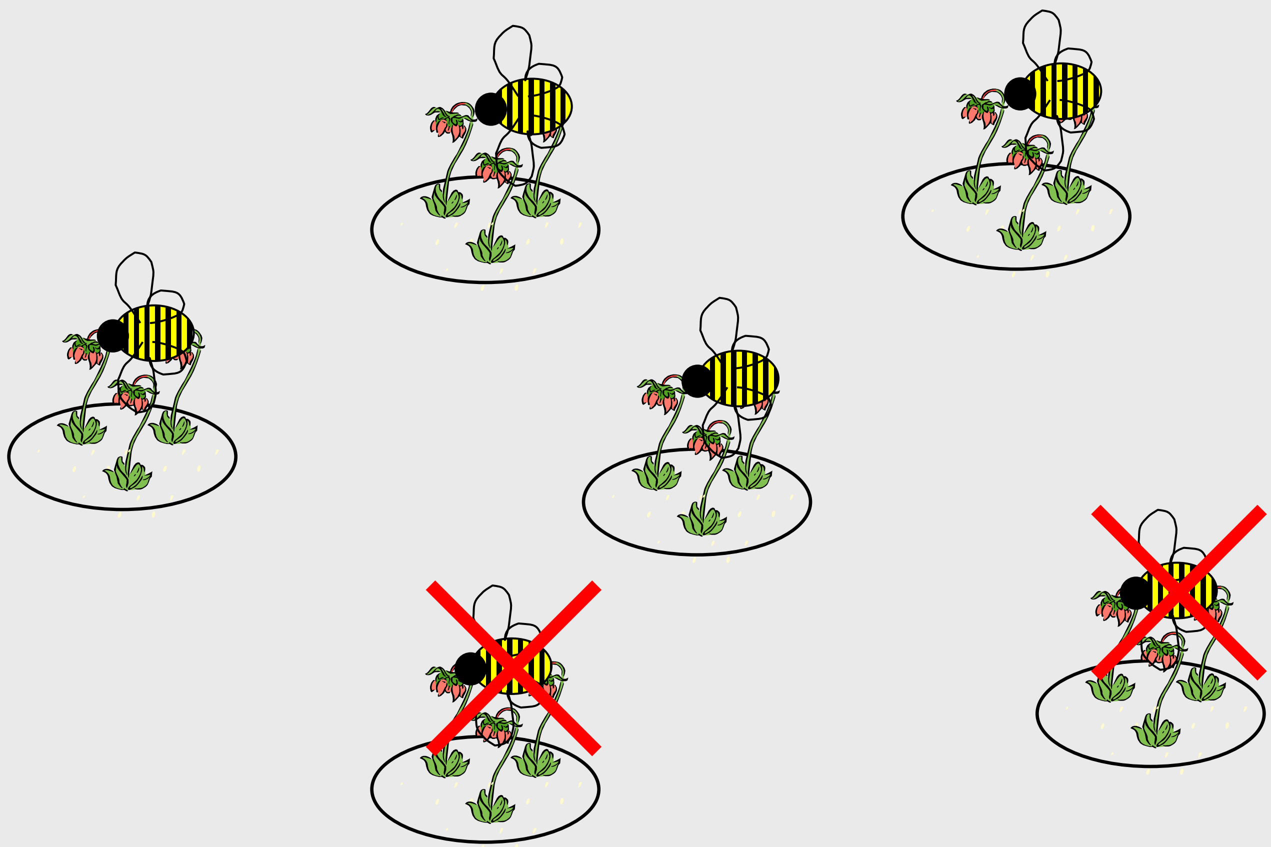
Life cycles

What if the order of events is different?

- selection gradient on dispersal rate may change direction when reproduction, dispersal and regulation happen in a different order (Johst & Brandl 1997)
- the order of reproduction, dispersal and regulation directly impact the evolution of local adaptation traits (Ravigné *et al*. 2004)

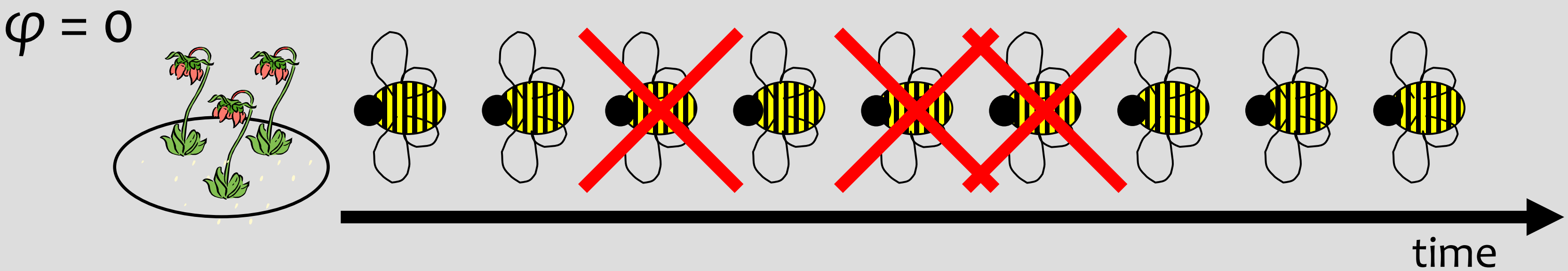
Measuring heterogeneity

First-order measure: proportion of type 1 patch, ρ



Measuring variability

temporal autocorrelation in patch state, φ



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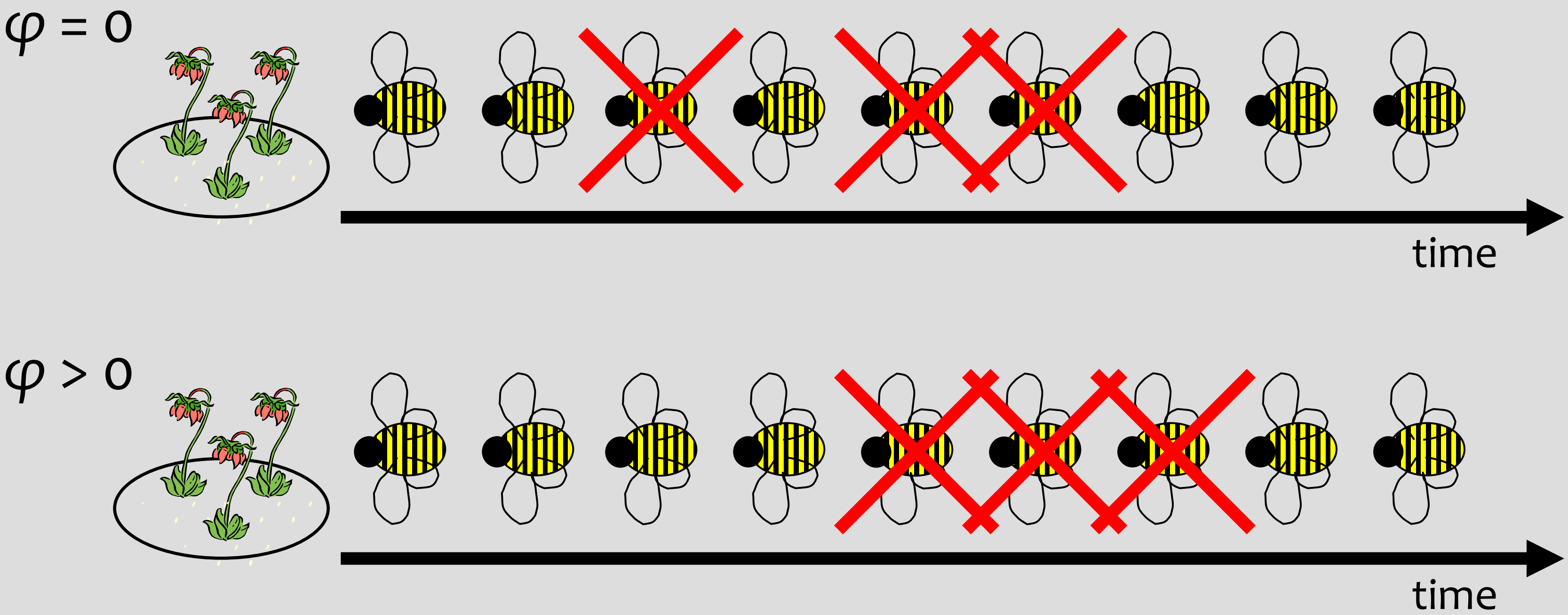

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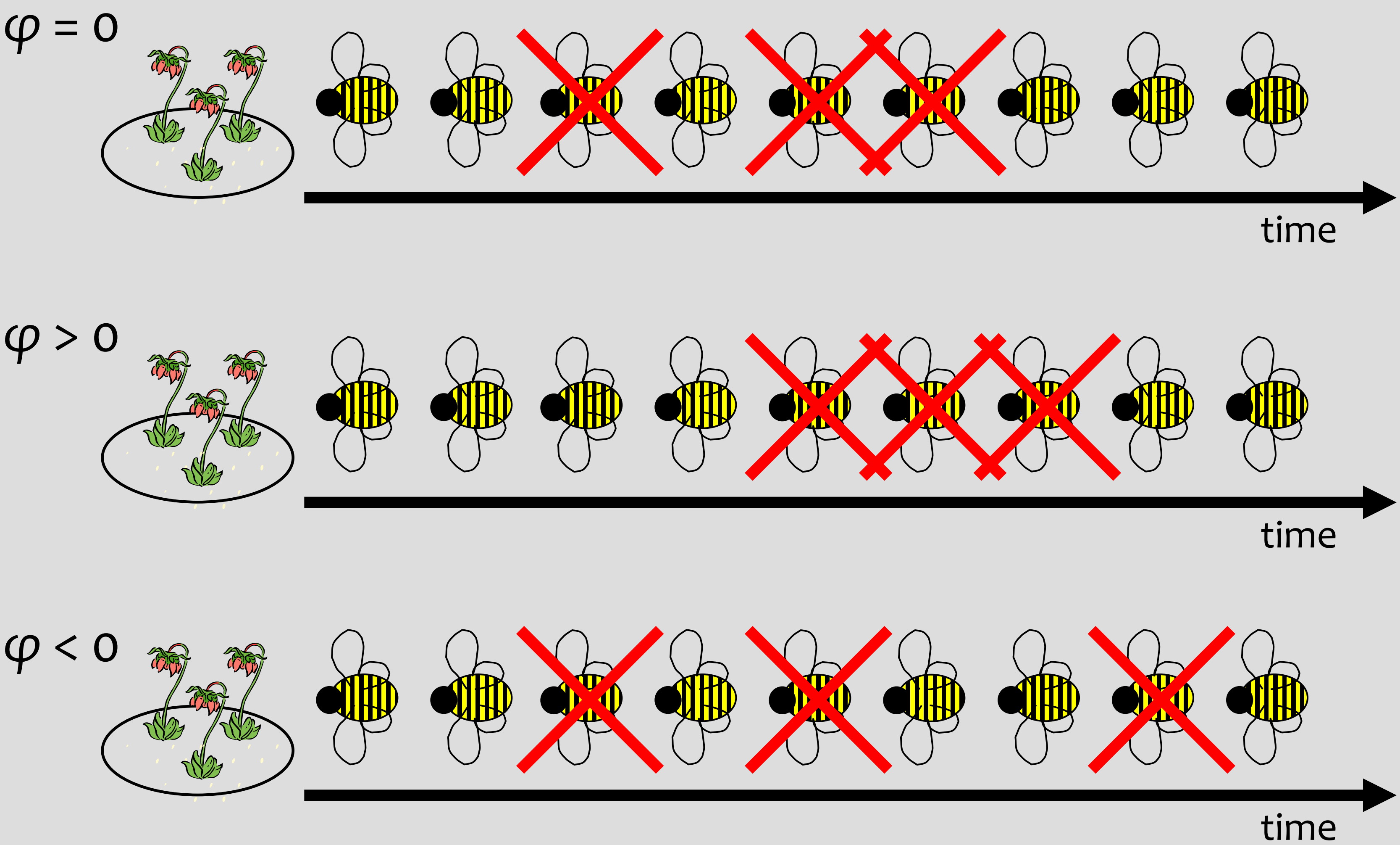


Heterogeneity and variability

Parameter reduction using

$$\beta = \frac{f_1 f_2}{\bar{f}^2}$$

~ comparison over two generations between dispersers and non-disperser lineages

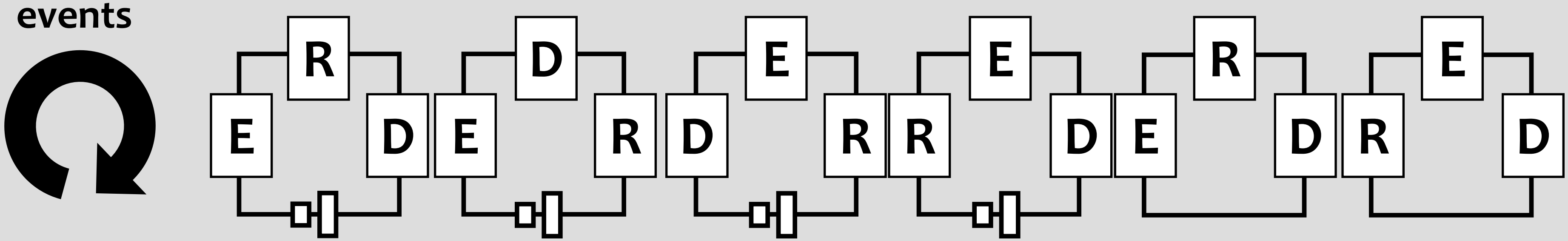
$$\gamma = \frac{\mathrm{var}[f]}{\bar{f}^2}$$

~ coefficient of variation of fecundity

Classification of life cycles

extended from Massol (2013)

Order of events



Ravigné *et al.*'s classification	***Ravigné type 3***	***Levene soft selection regime***	***Ravigné type 3***	***Dempster hard selection regime***
Modelling complexity	***Simple life cycles***	***Complex life cycles***		***Simple life cycles***

Fitness = obtained as eigenvalue of a next-generation matrix

Next-generation matrix = (non-commutative) product of event matrices

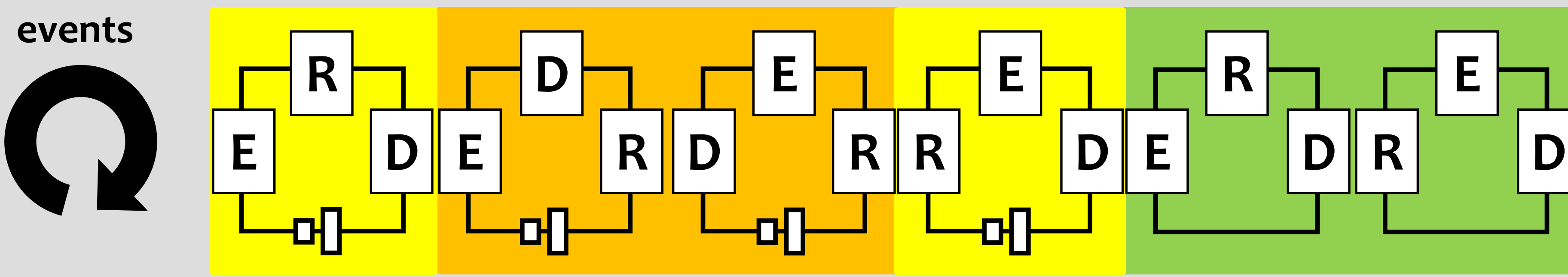
Cycle E,R,D,Regulation $\Rightarrow$ matrix Regulation.D.R.E

Classification of life cycles

extended from Massol (2013)

When dispersal is unconditional

Order of events



Ravigné *et al.*'s classification	*Ravigné type 3*	*Levene soft selection regime*	*Ravigné type 3*	*Dempster hard selection regime*

Classes of equivalence for fitness correspond to Ravigné *et al.*'s

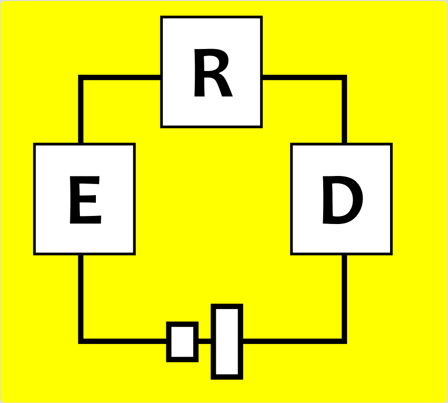
To the really interested audience:

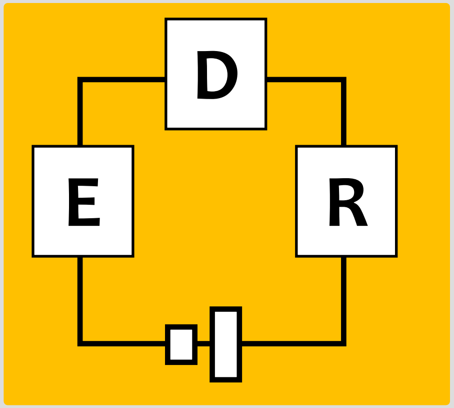
- **E** always commutes with regulation.
- With unconditional dispersal, **E** also commutes with dispersal.

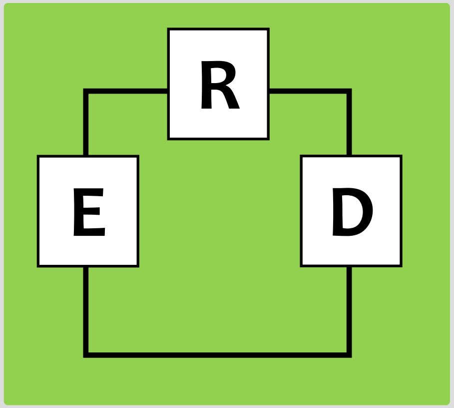
Evolution of dispersal

Massol & Débarre (2015)

Order of events







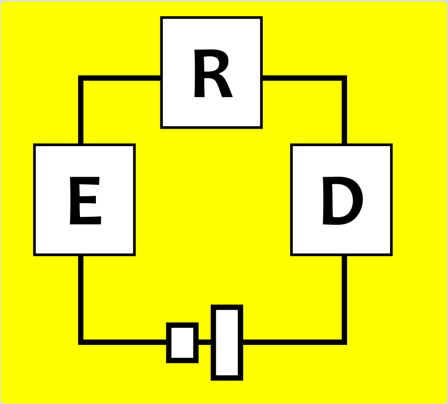
Ravigné *et al.*'s classification

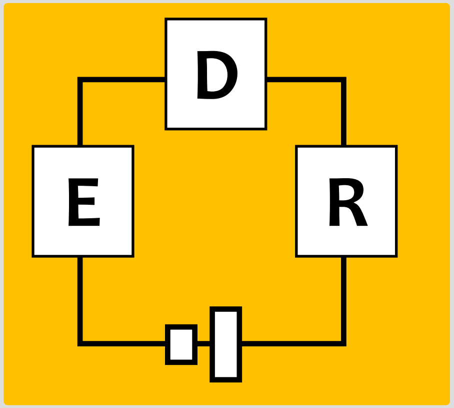
Ravigné	*Levene*	*Dempster*

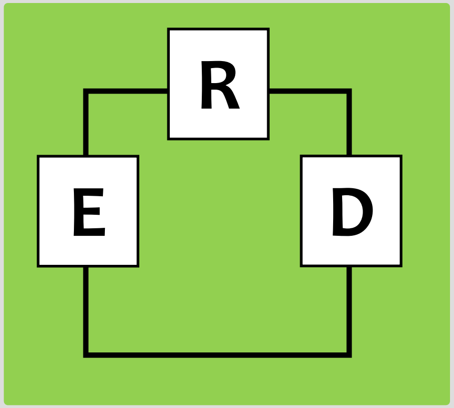
Evolution of dispersal

Massol & Débarre (2015)

Order of events







Ravigné *et al.*'s classification

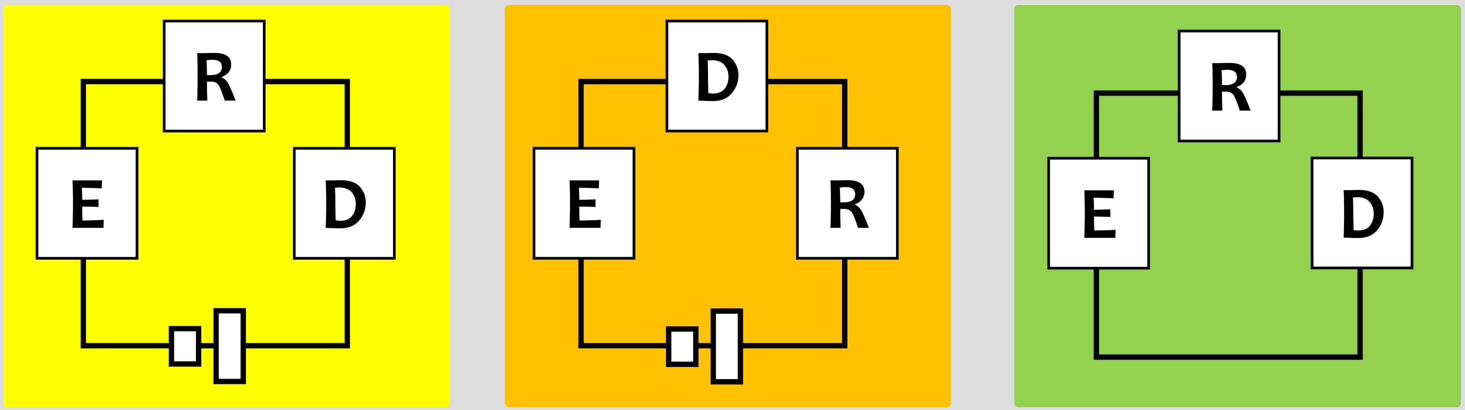
Ravigné	*Levene*	*Dempster*

evolution towards philopatry

Evolution of dispersal

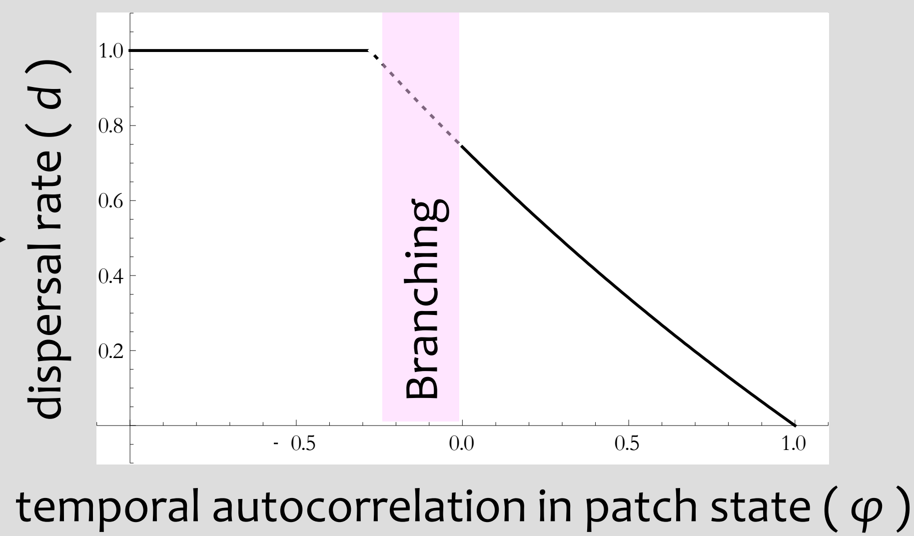
Massol & Débarre (2015)

Order of events



Ravigné *et al.*'s classification

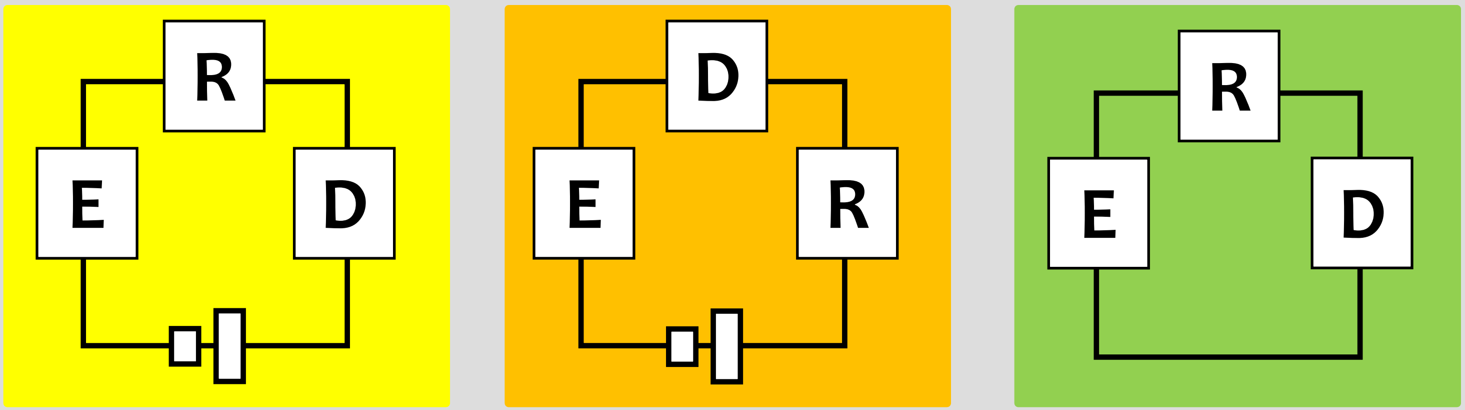
Ravigné	*Levene*	*Dempster*



Evolution of dispersal

Massol & Débarre (2015)

Order of events



Ravigné *et al.*'s classification

Ravigné	***Levene***	***Dempster***

Zero dispersal when $c > \dfrac{\gamma}{\gamma + \beta}$

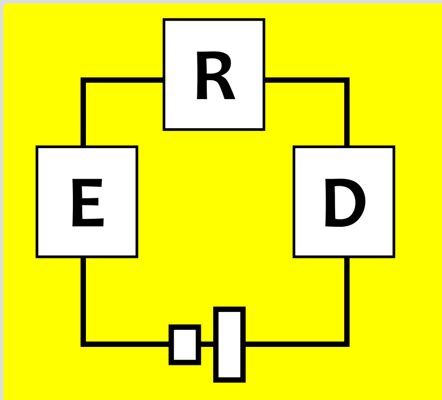
Total dispersal when $c < -\varphi\gamma$

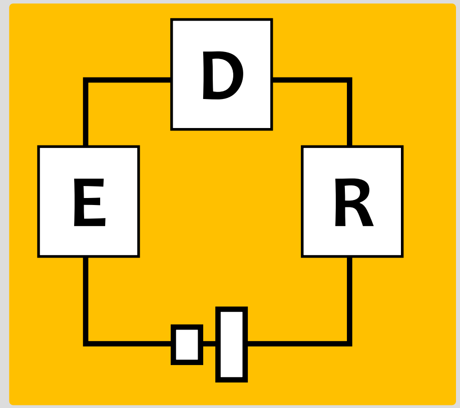
Branching when $\varphi < 0$

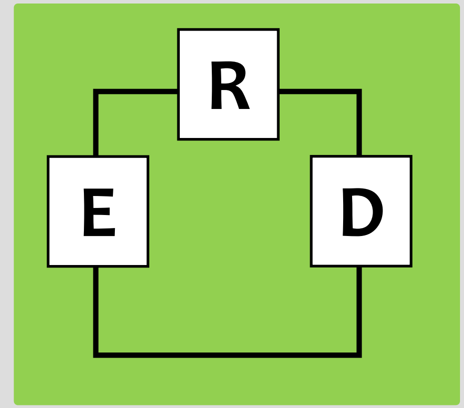
Evolution of dispersal

Massol & Débarre (2015)

Order of events





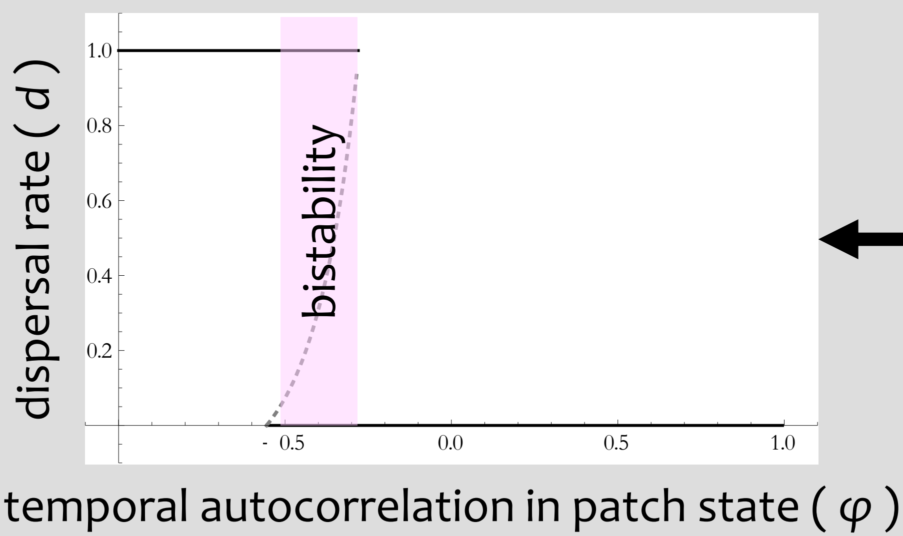


Ravigné *et al.*'s classification

Ravigné

Levene

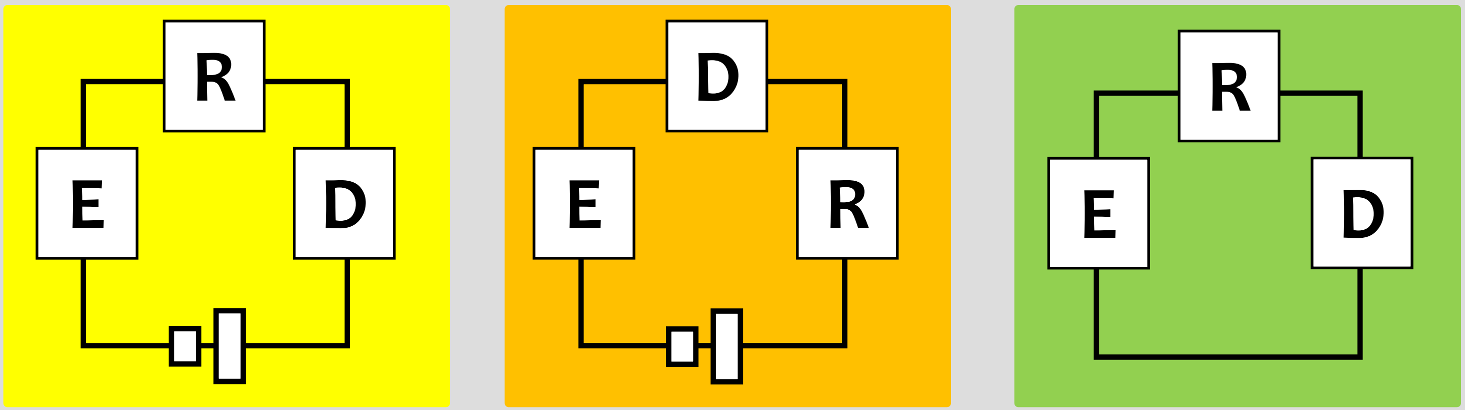
Dempster



Evolution of dispersal

Massol & Débarre (2015)

Order of events



Ravigné *et al.*'s classification | *Ravigné* | *Levene* | *Dempster*

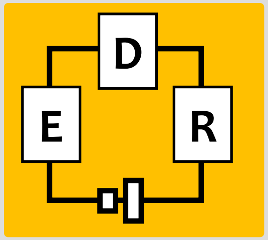
Zero dispersal when

$$c > -\frac{\left[(\beta+\gamma)\varphi-1\right]^2}{2\gamma}\left[\frac{1}{\varphi}+\sqrt{\frac{1}{\varphi^2}\left[1+\frac{4\varphi\gamma}{\left[(\beta+\gamma)\varphi-1\right]^2}\right]}\right]-1$$

Total dispersal when $c < -\varphi\gamma$

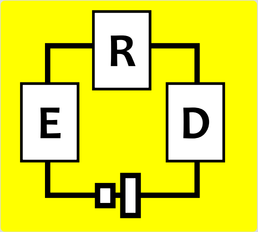
Conclusions

Massol & Débarre (2015)



Levene

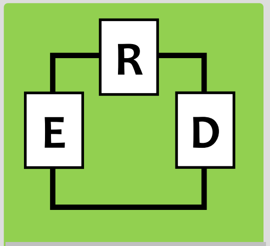
Evolution towards total philopatry



Ravigné

Intermediate dispersal rates are possible

Branching happens for negatively autocorrelated environments



Dempster

Either total philopatry or total dispersal

Bistability can happen

Final take-home messages

1. Environmental variability can affect the evolution of dispersal in a variety of ways, depending on what is variable, in time or in space

2. Disruptive selection on dispersal can happen when population densities are skewed or when juveniles disperse and patch quality is negatively autocorrelated in time

Perspectives

- Model 1: incorporating different types of cost; evolution of cost (mother vs. offspring)
- Merging both models (i.e. spatial variation in patch quality and population size)
- Model 2: evolution of conditional dispersal under different life cycles

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Ongoing collaborations

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Past students on the evolution of dispersal

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And also

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The "evolution of dispersal" workshop @ T. Hovestadt's lab