



DISPERSAL

Ophélie Ronce





EVOLUTION OF DISPERSAL

Review

A REVIEW WITH A COOL TITLE

How Does It Feel to Be
Like a Rolling Stone?
Ten Questions About
Dispersal Evolution

Ophélie Ronce

Annu. Rev. Ecol. Evol. Syst. 2007. 38:231–53

Ten years later...

What happened
since then?

Bob Dylan won a Nobel Prize!

1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?

Dispersal = Any movement of individuals or propagules with potential consequences for gene flow across space

Natal dispersal, breeding dispersal

Other types of movement: foraging, seasonal migration

1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?

Three stages of dispersal



DEPARTURE

TRANSIENCE

SETTLEMENT

1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?



Metatron
(Station for Theoretical and Experimental Ecology,
Moulis, France)

Discrete patches

Philopatric vs dispersing individuals

Resident vs immigrant individuals

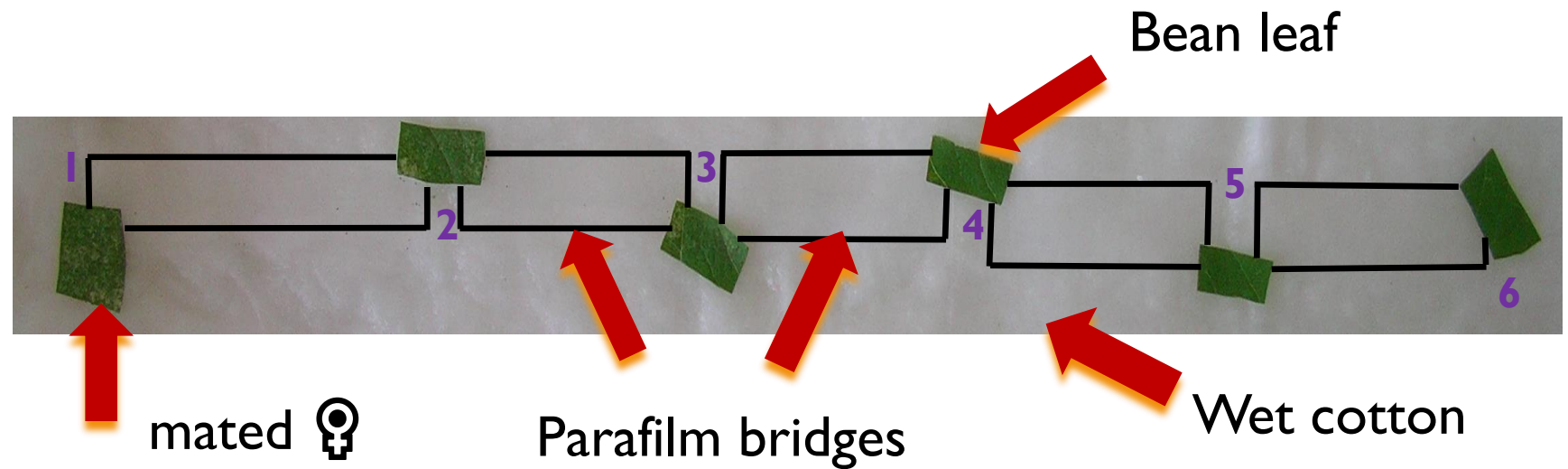
Dispersal/emigration rates

Legrand *et al.* 2012

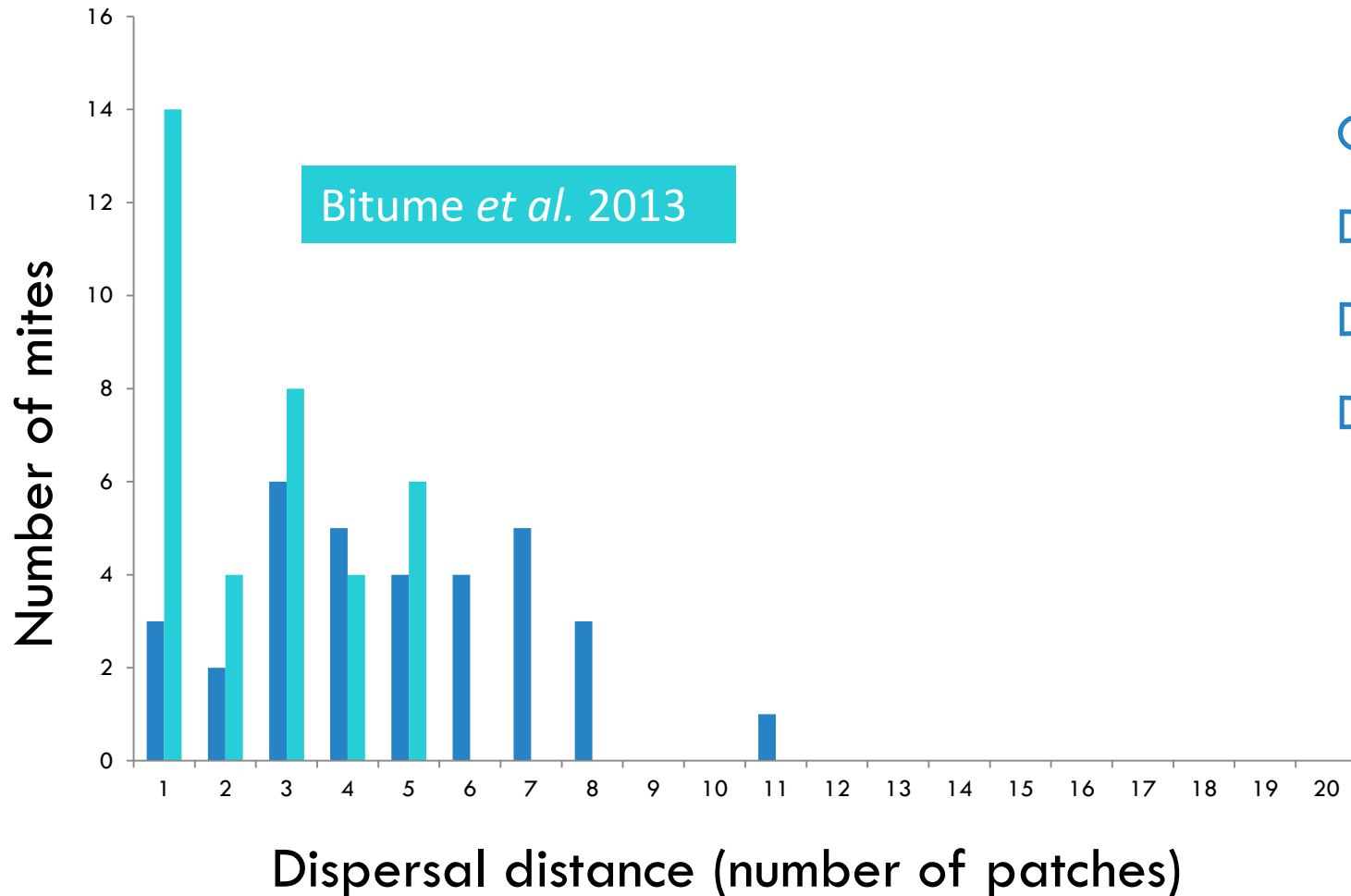
1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?

Dispersal assays in
Tetranychus urticae

Bitume *et al.* 2013



1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?



Continuous space

Dispersal distance

Dispersal kernels

Distribution moments: mean, kurtosis

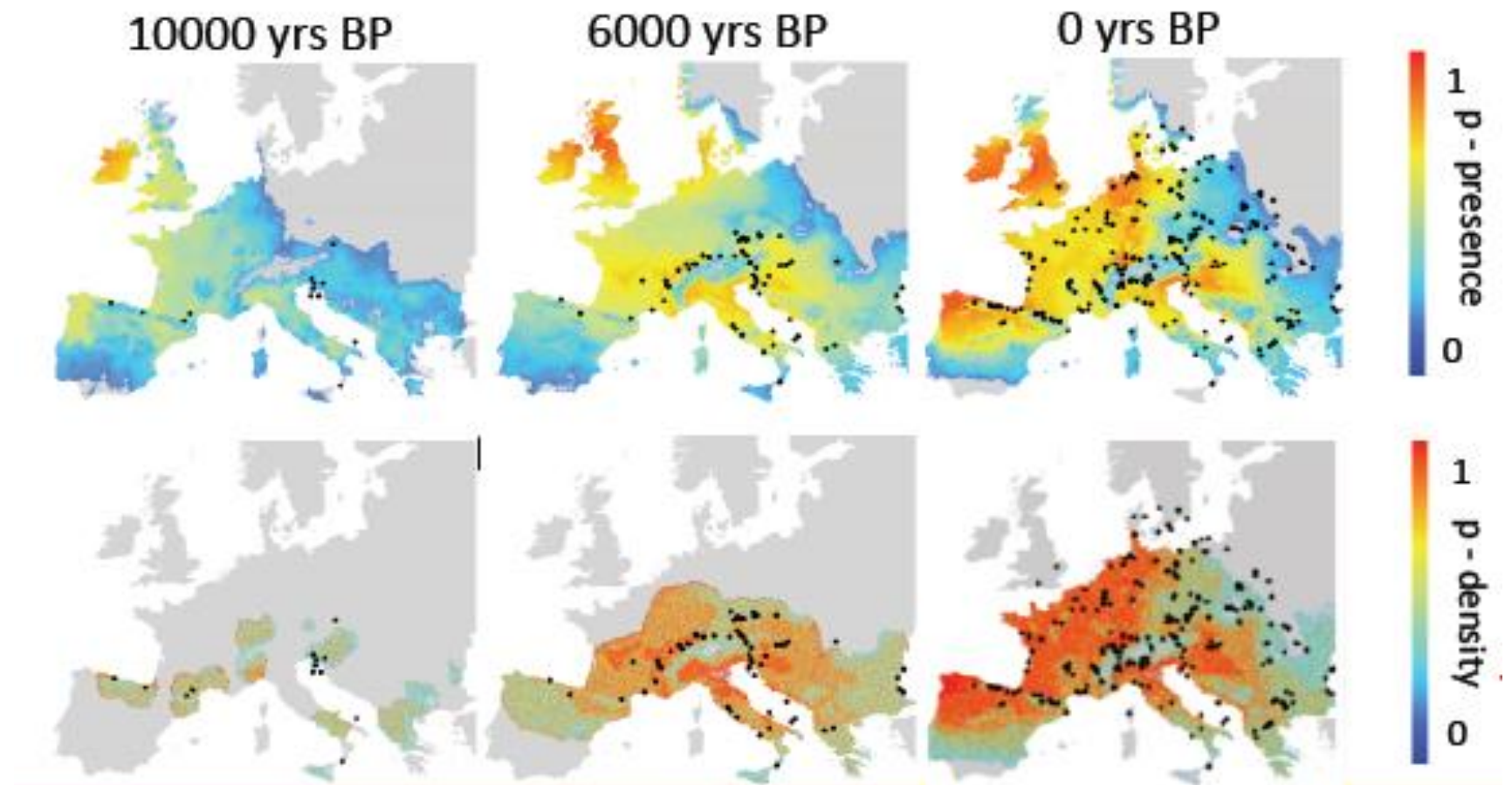
1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?

Saltré *et al.* 2013, 2015

Modelling recolonization of Europe by common Beech after last glaciation

Modelling climatic niche only

Modelling climatic niche and dispersal



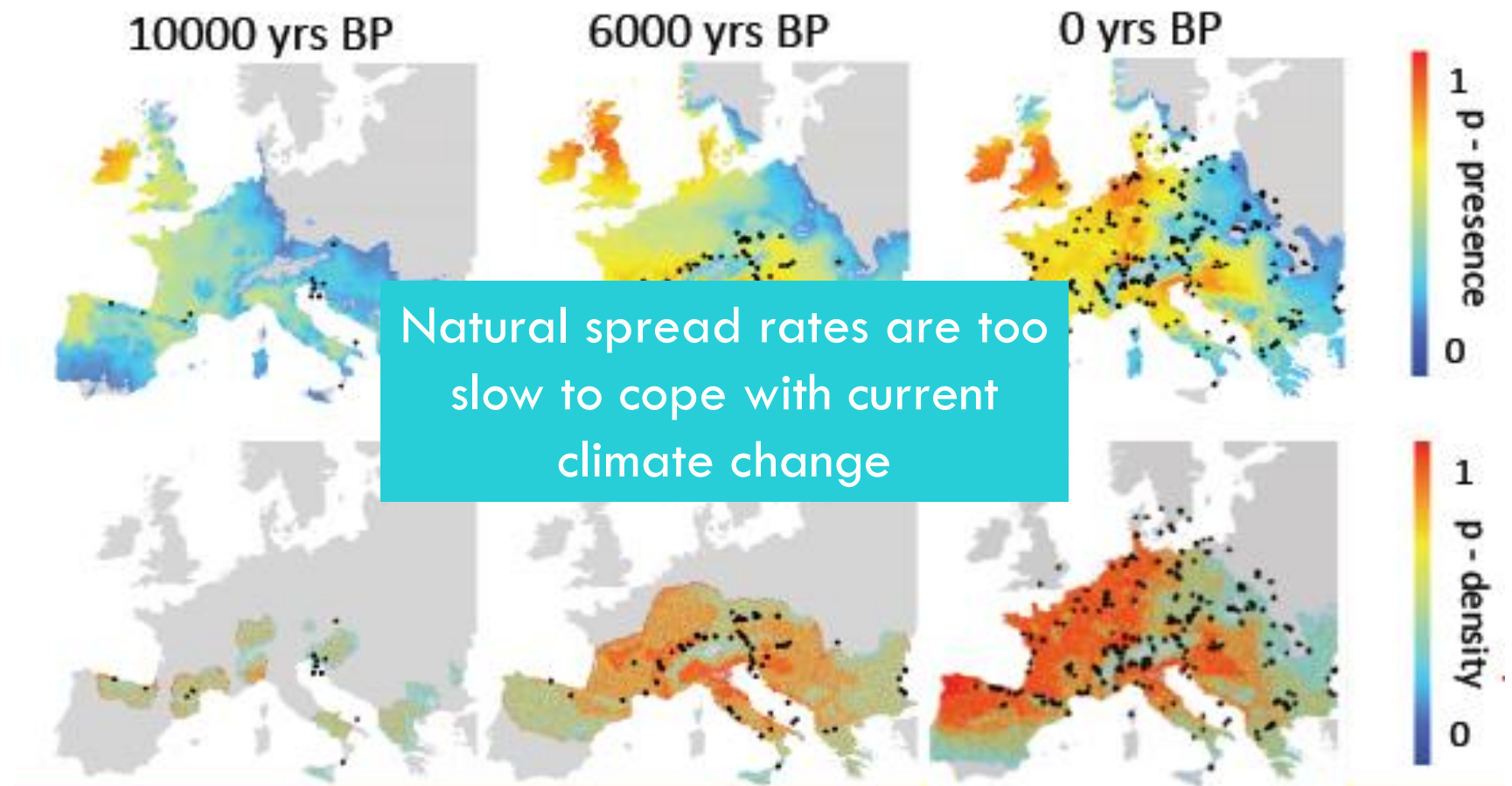
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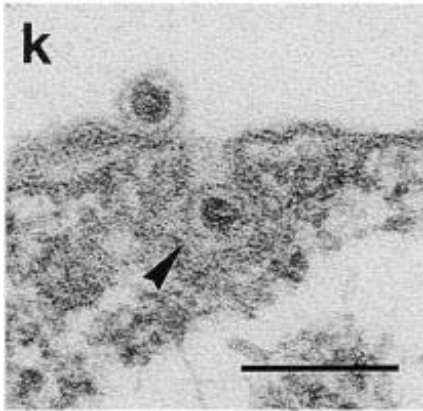
Modelling climatic niche and dispersal



1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?

Experimental adaptation of Phage Phi6 to a new bacterial host

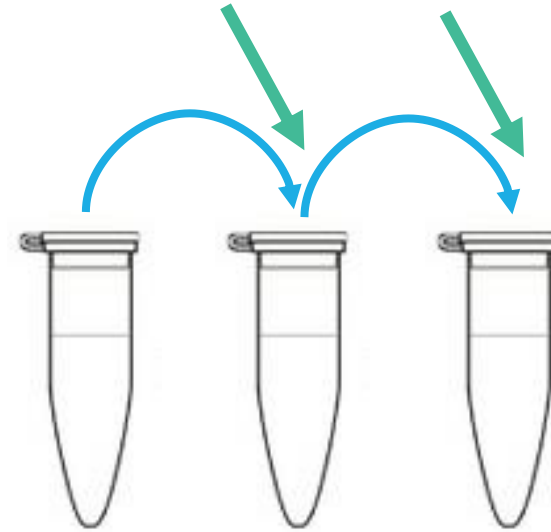
Ching *et al.* 2013



Serial passages

Addition of phages mimicking
immigration

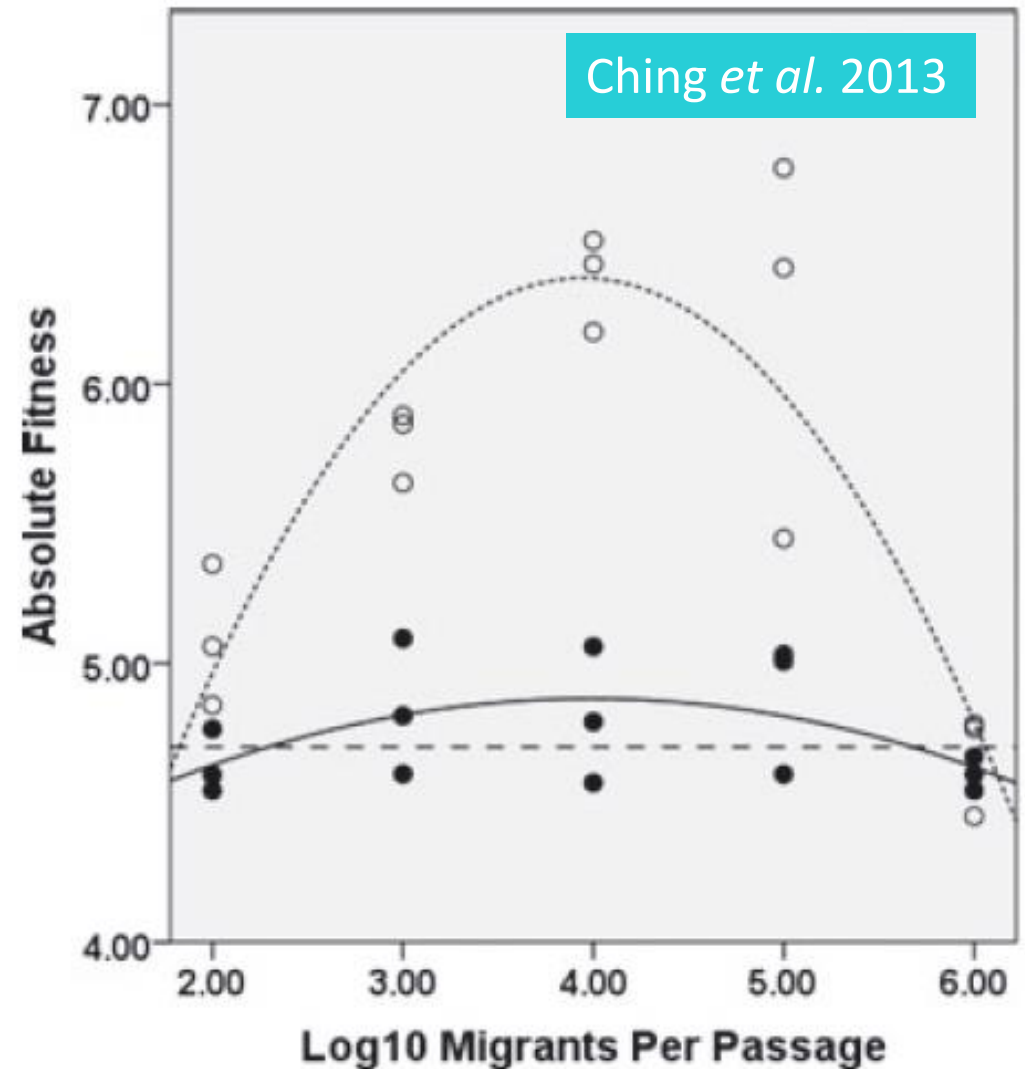
Fitness assays after 30 passages



1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?

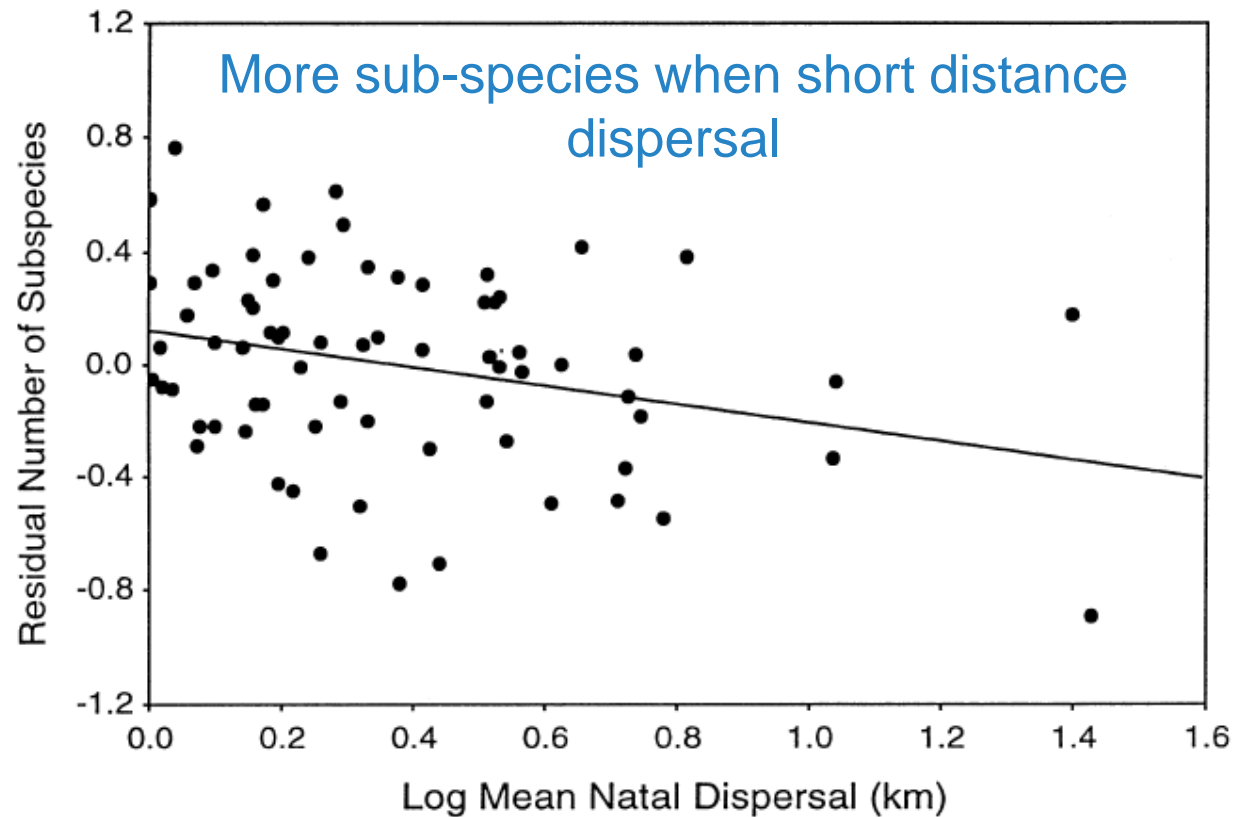
Adaptation of Phage Φ 6 to a new bacterial host is maximized for intermediate migration rates

Dispersal affects the evolution of the ecological niche



1. WHAT IS DISPERSAL AND WHY IS IT IMPORTANT?

Diversification and dispersal distance in birds



Belliure et al. 2000

75 species



2. IS DISPERSAL PLASTIC? YES

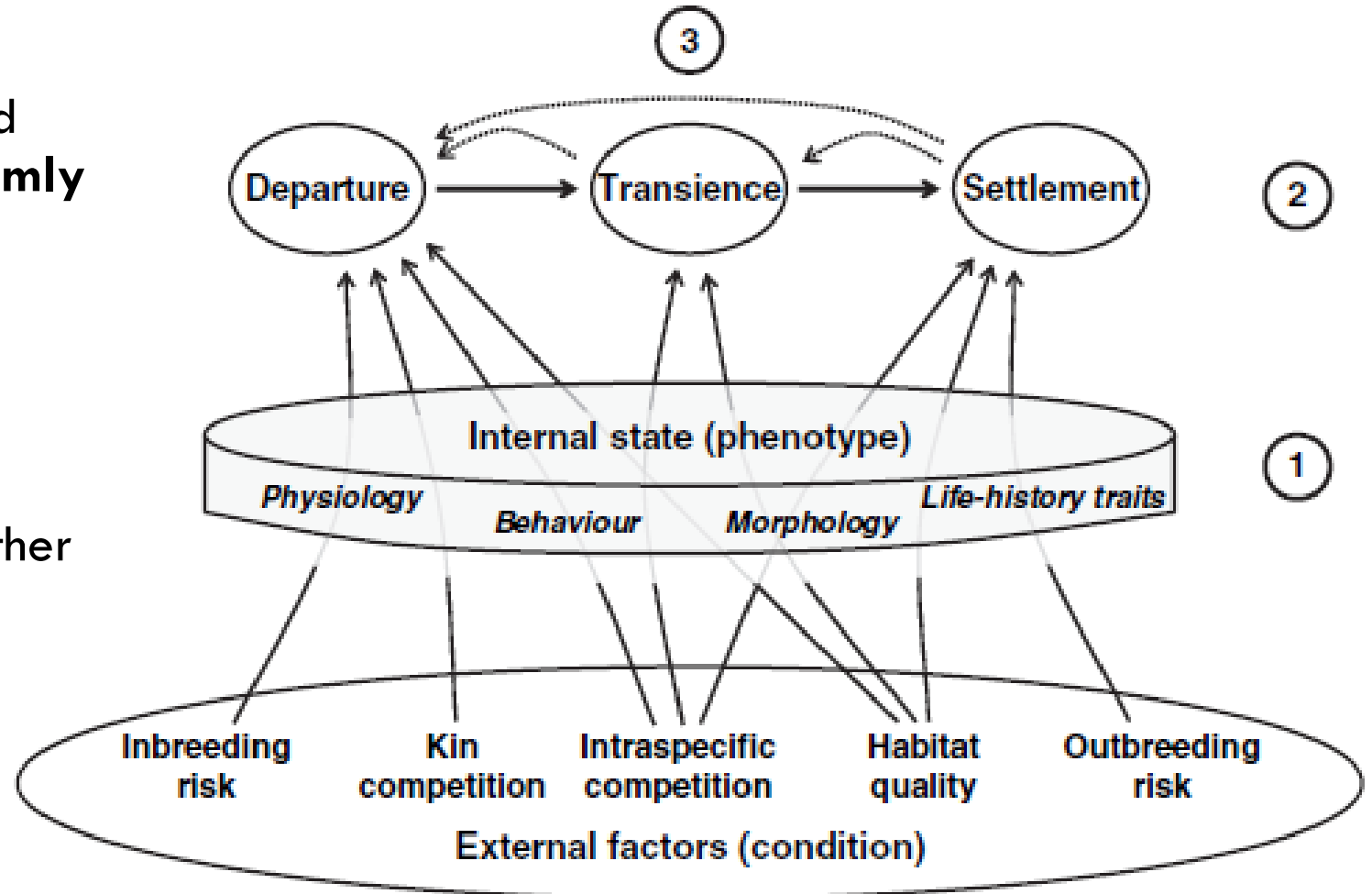
Clobert *et al.* 2009

Individuals leave their natal area and select a breeding habitat **non-randomly**

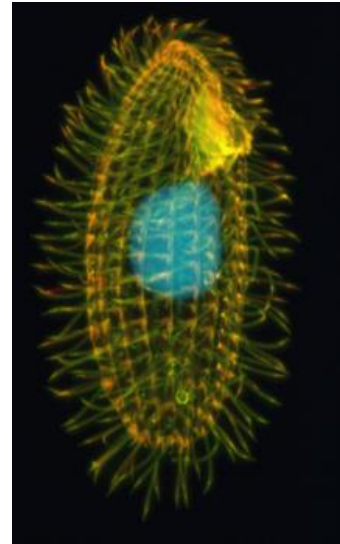
condition dependence

phenotype dependence

Informed dispersal = individuals gather and transfer information before and during their movements through the landscape

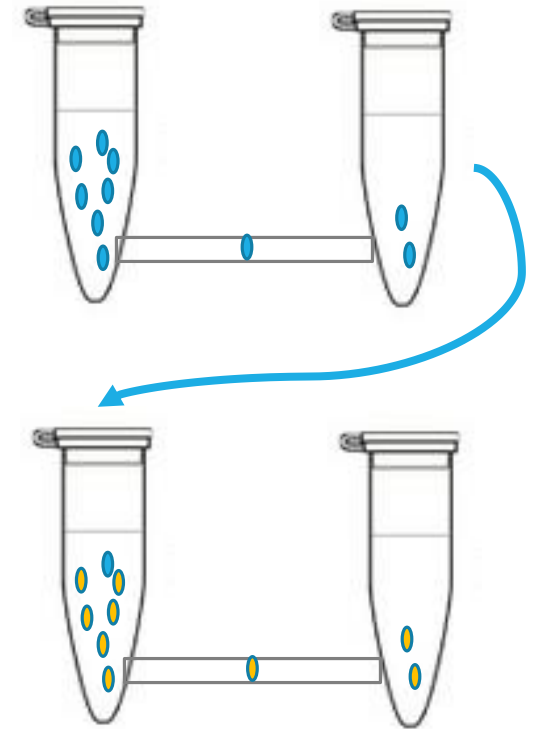


2. IS DISPERSAL INFORMED?



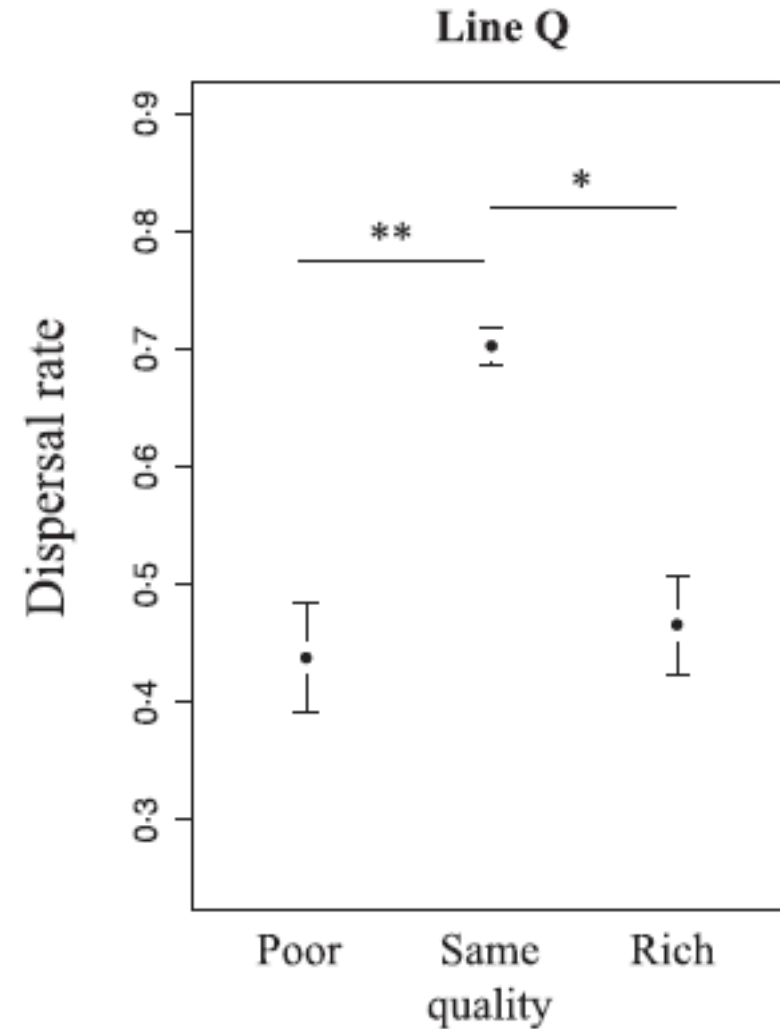
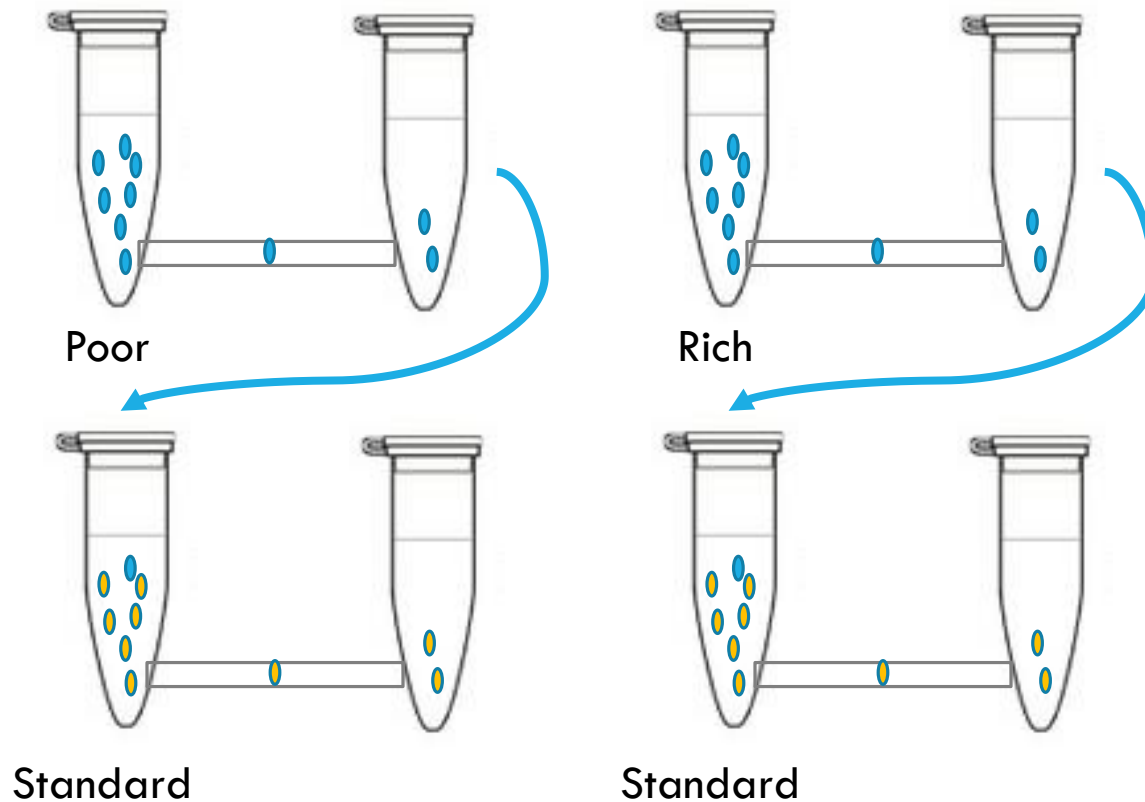
Dispersal assays in
Tetrahymena thermophila

Jakob *et al.* 2015



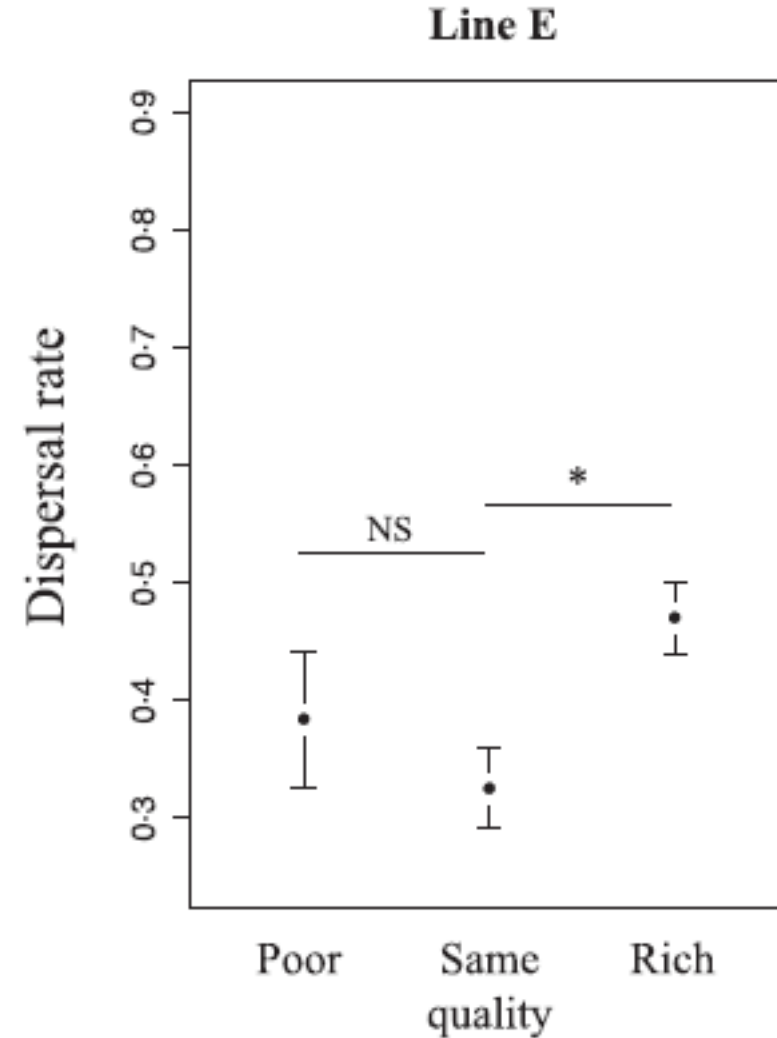
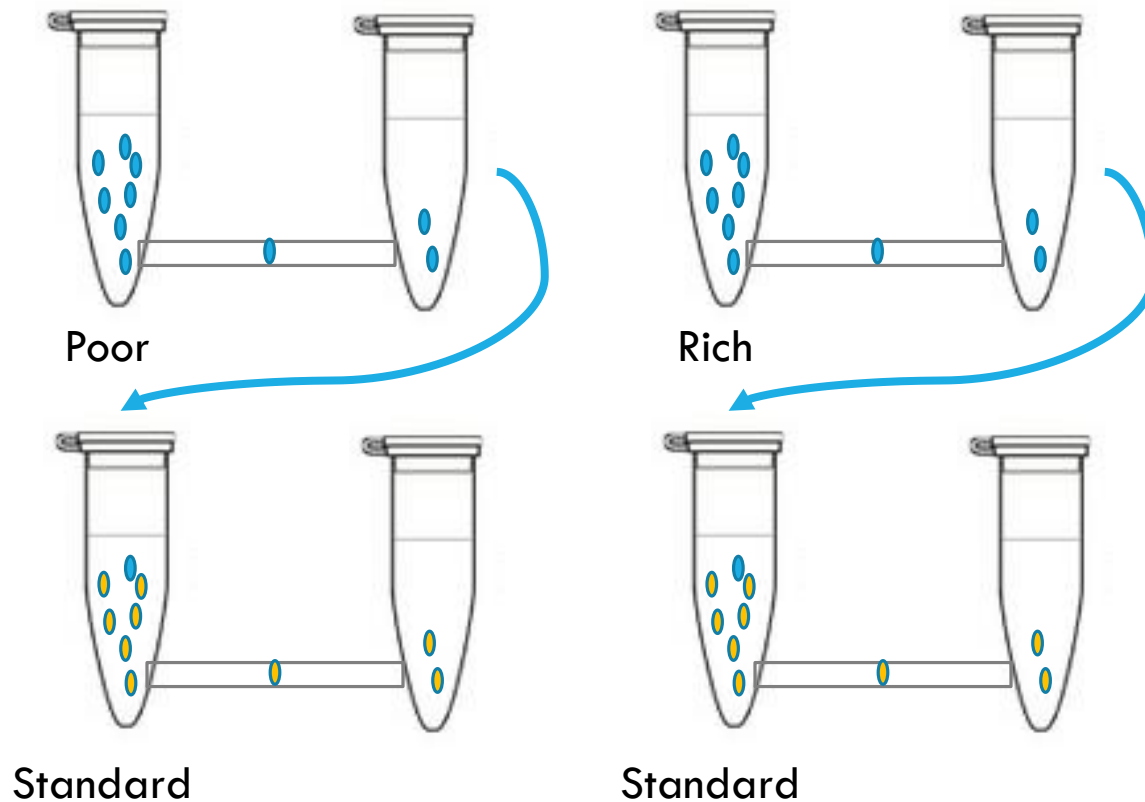
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Jakob *et al.* 2015



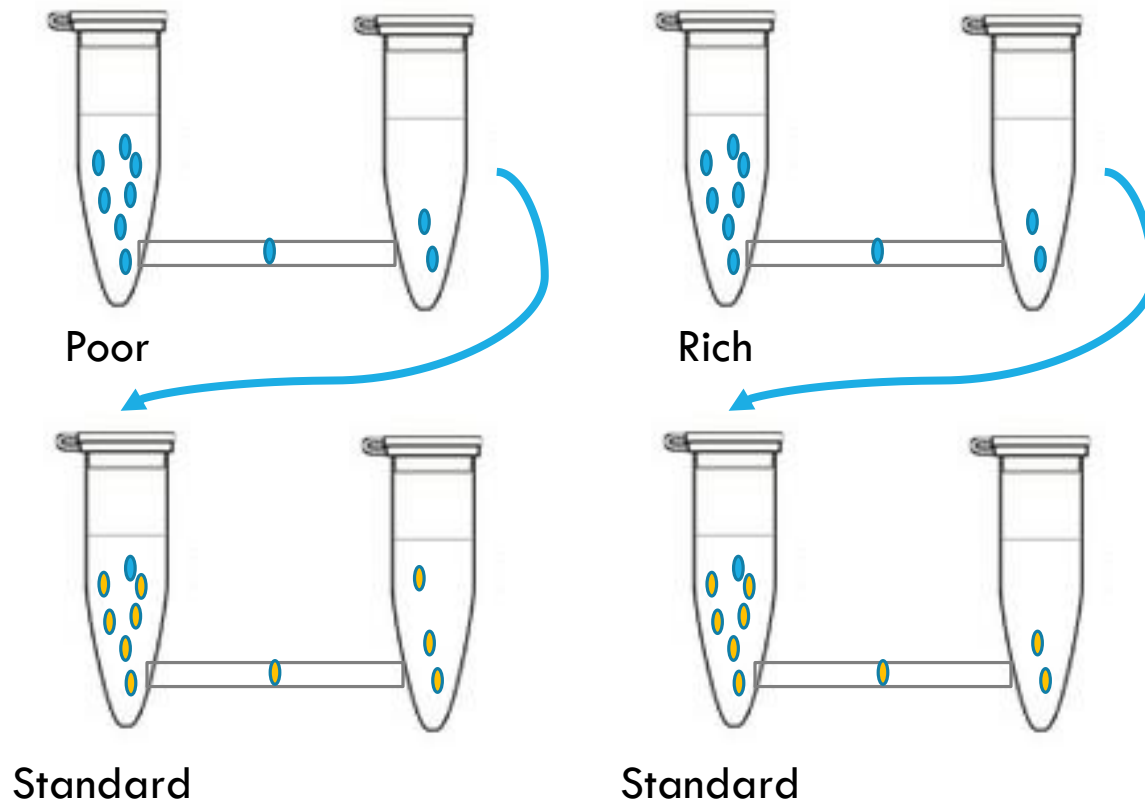
2. IS DISPERSAL INFORMED?

Jakob *et al.* 2015



2. IS DISPERSAL INFORMED?

Jakob *et al.* 2015



Dispersal is modified by the presence of immigrants coming from a different environment

But highly idiosyncratic responses

Information?

3. HOW FAST CAN DISPERSAL EVOLVE?

Rollins *et al.* 2015

Evolution along invasions

Cane toads (*Rhinella marina*) introduced to Australia in 1935

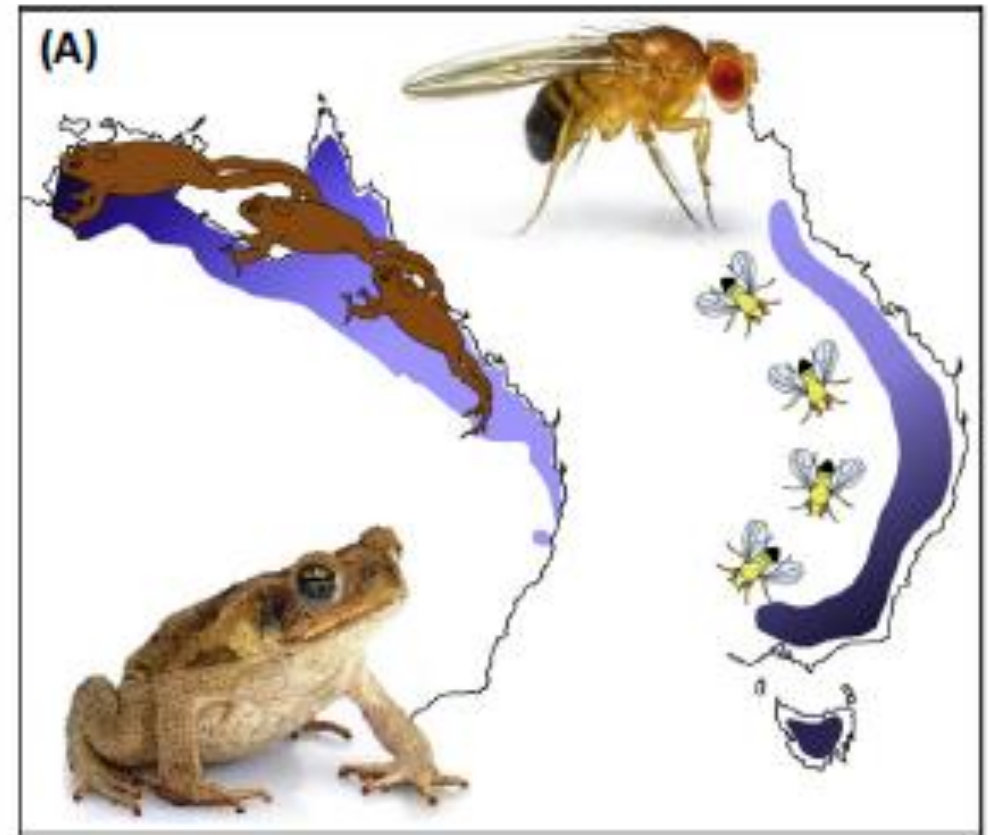
80 generations of continuous spatial expansion

Heritable differences between toads at the expanding front and long-established populations:

Larval growth rate, immune function, dispersal rate, path straightness, morphology



Hudson *et al.* 2016



Canestrellis *et al.* 2016

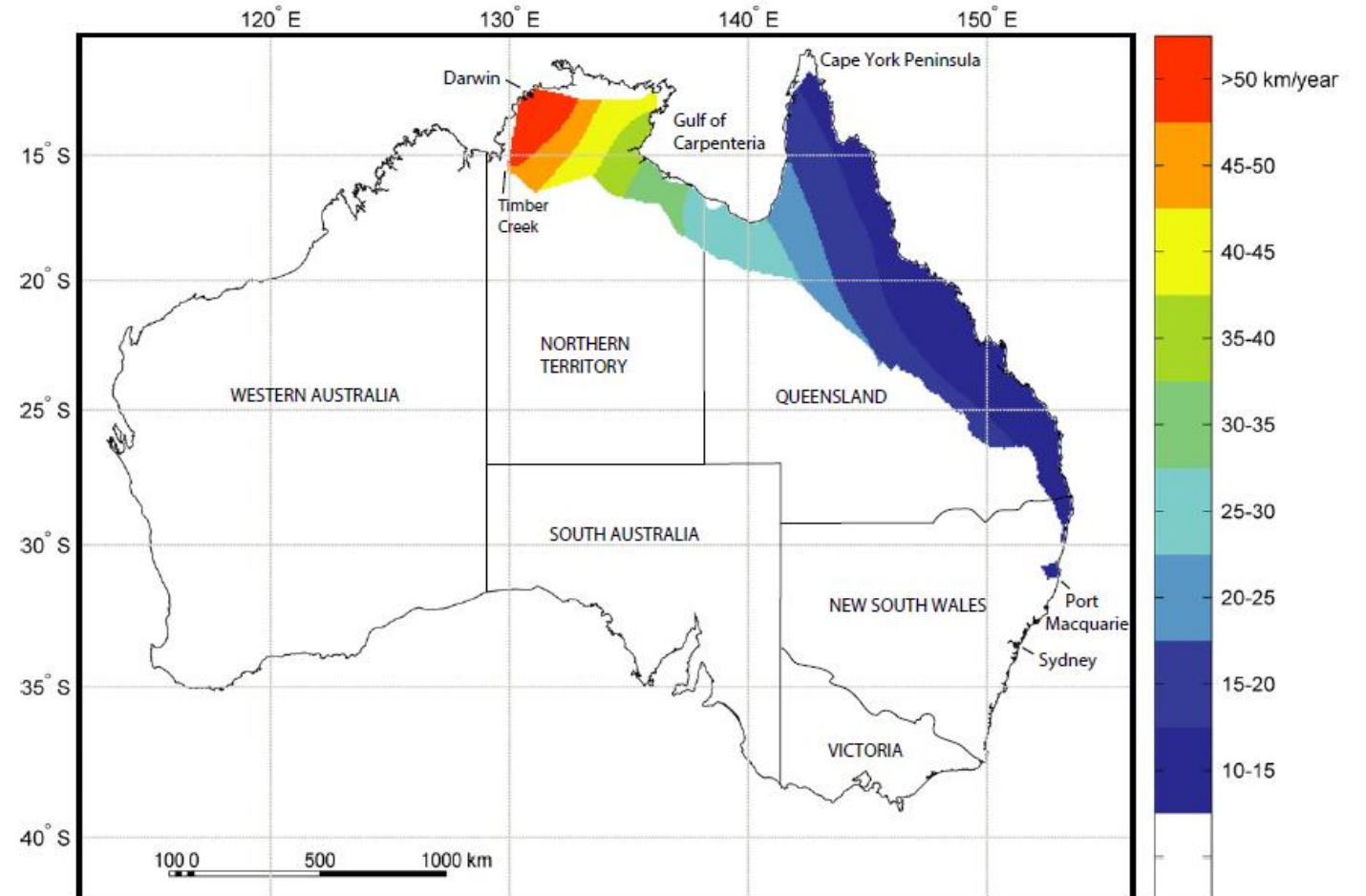
3. HOW FAST CAN DISPERSAL EVOLVE?

Urban *et al.* 2008

Fast evolution of dispersal has
accelerated the invasion

Spread rates increased from
10-15 km /year after
introduction to to 60 km/year
in 2006

Spatial sorting speeds up
evolution



3. HOW FAST CAN DISPERSAL EVOLVE?

From phenotype to dispersal



Arabidopsis thaliana



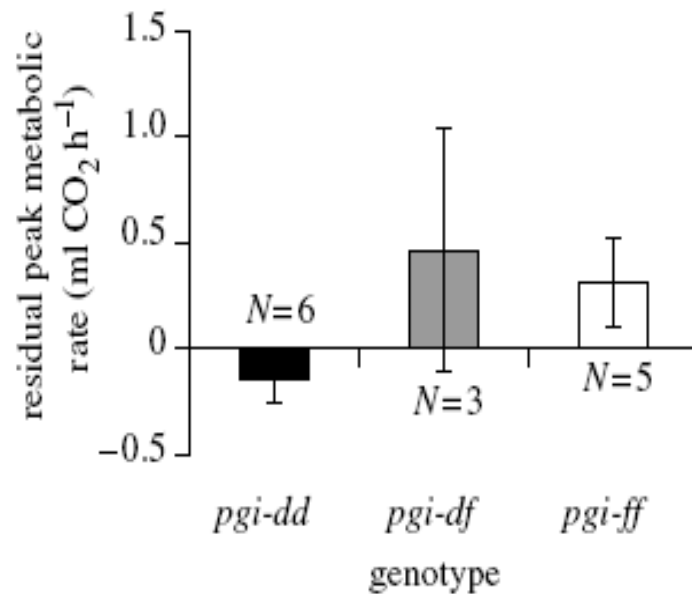
Donohue et al. 2005

	Distance	SD distance	Kurtosis
High density:			
Fruits	NE	NE	NE
Branches	-1.00***	NE	-.76
Height	.47	NE	-.31
Branch length	.12	NE	-.50
Branch angle	.52**	NE	.20
Silique length	-1.00	NE	1.00
Proportion dehiscence	.25	NE	.22
Low density:			
Fruits	-.61**	-.55**	.70***
Branches	-.75***	-.87***	.81***
Height	.15	.74***	-.82***
Branch length	.42**	.68***	-.77***
Branch angle	.22 ⁺	.36*	-.69***
Silique length	.17	.76***	-.82***
Proportion dehiscence	.58**	.46*	-.45***

3. HOW FAST CAN DISPERSAL EVOLVE?

Genetic variation for dispersal

Haag et al. 2005



Melitea cinxia

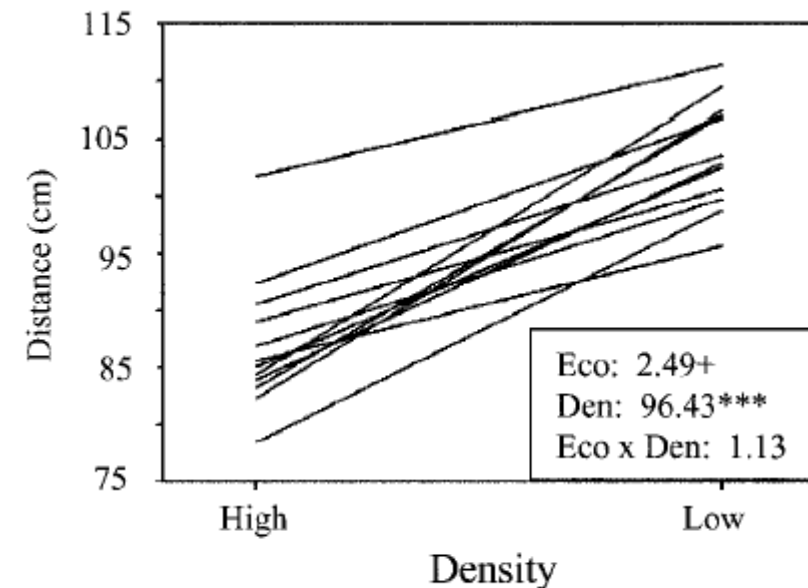


pgi-f: a major gene?



Arabidopsis thaliana

Donohue et al. 2005



4. WHICH MODEL ASSUMPTIONS MATTER?

Assumptions allowing mathematical tractability:

Discrete patches

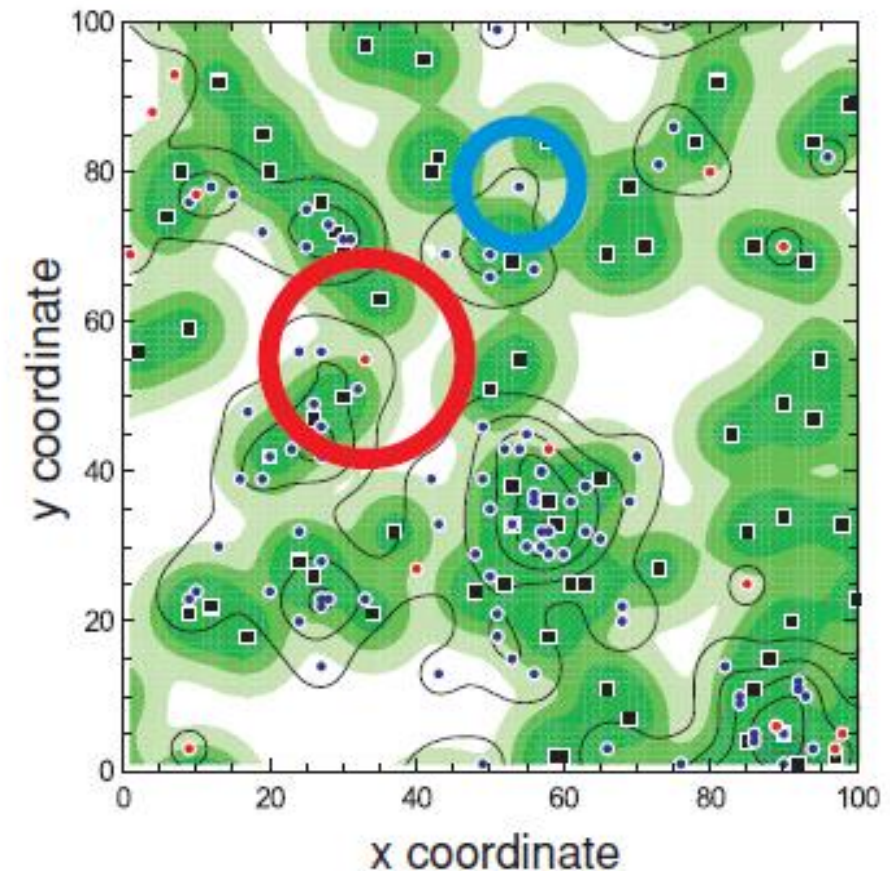
Very few/ infinite number of patches

Very few/ infinite number of individuals per patch

Implicit descriptions of space (e.g. equal connectivity)

Neglecting higher moments of spatial interactions

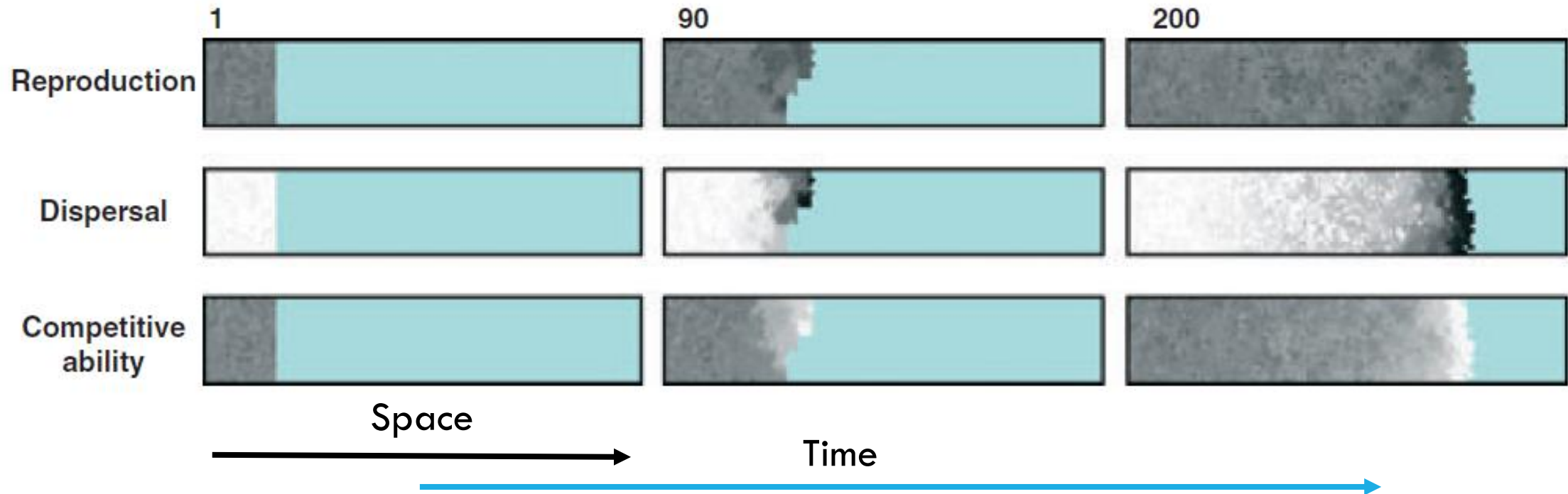
North *et al.* 2011



4. WHICH MODEL ASSUMPTIONS MATTER?

Spatially explicit Individual-based simulations

Burton *et al.* 2010



4. WHICH MODEL ASSUMPTIONS MATTER?

All models make assumptions...

VOL. 179, NO. 5 THE AMERICAN NATURALIST MAY 2012

Uncertainty and the Role of Information Acquisition in the Evolution of Context-Dependent Emigration

Greta Bocedi,^{*,†} Johannes Heinonen,^{*} and Justin M. J. Travis

VOL. 187, NO. 1 THE AMERICAN NATURALIST JANUARY 2016

REPLY

Models of Dispersal Evolution Highlight Several Important Issues in Evolutionary and Ecological Modeling

(A Reply to Poethke et al.)

Greta Bocedi^{*} and Justin M. J. Travis

VOL. 187, NO. 1 THE AMERICAN NATURALIST JANUARY 2016

COMMENT

The Adequate Use of Limited Information in Dispersal Decisions

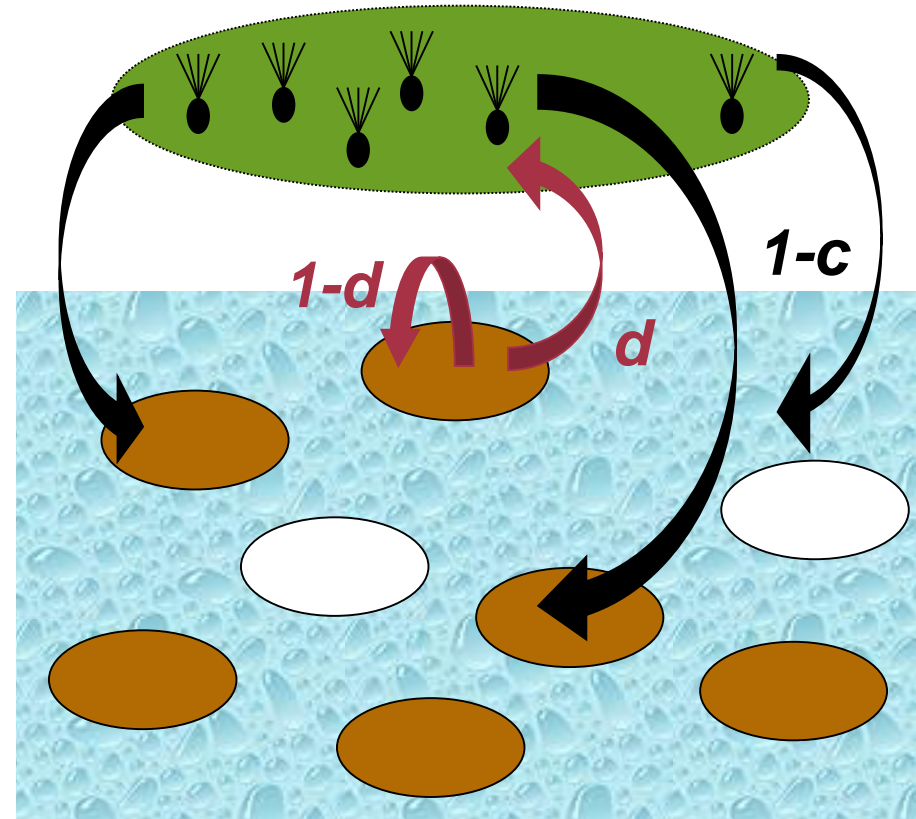
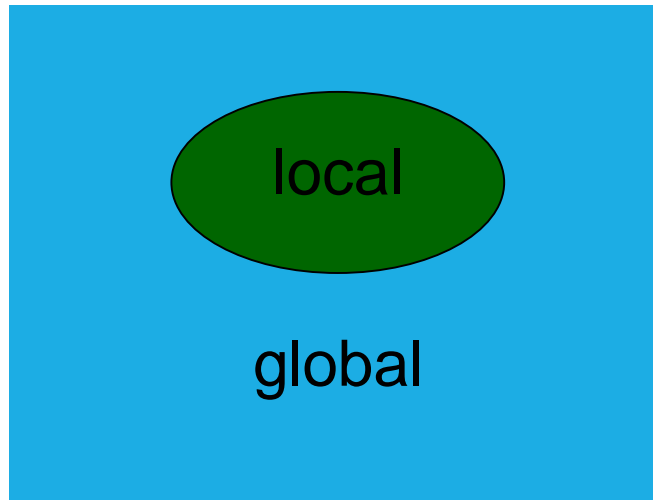
(A Comment on Bocedi et al., “Uncertainty and the Role of Information Acquisition in the Evolution of Context-Dependent Emigration”)

Hans Joachim Poethke,^{1,*} Alexander Kubisch,² Oliver Mitesser,¹ and Thomas Hovestadt^{1,3}

5. HOW DO WE MODEL SELECTION ON DISPERSAL?

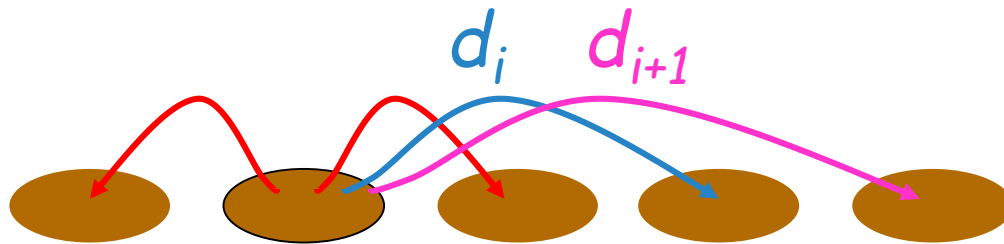
Analytical approaches: which aspects of space to keep in the model?

The island model

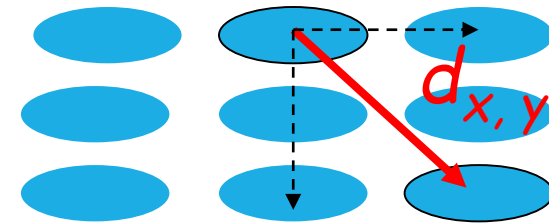
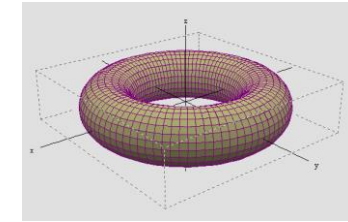


5. HOW DO WE MODEL SELECTION ON DISPERSAL?

« stepping-stone » model

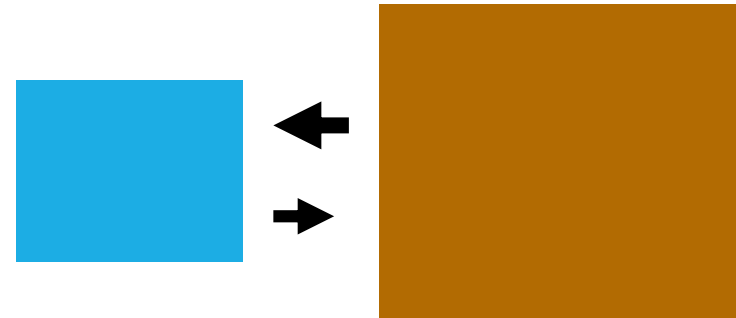


Rousset & Gandon 2002



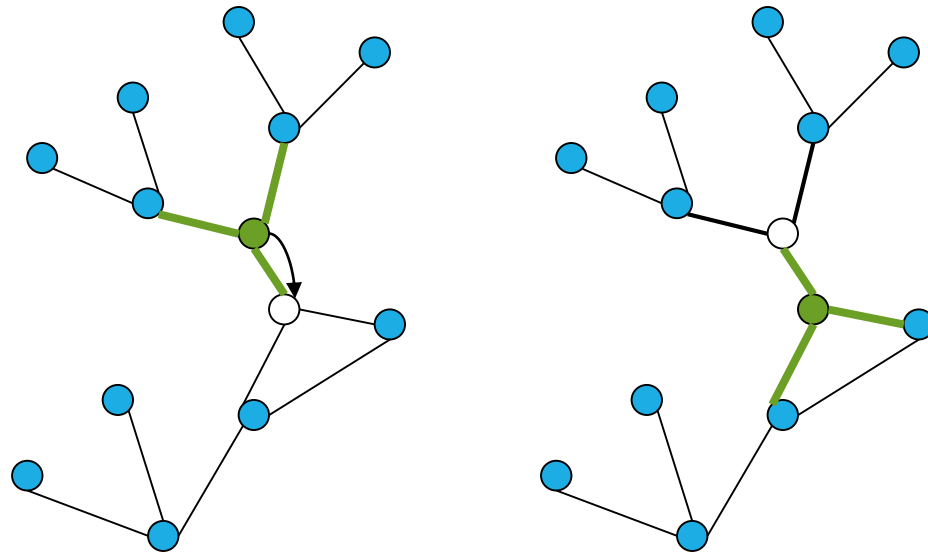
Two sub-populations

McPeck & Holt 1992



5. HOW DO WE MODEL SELECTION ON DISPERSAL?

Random network model



Le Galliard et al. 2005

5. HOW DO WE MODEL SELECTION ON DISPERSAL?

Allele M: dispersal rate

$$z$$

Allele m: dispersal rate

$$z^* = z + \delta$$

Fitness of individuals with
allele m when competing with
individuals with M allele

$$w(z^* | z)$$

$$\left. \frac{\partial w(z^* | z)}{\partial \delta} \right|_{\delta=0}$$

>0 : the allele with higher dispersal is favored

<0: the allele with lower dispersal is favored

5. HOW DO WE MODEL SELECTION ON DISPERSAL?

Fitness= number of surviving offspring

$$w(z_{\bullet}) = f(1 - z_{\bullet})w_{philo} + fz_{\bullet}(1 - c)w_{disp}$$

Dispersal rate of a focal individual

Survival probability in natal patch

Survival probability if immigrating elsewhere

5. HOW DO WE MODEL SELECTION ON DISPERSAL?

Direct and indirect selective effects

$$\frac{\partial w(z^*)}{\partial \delta} \propto \underbrace{-w_{philo} + (1-c)w_{disp}}_{\text{Difference in survival between philopatric and dispersing individuals}} + \underbrace{(1-z^*)\frac{\partial w_{philo}}{\partial \delta} + z^*(1-c)\frac{\partial w_{disp}}{\partial \delta}}_{\text{Indirect effect of genotype on those survival}}$$

$$\frac{\partial w_{philo}}{\partial \delta} = \frac{\partial w_{philo}}{\partial z_0} \boxed{\frac{\partial z_0}{\partial \delta}} + \frac{\partial w_{philo}}{\partial z_1} \boxed{\frac{\partial z_1}{\partial \delta}}$$

Average dispersal rate in
natal patch

Average dispersal rate in
other patches

Does the genotype of a focal
individual predicts the phenotype
of its neighbors?

5. HOW DO WE MODEL SELECTION ON DISPERSAL?

Population genetics (multilocus)

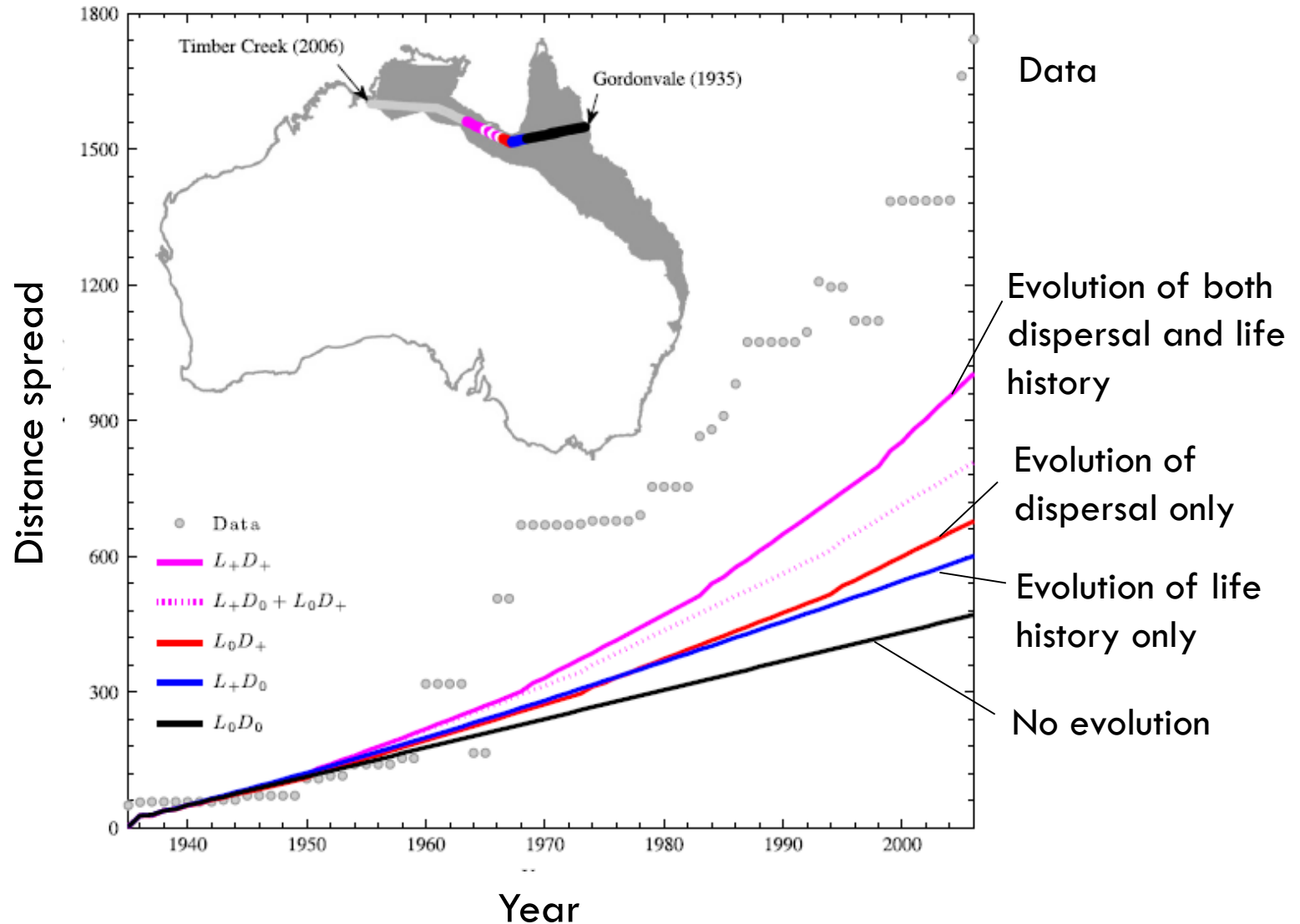
Adaptive dynamics

Long-term evolutionary equilibria

Short-term quantitative genetics prediction?

Perkins *et al.* 2013

470 km without evolution in 72 years,
1004 km with evolution



6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

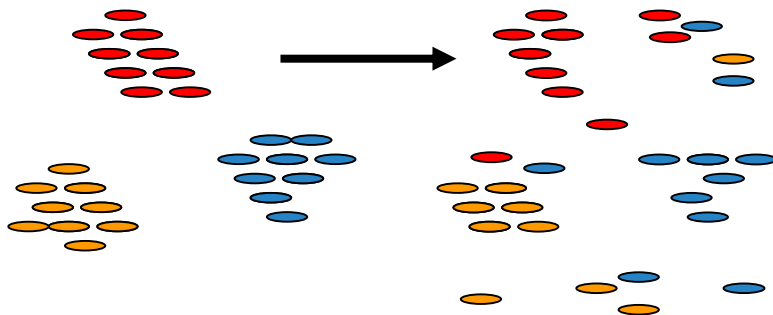


Trillium grandiflorum

Kalisz et al. 1999

Elaiosome
Self-incompatible

Radio-labeled seeds
+ color-tag

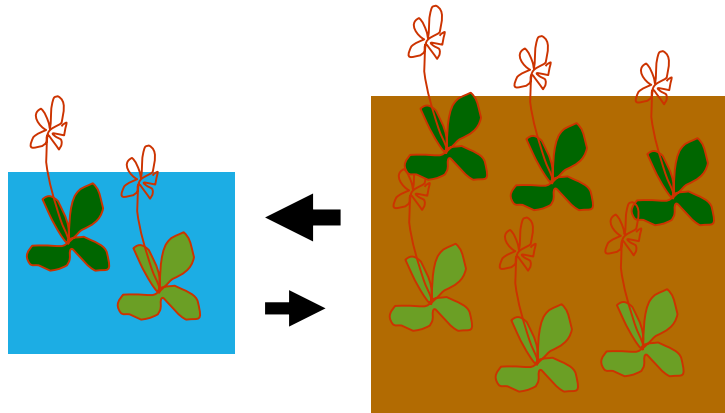


Decreased aggregation

6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Avoiding crowded conditions

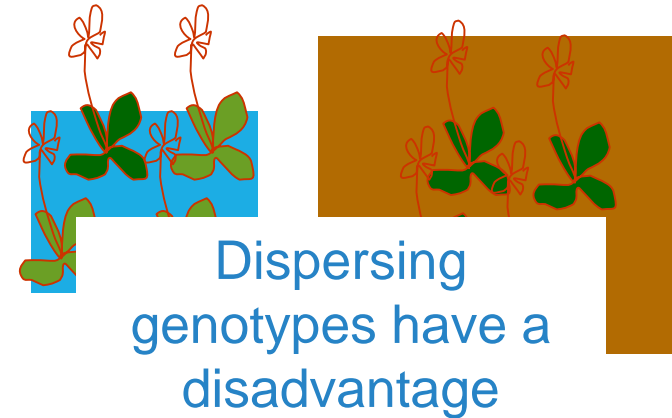
Passive dispersal



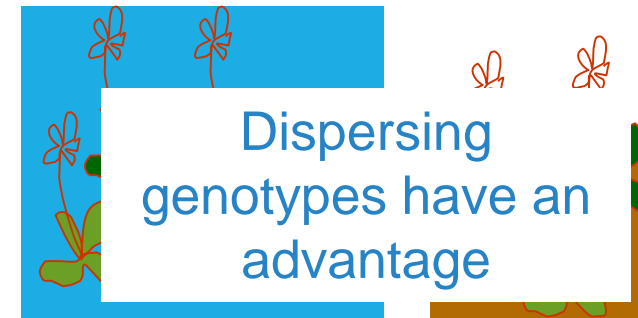
Hastings 1983

McPeck et Holt 1992

Stable heterogeneous habitat



Heterogeneous habitat variable in time



6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Catastrophic extinctions

Van Valen 1971

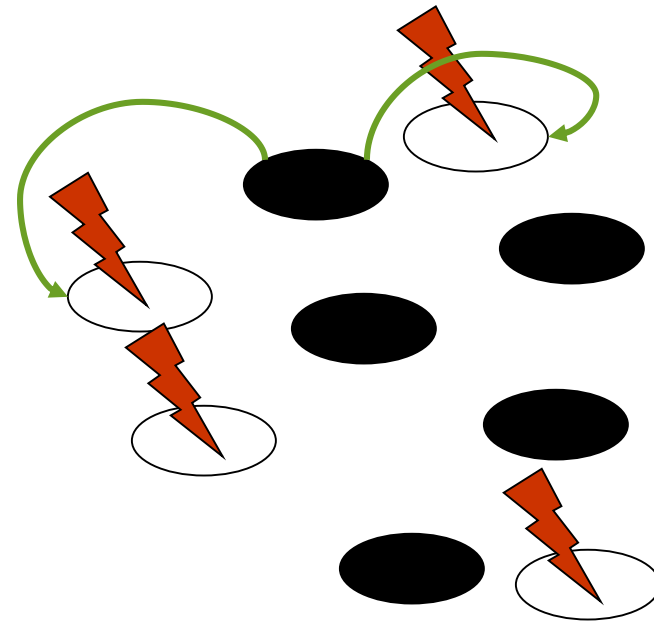
ESS dispersal rate =
Extinction rate

if

cost of dispersal is very high,

large population size

fast population growth



Levin *et al.* 84

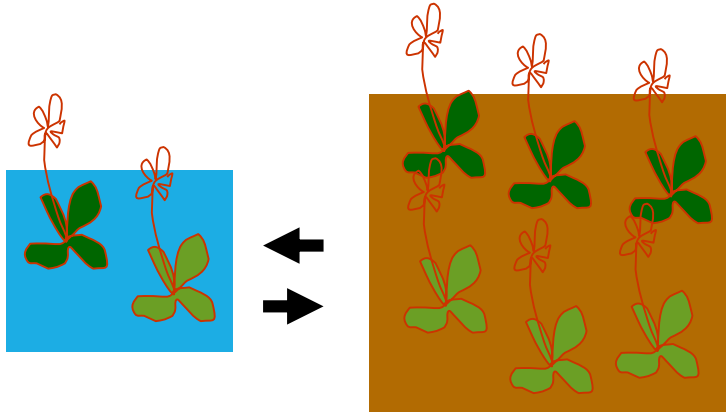
Comins *et al.* 82

Olivieri *et al.* 95

6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Plasticity of dispersal

Stable heterogeneous habitat

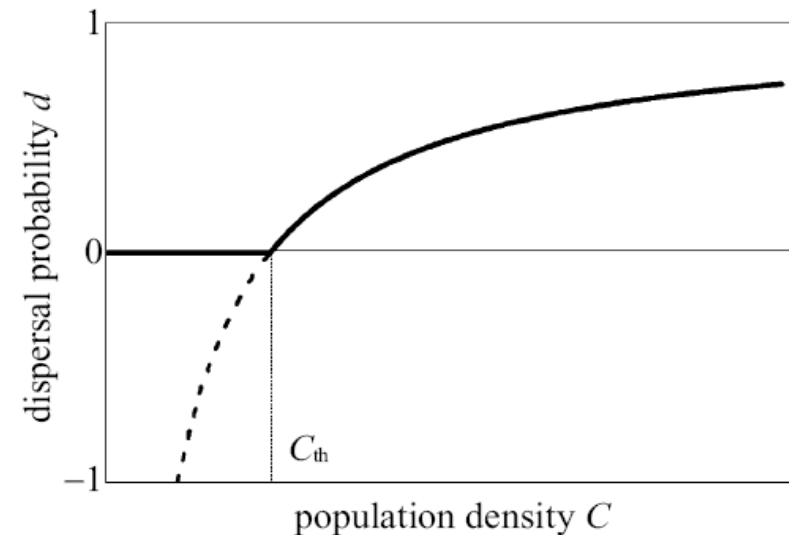


McPeck & Holt 1992

Equal **number** of migrants

Dispersal >> Dispersal

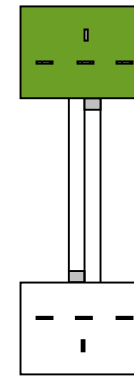
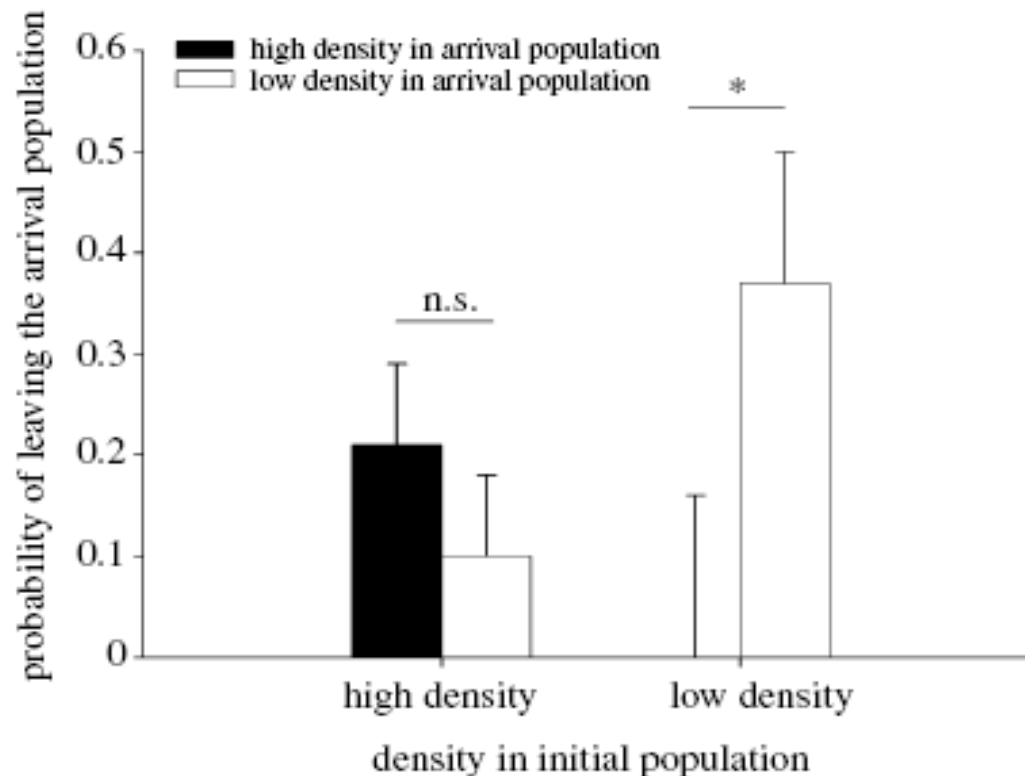
Unstable habitat



Poethke & Hovestadt 2002

6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Complex data



Lacerta vivipara



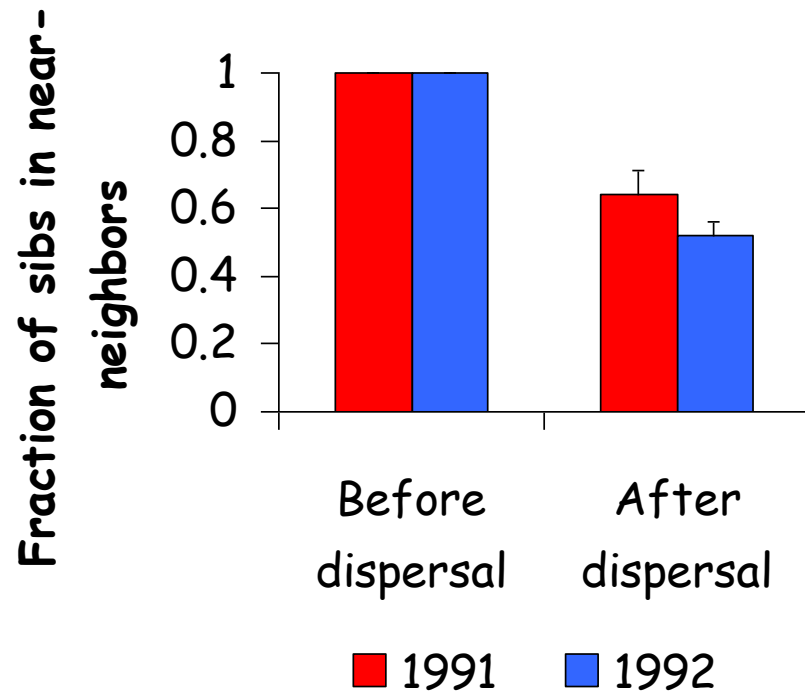
Côte & Clobert 2007

Density also affects
the personality of
dispersing
individuals!

6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Kin competition

Kalish et al. 1999



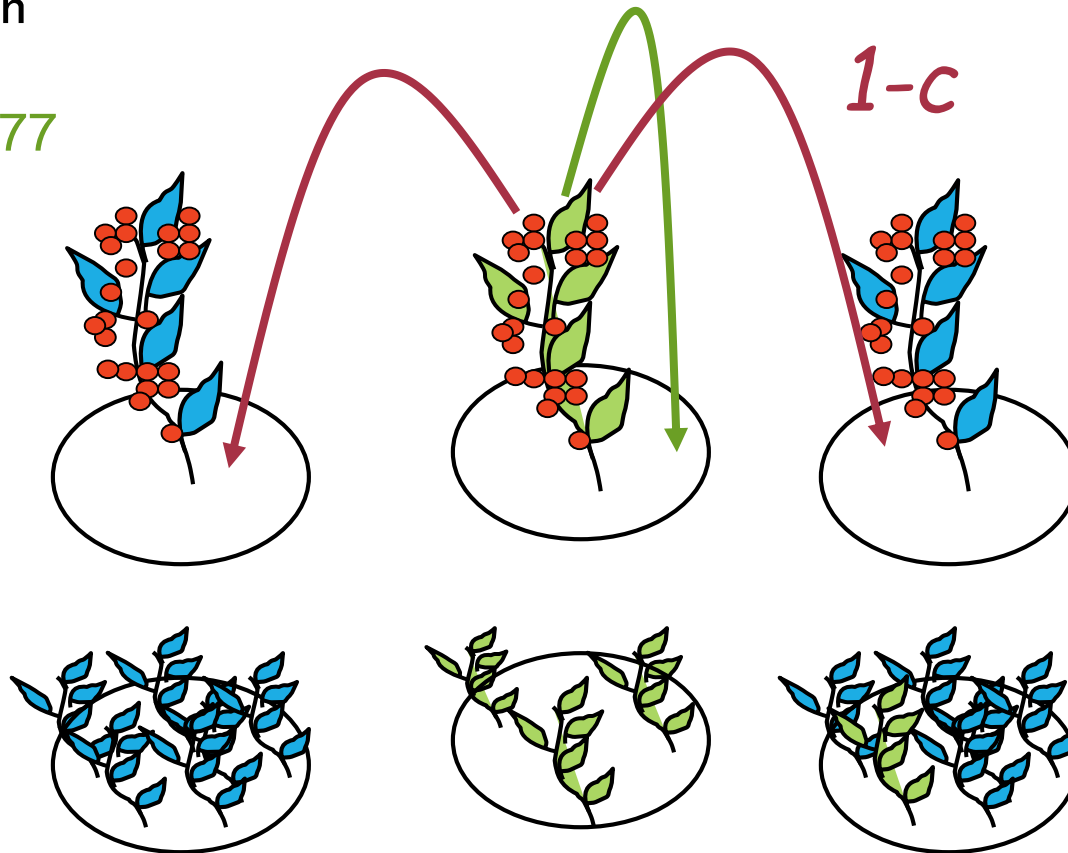
Weaker relatedness
between neighbors



6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Kin competition

Hamilton et May 1977



$$d_{ess} = 1/(1+c)$$

Min 50%
dispersal

Is dispersal an
altruistic
behavior?

6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Kin competition

Frank 1986

Gandon et Rousset 1999

N individuals per site

Draw two identical genes
in two individuals in the
same site

$$R = \frac{Q_0 - Q_1}{1 - Q_1}$$

In different sites

$$d_{ess} = \frac{R - c}{R - c^2}$$

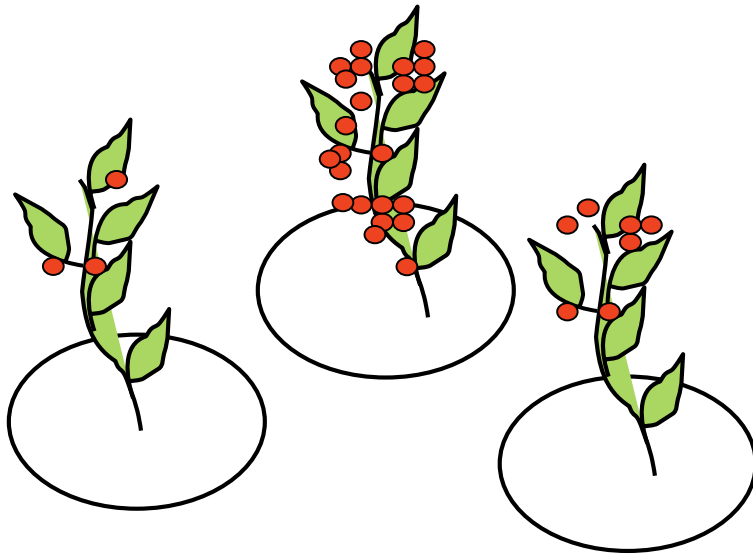
Depends on dispersal!

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

6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Variation in kin competition
due to number of sibs

Kisdi 2006



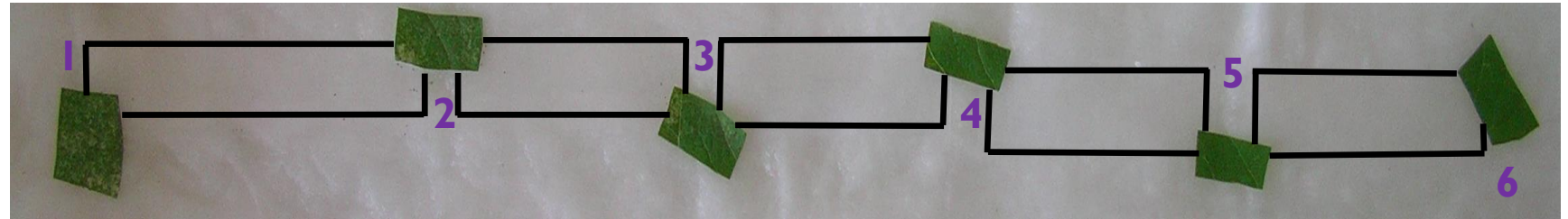
ESS:
Fixed number of philopatric
offspring

Large sibship:
large dispersal
rate

Few sibs: low
dispersal rate

6. DOES DISPERSAL ALLOW ESCAPE FROM (KIN) COMPETITION?

Bitume *et al.* 2013



Theoretical expectations:

Dispersal distance should increase with density in departure patch

Poethke *et al.* 2011

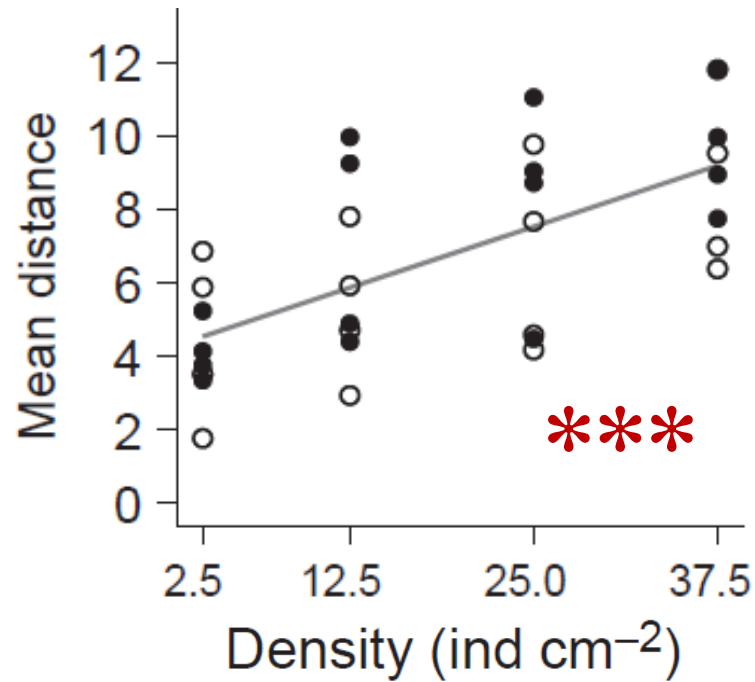
Dispersal distance should increase with genetic resemblance among competitors

Gandon & Rousset 2002

Manipulation of density and genetic resemblance in the starting patch

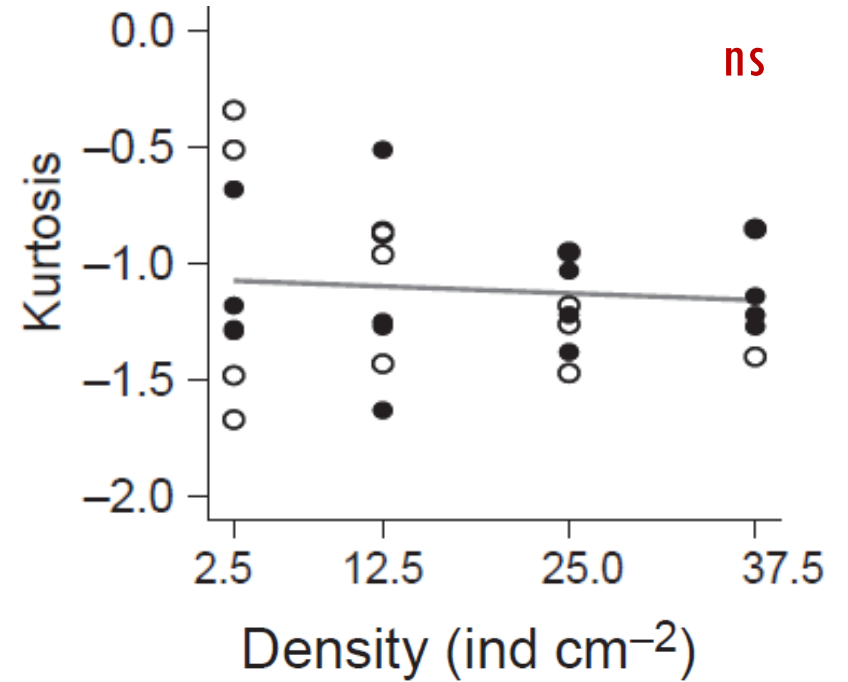
6. DOES DISPERSAL ALLOW ESCAPE FROM COMPETITION?

Dispersal distance increases with density



Mites move further

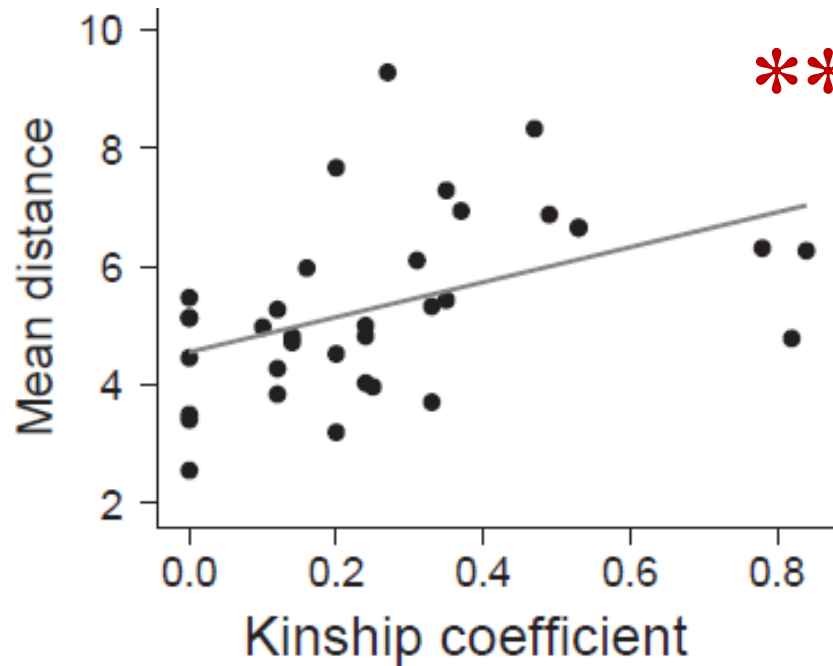
Bitume *et al.* 2013



The shape of the dispersal kernel is unaffected

6. DOES DISPERSAL ALLOW ESCAPE FROM KIN COMPETITION?

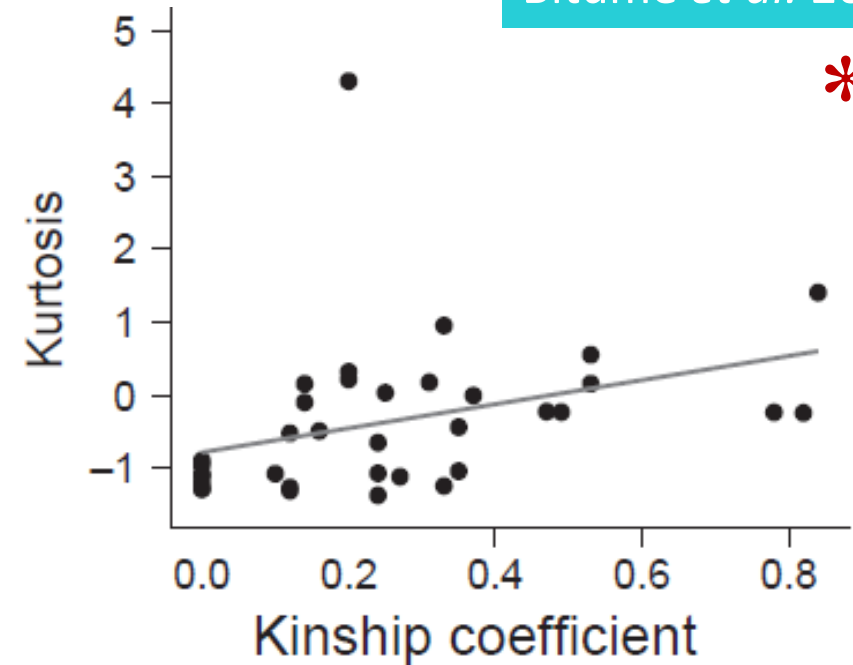
Dispersal distance increases with genetic resemblance



A few mites move much further

Mites move further

Bitume *et al.* 2013



The shape of the dispersal kernel is affected

7. IS DISPERSAL AN INBREEDING AVOIDANCE STRATEGY?

Wolff 1992



*Peromyscus
leucopus*

Removal of parents of one sex



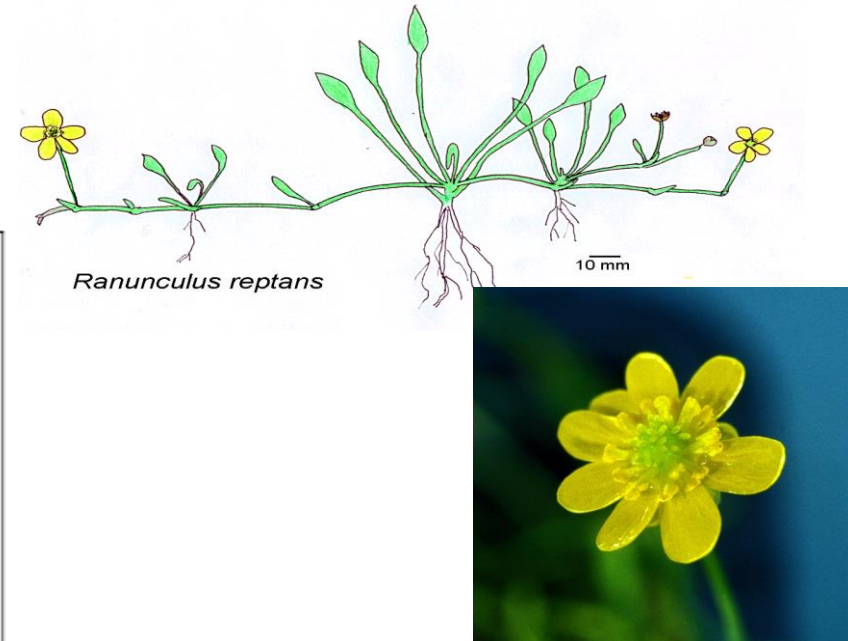
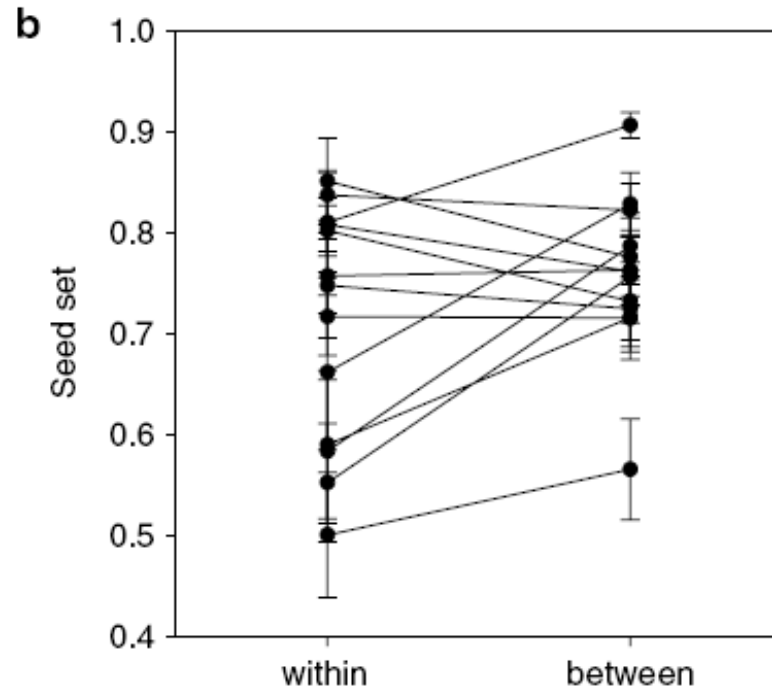
Later dispersal of offspring of
opposite sex

Frequent sex-biased dispersal

Avoidance of inbreeding or of sex-specific competition?

7. IS DISPERSAL AN INBREEDING AVOIDANCE STRATEGY?

Heterosis: data

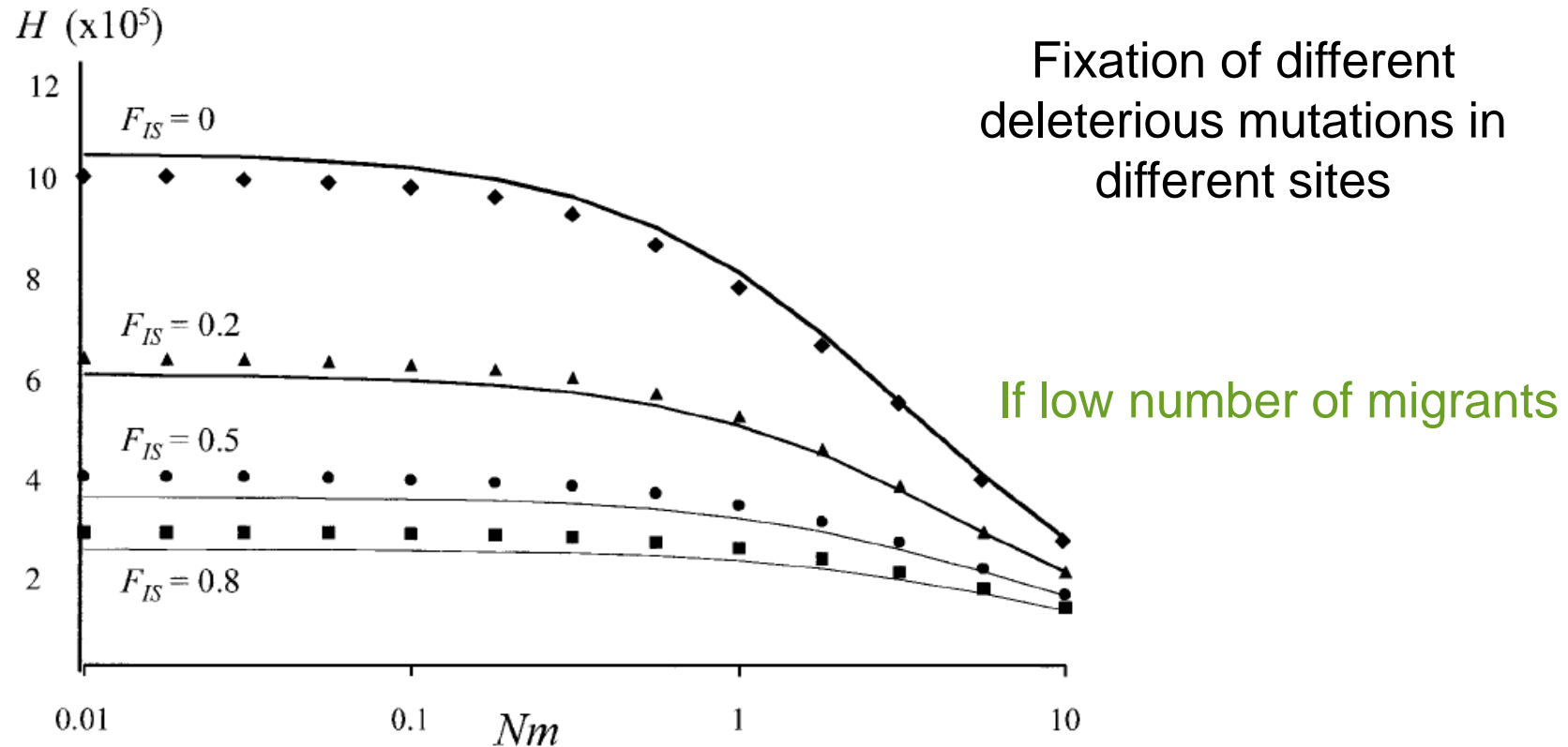


Heterosis higher in small populations

7. IS DISPERSAL AN INBREEDING AVOIDANCE STRATEGY?

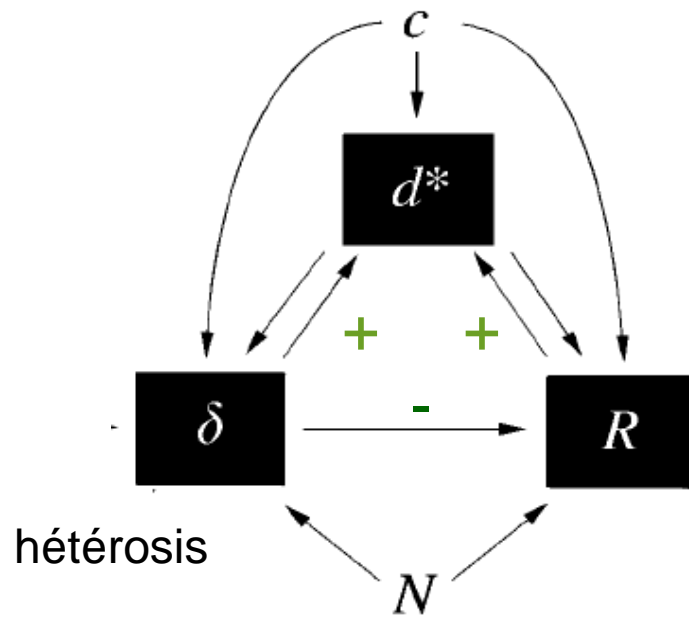
Glémin et al. 2003

Heterosis: theoretical predictions



7. IS DISPERSAL AN INBREEDING AVOIDANCE STRATEGY?

Kin competition and heterosis



Gandon 1999

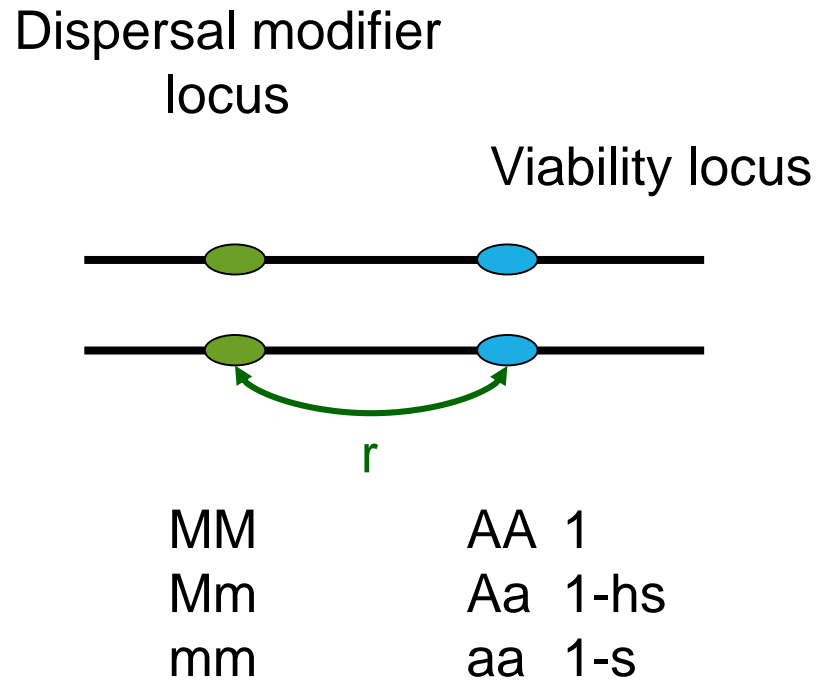
Perrin & Goudet 2001

High heterosis AND high kin competition in small isolated population

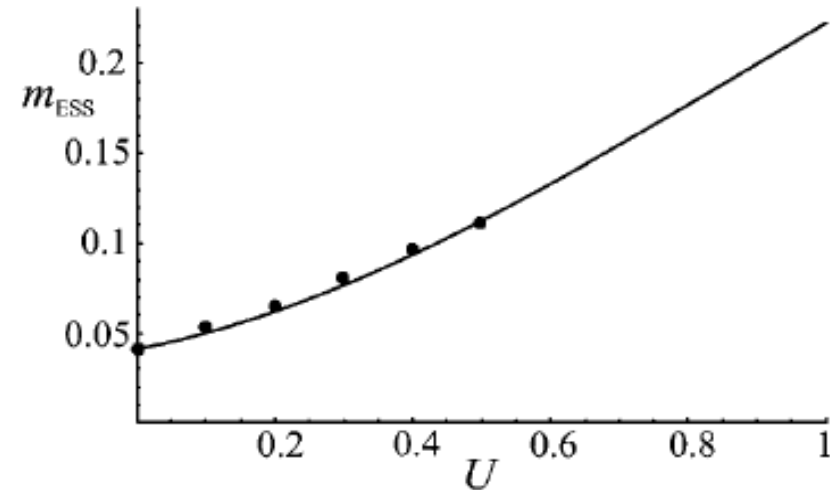
Complex interactions

7. IS DISPERSAL AN INBREEDING AVOIDANCE STRATEGY?

Kin competition and heterosis



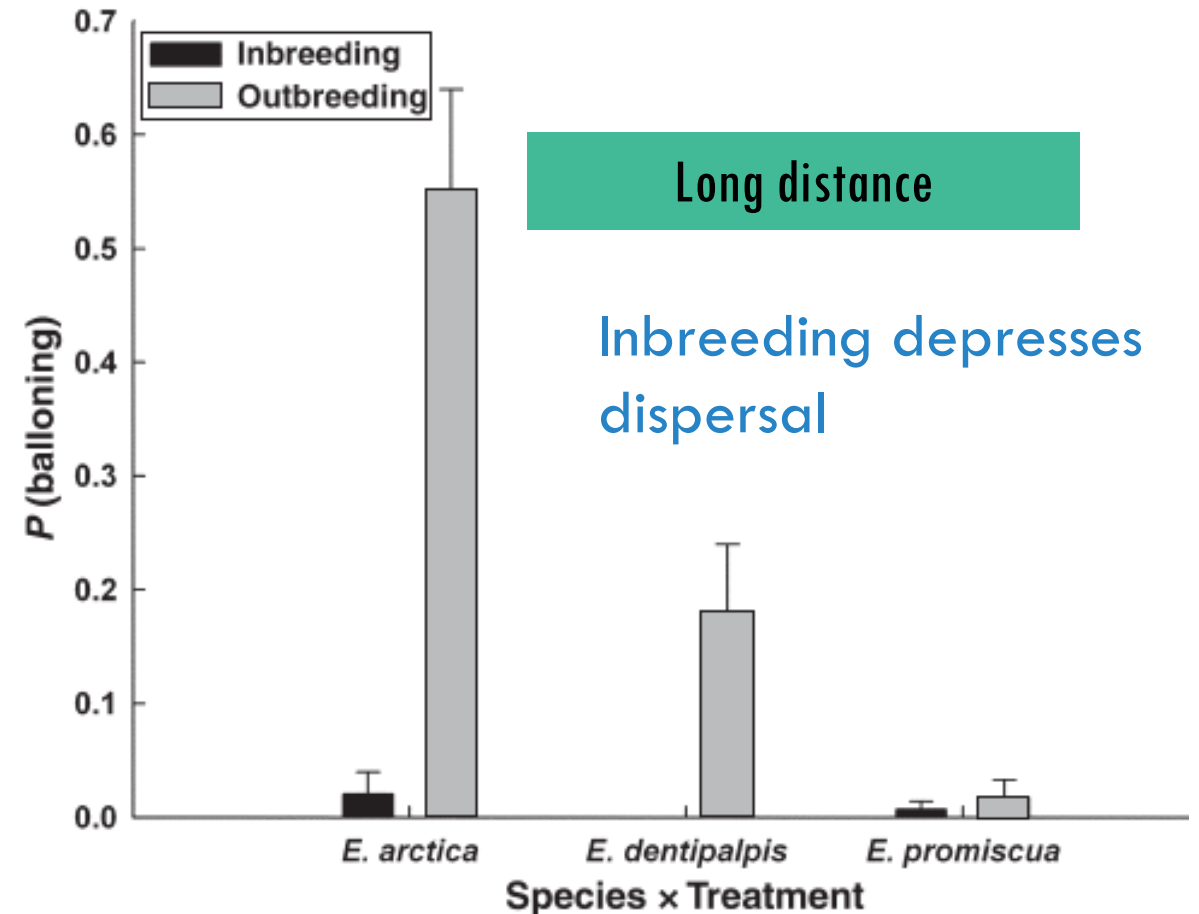
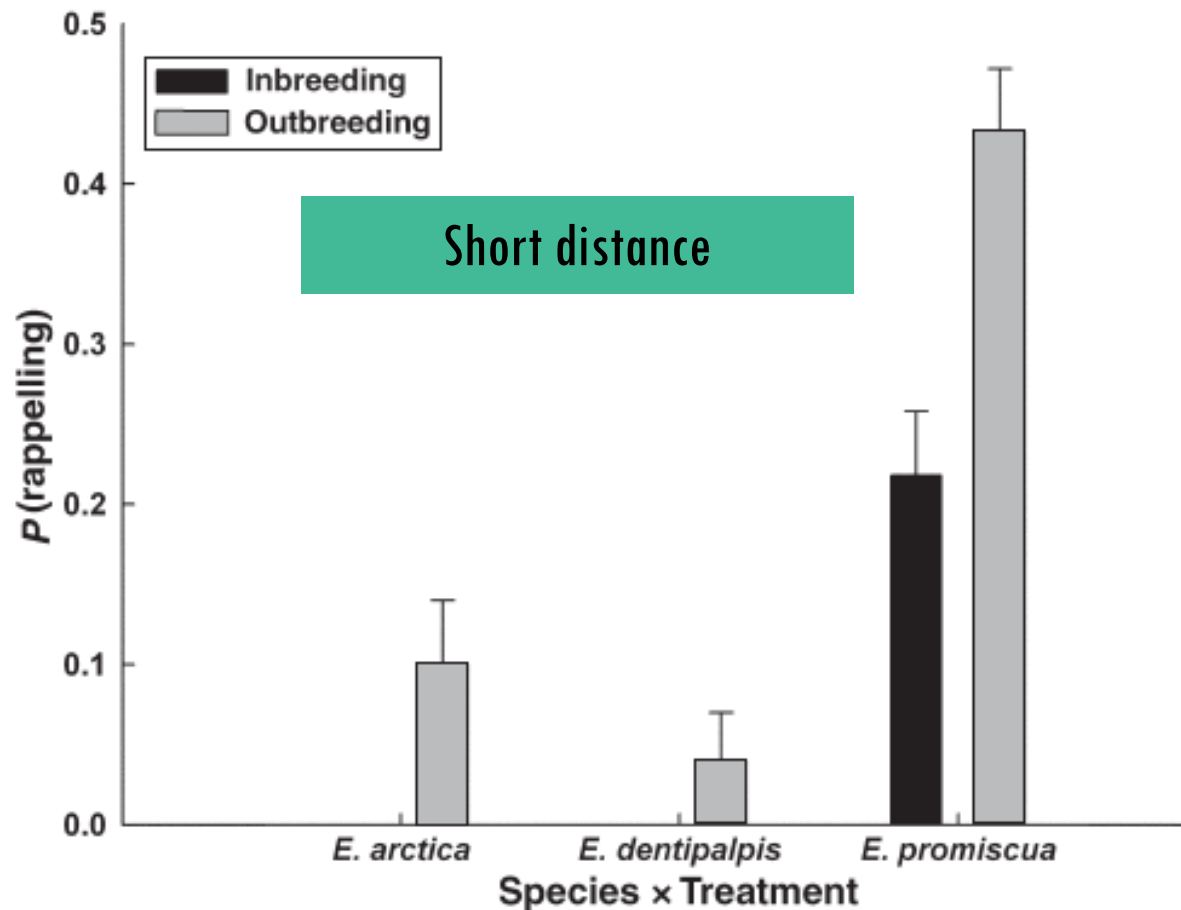
Roze et Rousset 2005



Genomics deleterious
mutation rate

7. IS DISPERSAL AN INBREEDING AVOIDANCE STRATEGY?

Bonte 2010

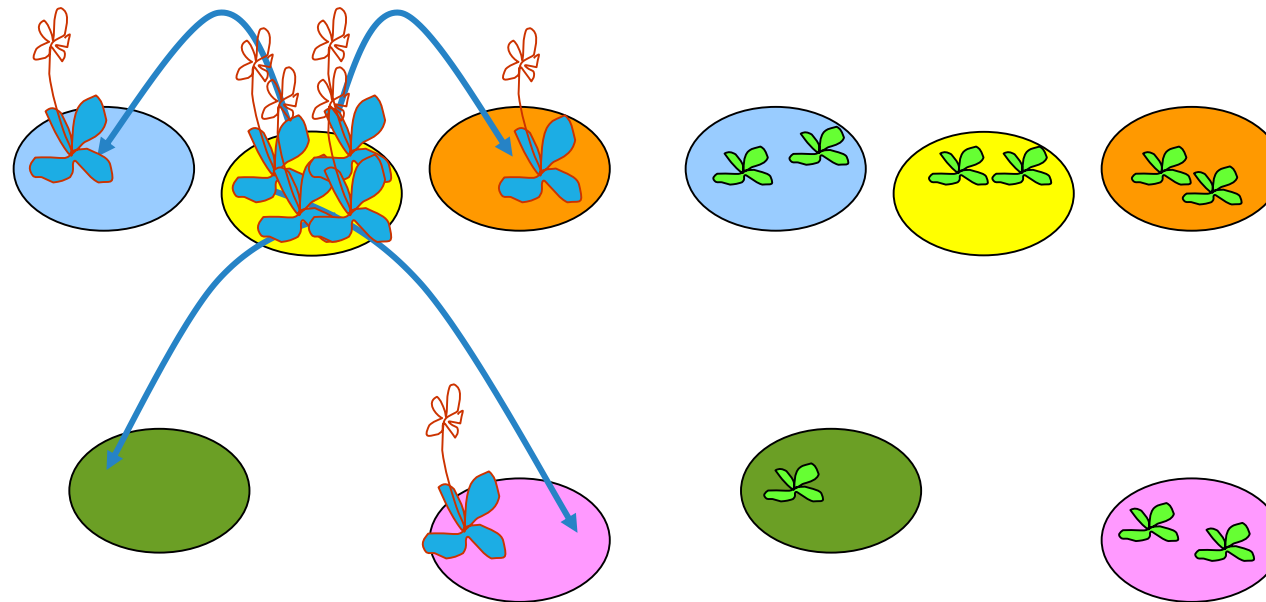


8. IS DISPERSAL AN ADAPTATION TO EPHEMERAL HABITATS?

Random fluctuations

van Valen 1971
Levin et al. 1984
Olivieri et al 1995

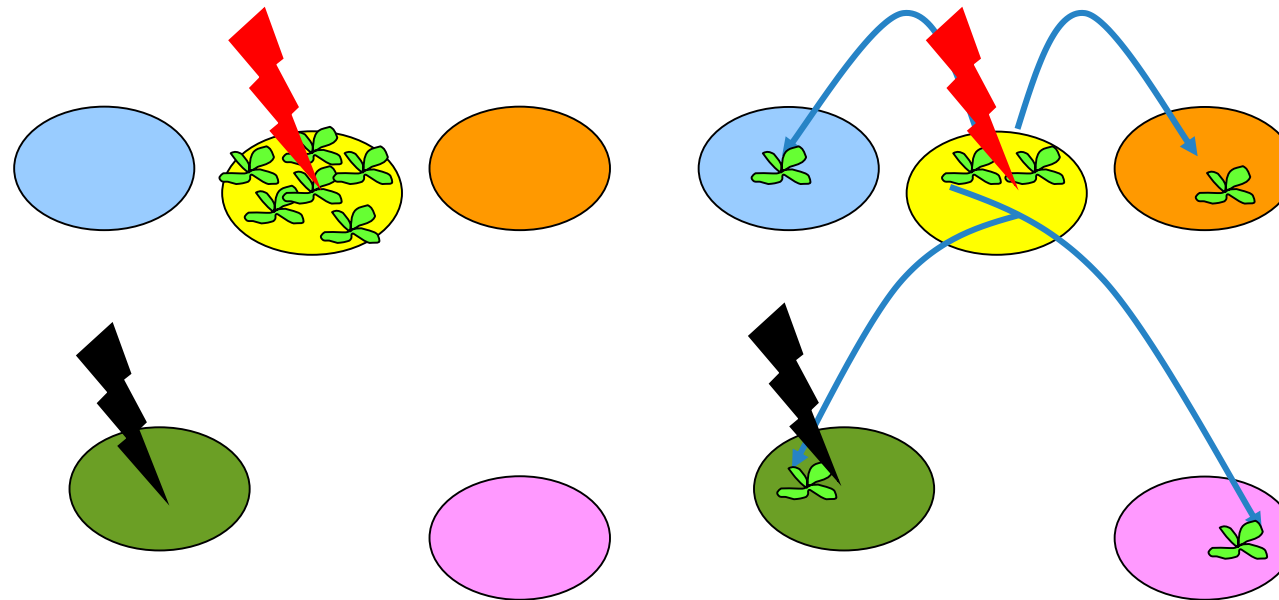
Avoiding crowded
conditions



8. IS DISPERSAL AN ADAPTATION TO EPHEMERAL HABITATS?

Random fluctuations

bet-hedging



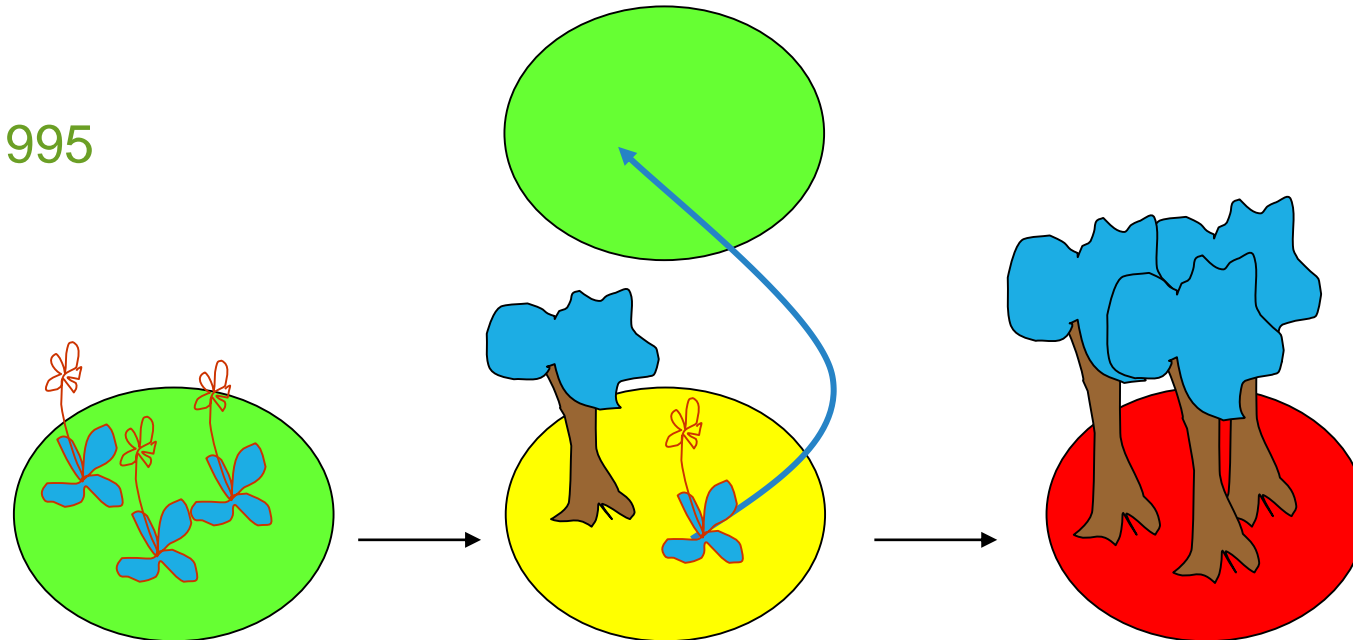
Venable and
Brown 1988

8. IS DISPERSAL AN ADAPTATION TO EPHEMERAL HABITATS?

Predictable changes

Avoiding deteriorated habitat

Olivieri et al. 1995

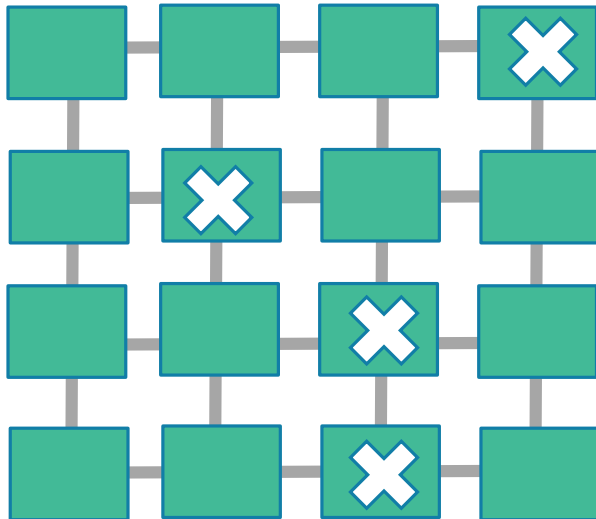


8. IS DISPERSAL AN ADAPTATION TO EPHEMERAL HABITATS?

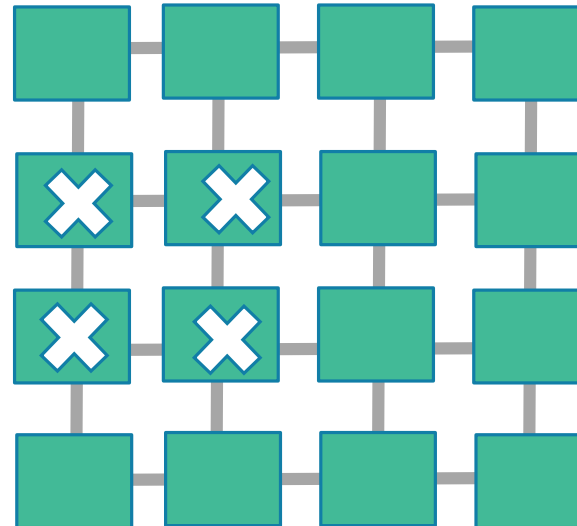
Experimental evolution of dispersal

Fronhofer *et al.* 2014

Random extinction



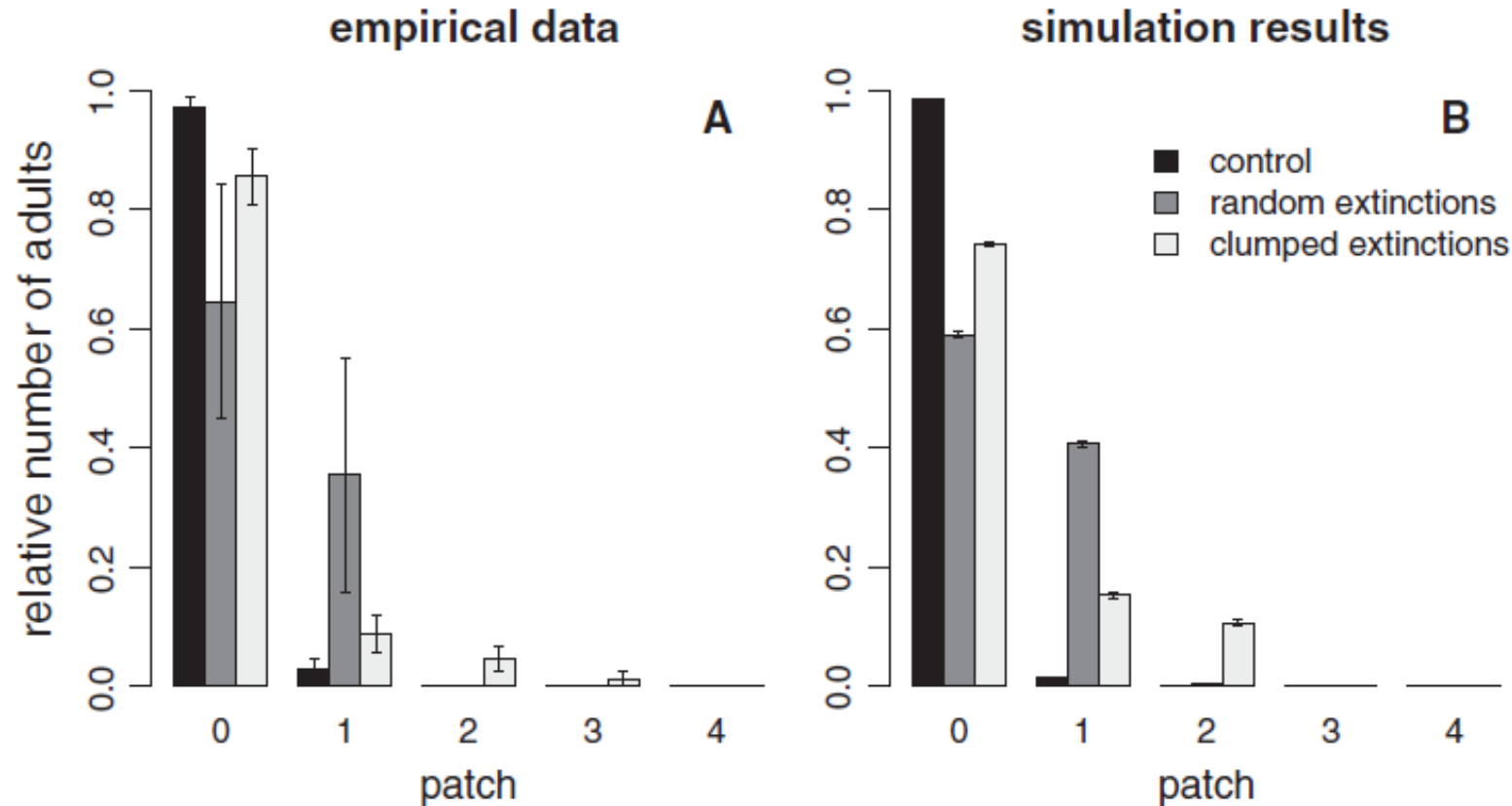
Clumped extinction



10 generations:
Dispersal assays

8. IS DISPERSAL AN ADAPTATION TO EPHEMERAL HABITATS?

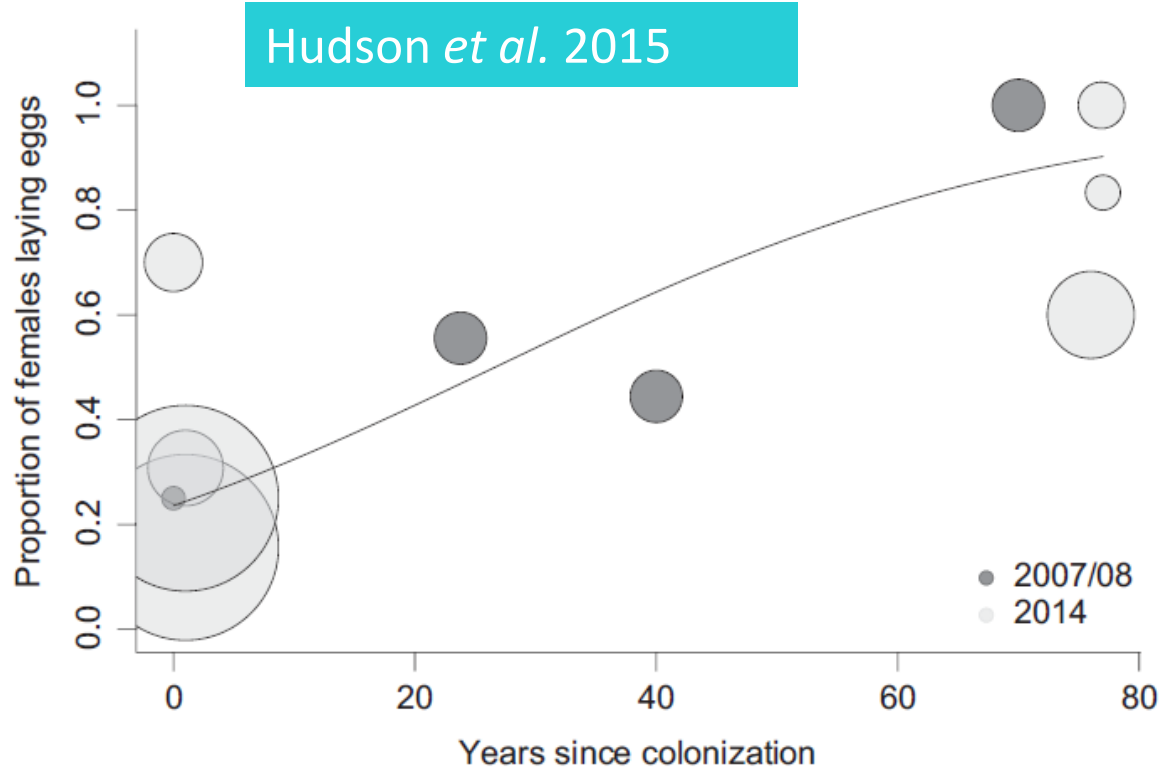
Fronhofer *et al.* 2014



Dispersal distance and emigration increase with random extinction

Higher dispersal distance but lower emigration with clumped extinction

9. HOW COSTLY IS DISPERSAL?



Cane toads from the front edge have a delayed reproduction

Cost of dispersal or evolution of different life history at the front edge?

For a review see

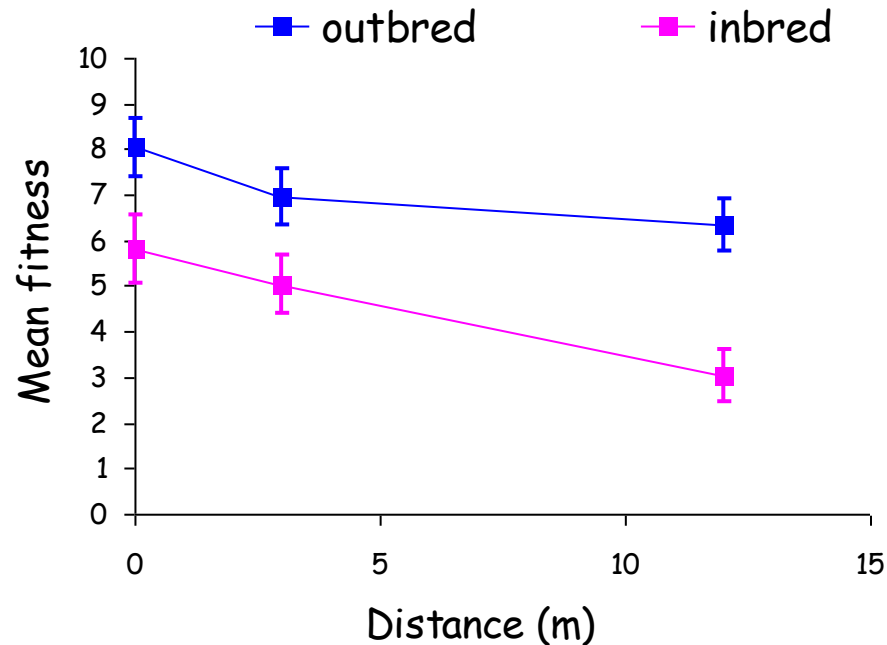
Bonte *et al.* 2012

9. HOW COSTLY IS DISPERSAL?

Foreign environments are dangerous

Social

Local adaptation

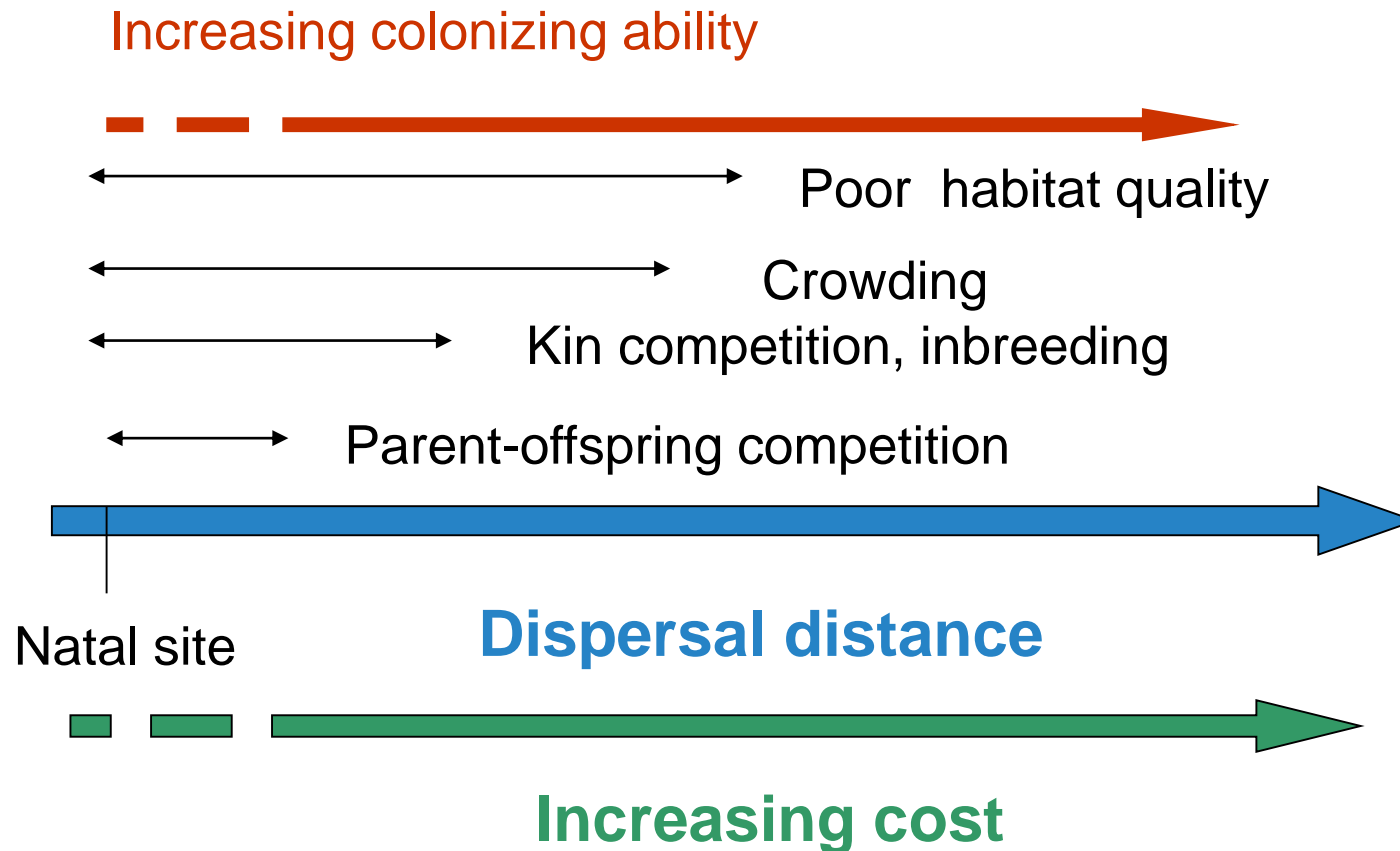


Xenophobia in mole-rats

Schmitt et Gamble 1990

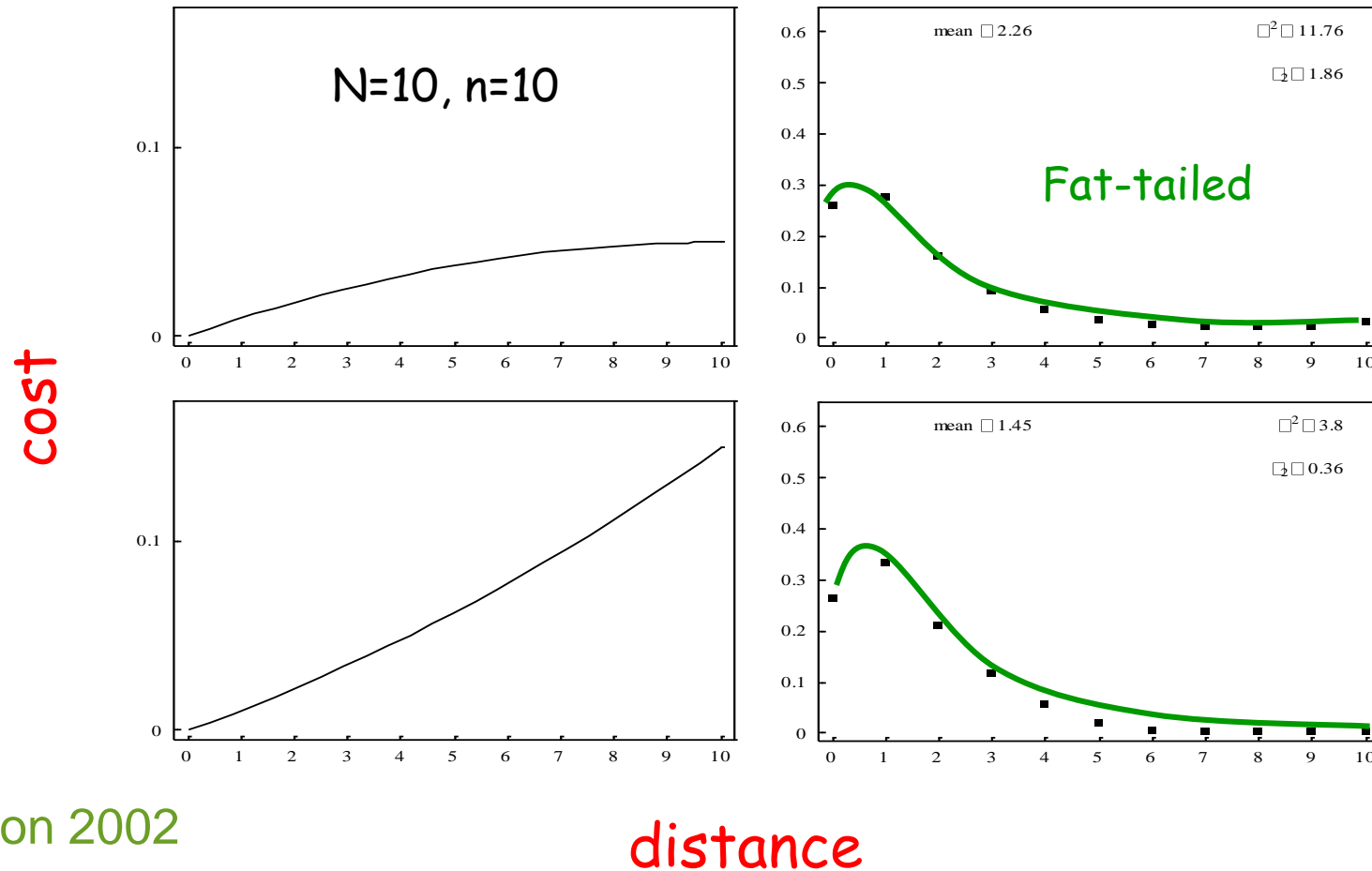
Mastomys natalensis

10. IS LONG-DISTANCE DISPERSAL A CONSEQUENCE OF SELECTION FOR SHORT-DISTANCE DISPERSAL?



10. IS LONG-DISTANCE DISPERSAL A CONSEQUENCE OF SELECTION FOR SHORT-DISTANCE DISPERSAL?

Models



10. IS LONG-DISTANCE DISPERSAL A CONSEQUENCE OF SELECTION FOR SHORT-DISTANCE DISPERSAL?

Several studies suggest that short and long distance dispersal evolve independantly or respond differently to various cues

Fronhofer *et al.* 2014

Bitume *et al.* 2013

Mechanistic models of seed dispersal suggest that different traits (different vectors, different process) explain short and long distance dispersal

Schurr *et al.* In prep

FUTURE ISSUES

1. We need more information about both the heritability of dispersal kernels and the heritability of dispersal reaction norms to environmental cues.
2. We need models to focus on the evolution of the distribution of dispersal distances to better understand how the different evolutionary forces shape such distribution and to better relate theoretical predictions to data.
3. We need to better understand empirically and model theoretically the ontogeny of dispersal to predict the evolution of environmental effects on dispersal.
4. We need to produce short-term predictions about evolutionary changes in dispersal in the context of global change.

On-going

On-going

On-
going?

Starting



DISPERSAL AND AGING

Original research

DISPERSAL SYNDROMES

Dispersal syndrome = patterns of covariation of morphological, behavioural, and/or life history traits associated with dispersal

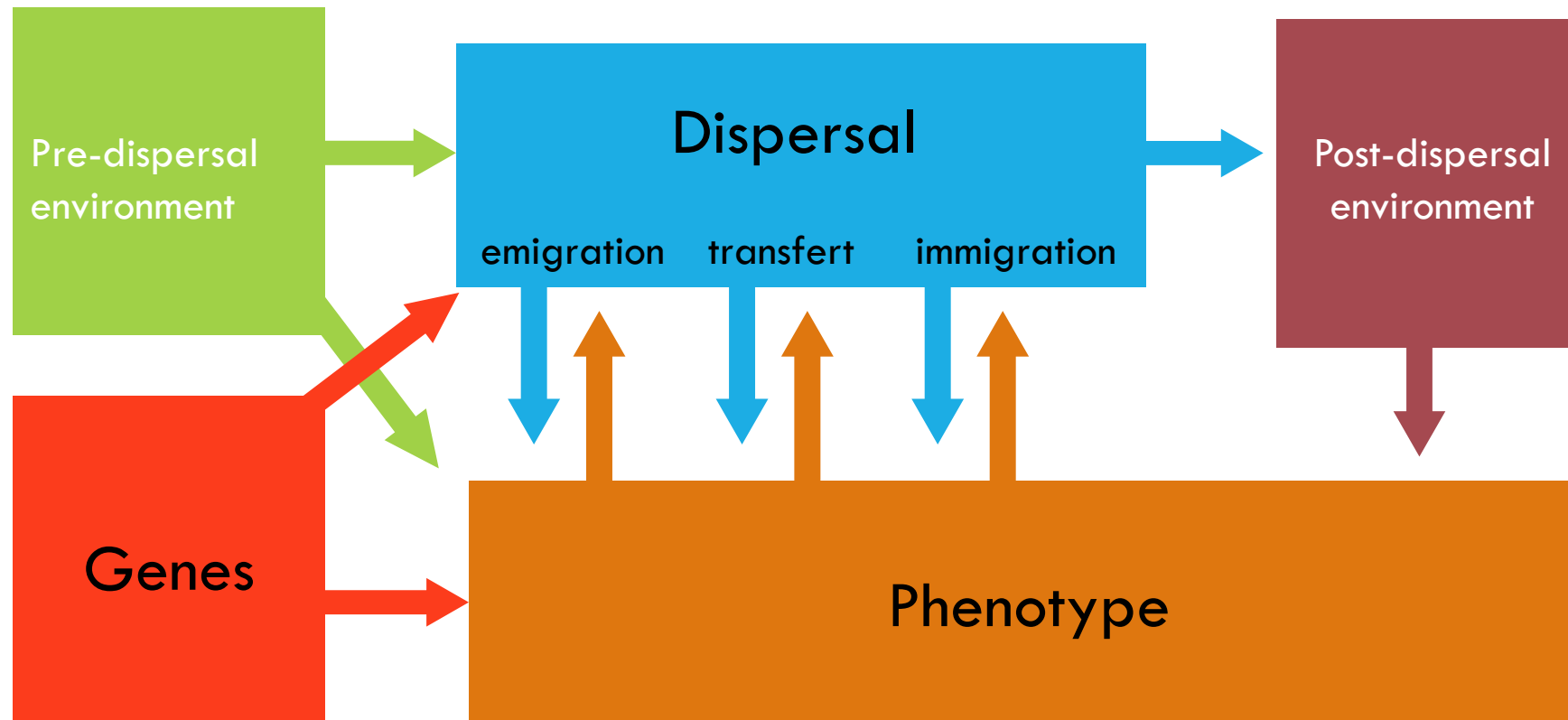
Proximate causes

Ronce & Clobert 2012

Ultimate causes

DISPERSAL SYNDROMES

Ronce & Clobert 2012

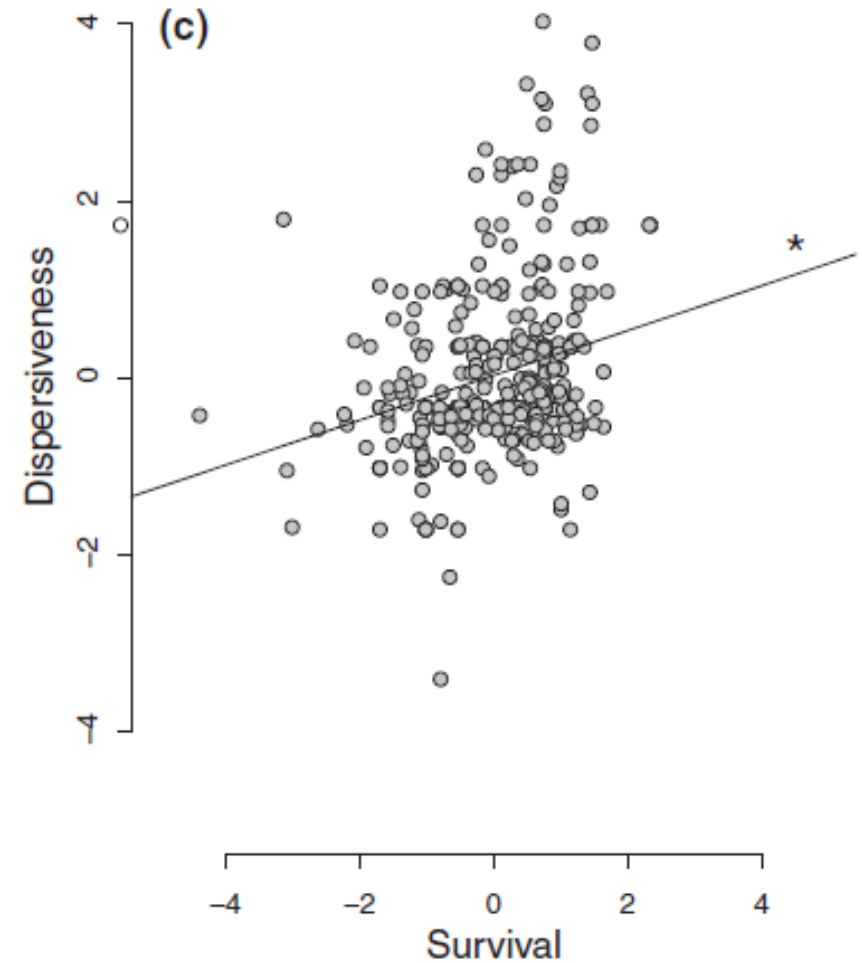
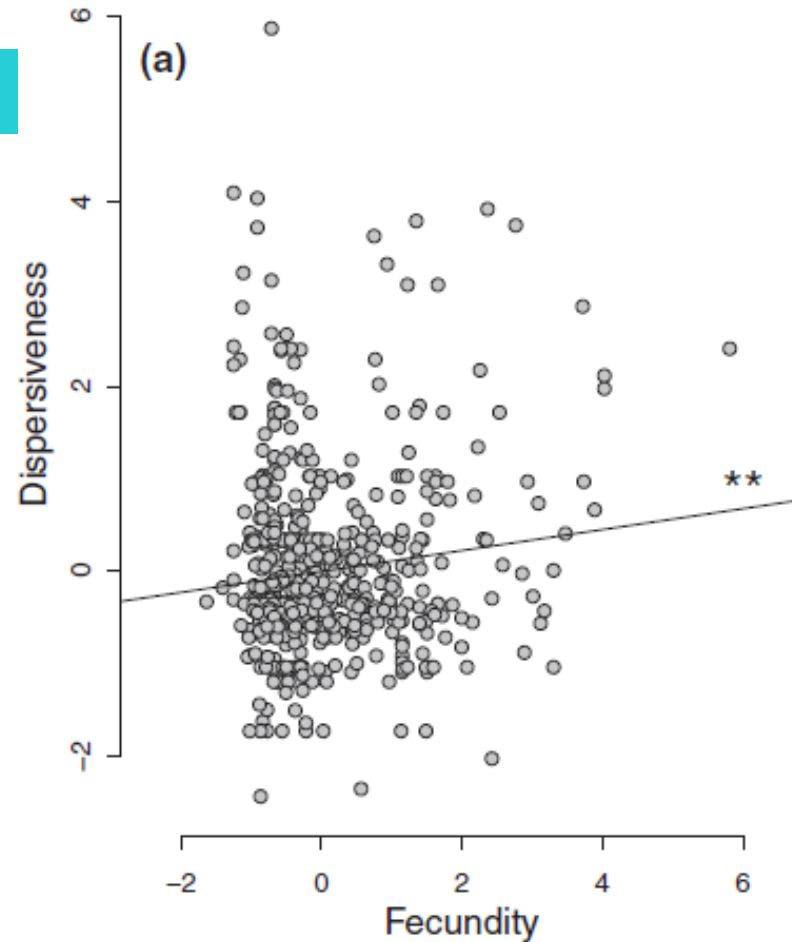


DISPERSAL SYNDROMES

Stevens et al. 2014

> 700 species

High level of
idiosynchrasy



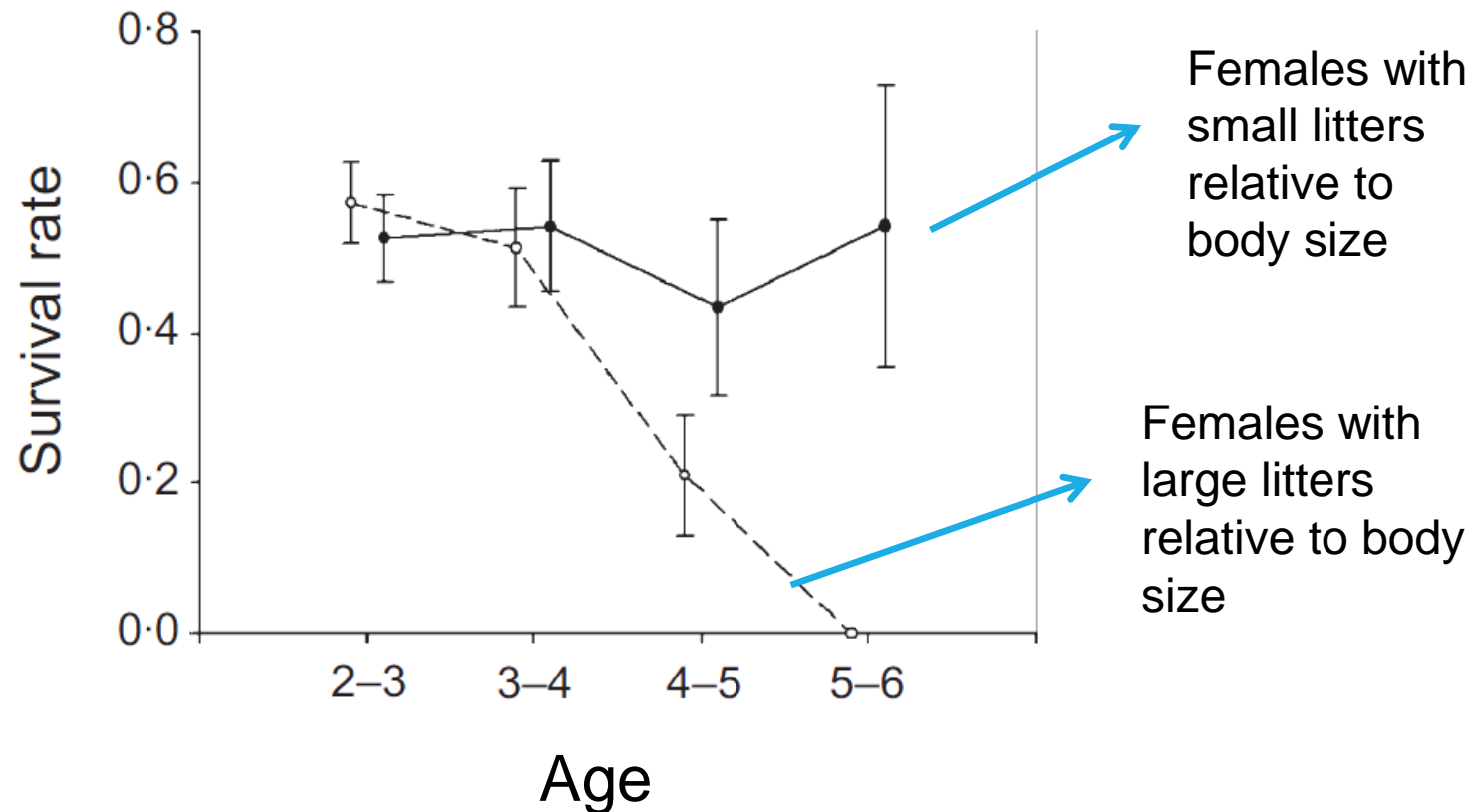
DISPERSAL SYNDROMES

Life history traits vary with age

Do dispersal syndromes vary with age ?

Does dispersal influence the aging trajectory?

AGING IN A LIZARD

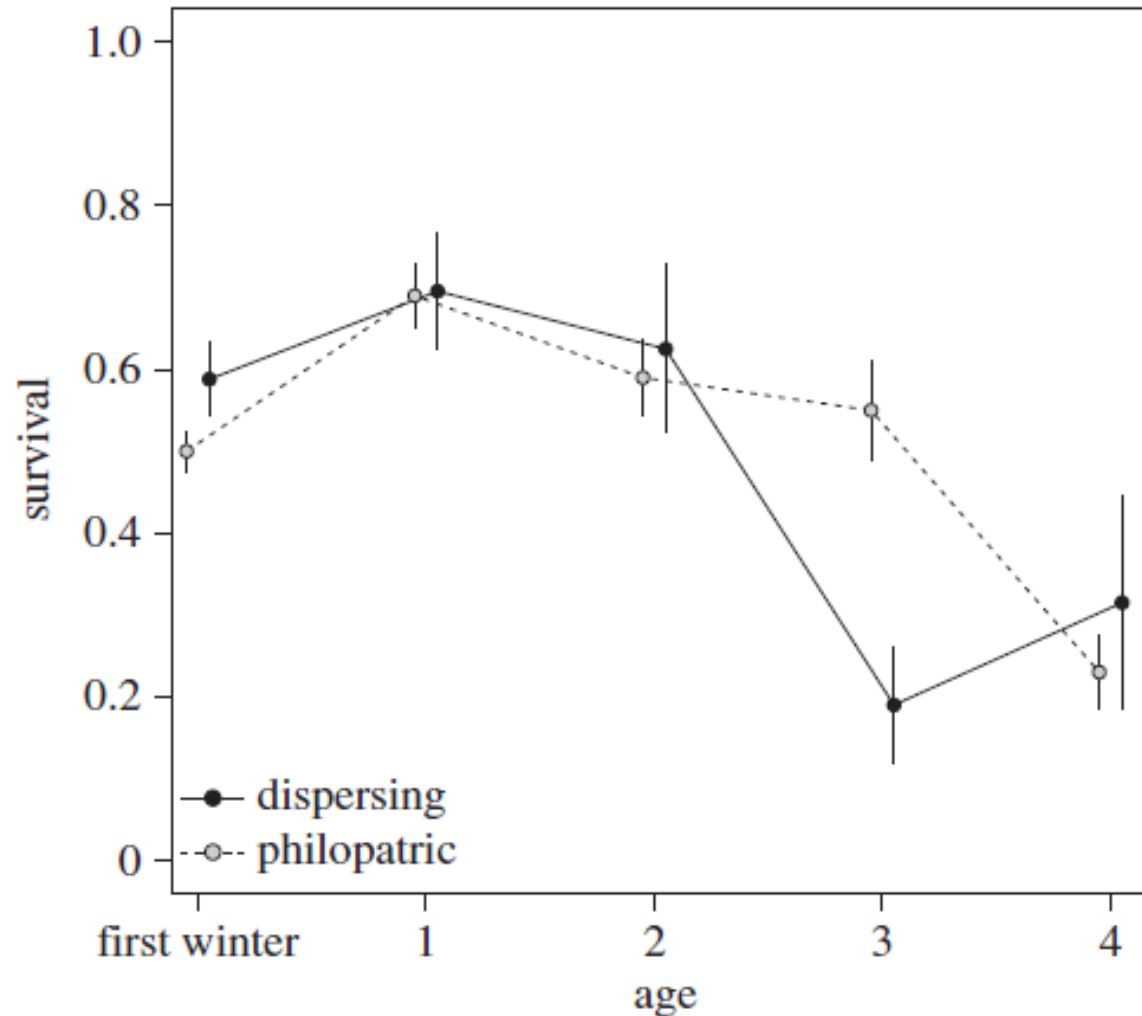


Zooteca vivipara

Massot et al. 2011

Females with a high reproductive effort age more rapidly

AGING IN A LIZARD

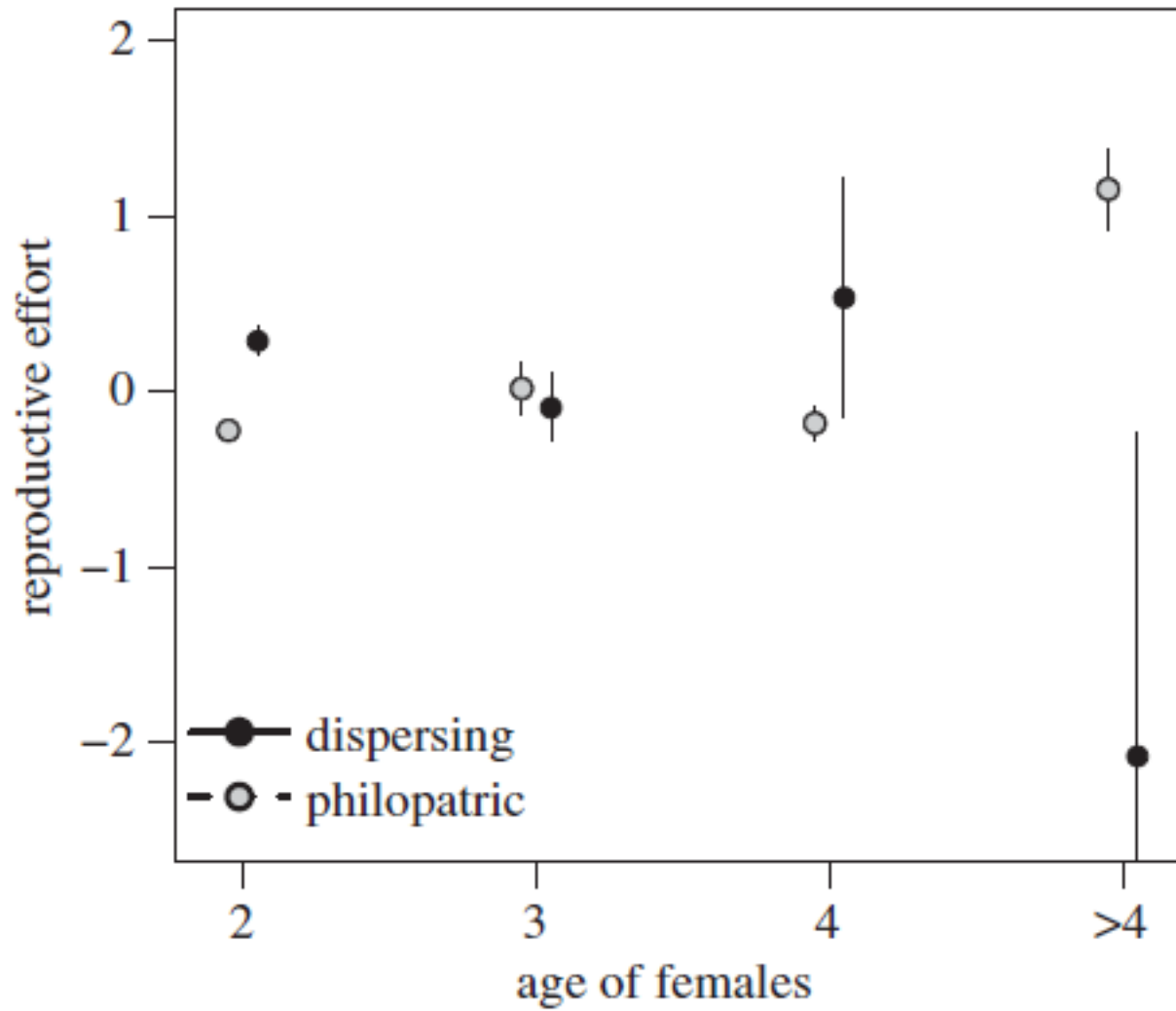


Zooteca vivipara

Cotto et al. 2015

Philopatric females age more slowly than females that have dispersed when young

AGING IN A LIZARD



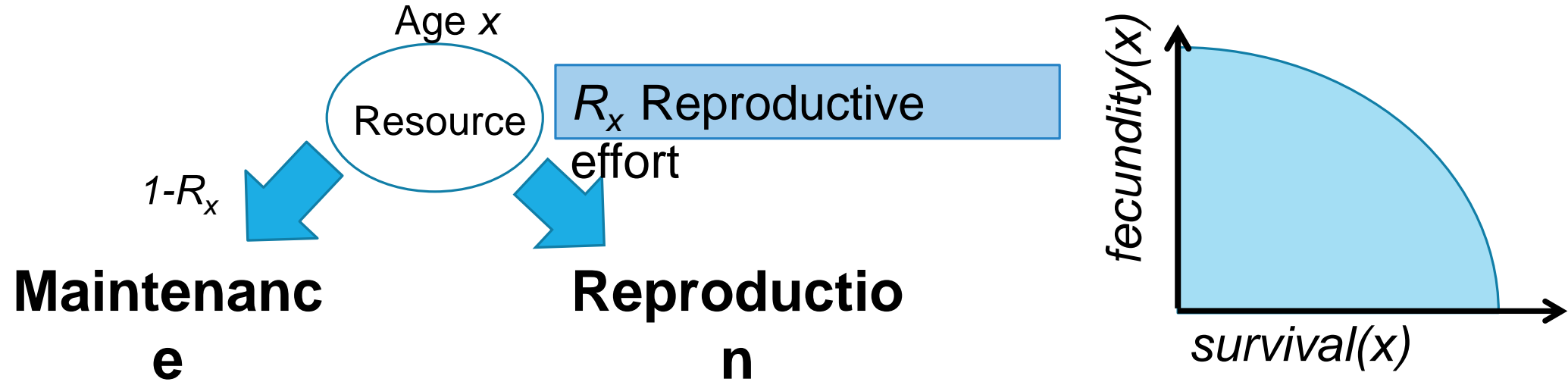
Cotto et al. 2015

Young philopatric females have a lower reproductive effort than young females having dispersed

Reverse pattern in old females

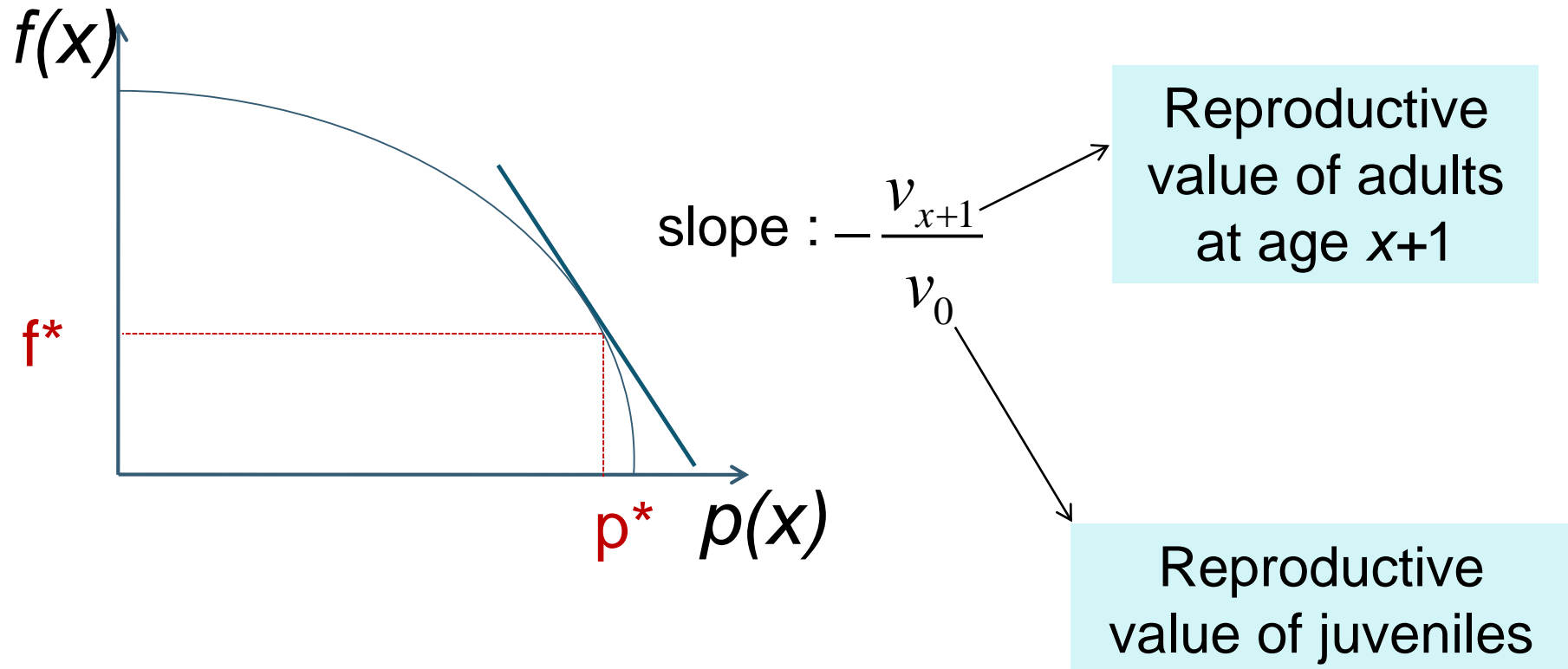
EVOLUTION OF AGE SPECIFIC REPRODUCTIVE EFFORT

Antagonistic pleiotropy: trade-off between survival and reproduction



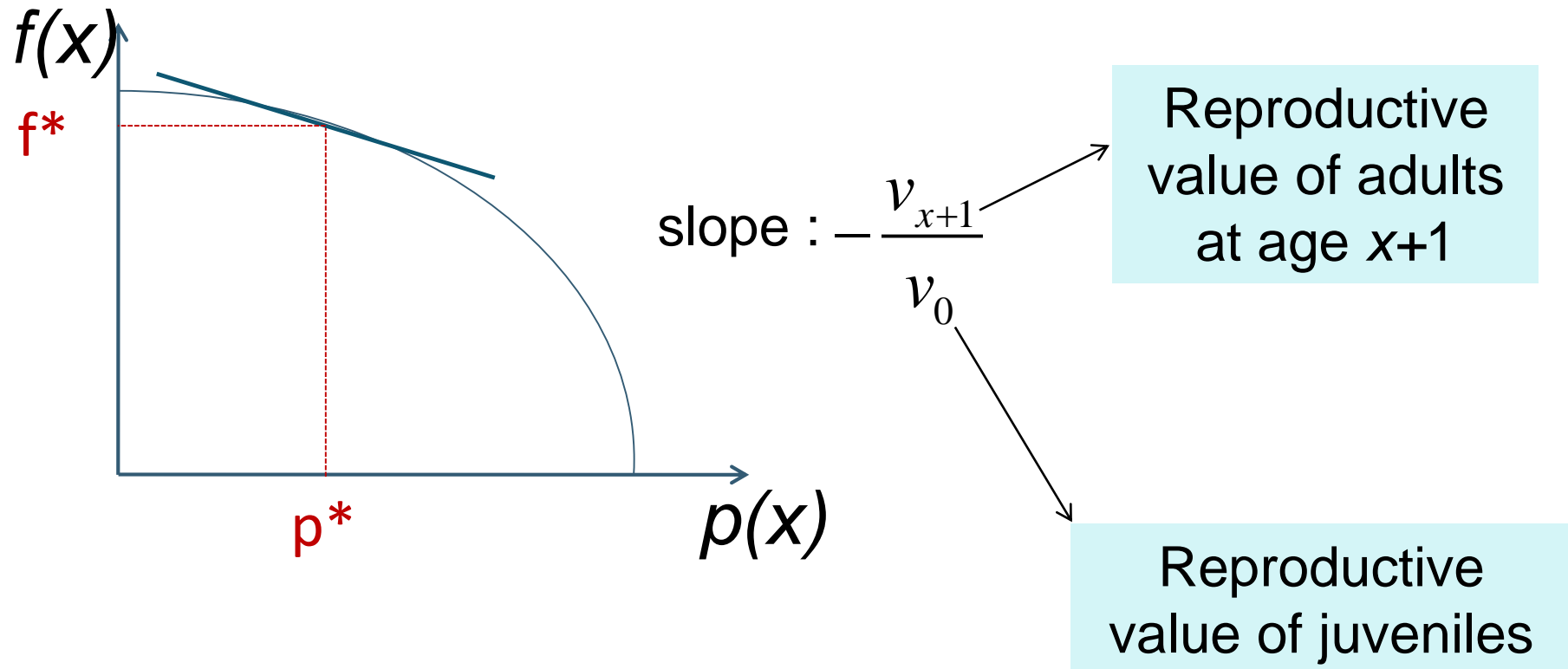
EVOLUTION OF AGE SPECIFIC REPRODUCTIVE EFFORT

Optimal allocation



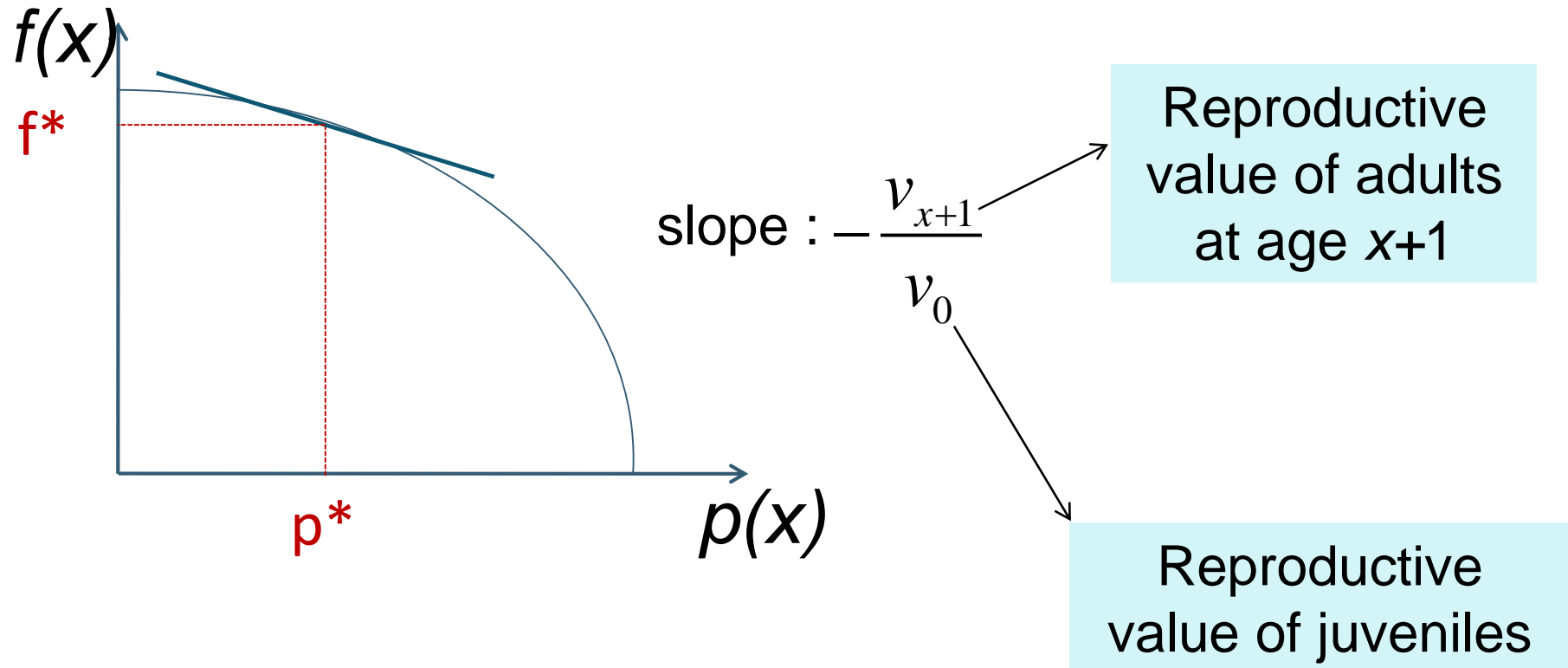
EVOLUTION OF AGE SPECIFIC REPRODUCTIVE EFFORT

If the reproductive value of adults decline when they age: **reproductive effort increases with age**

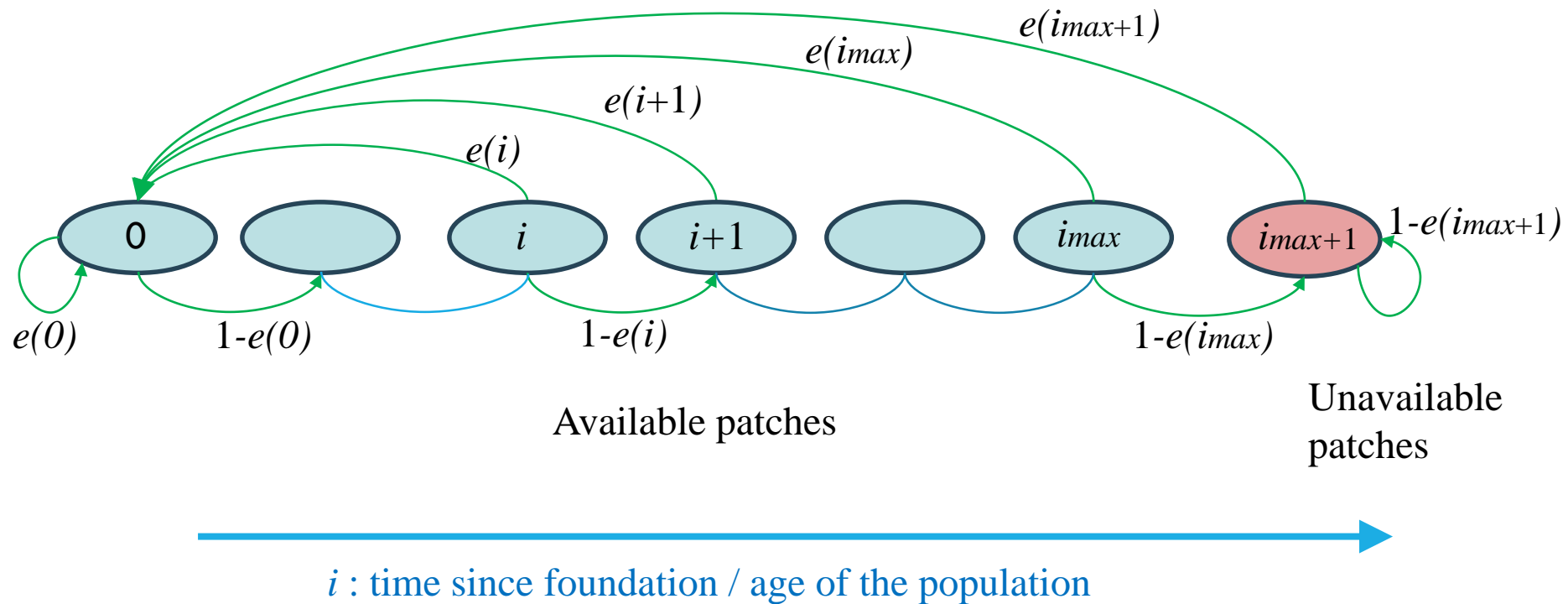


EVOLUTION OF AGE SPECIFIC REPRODUCTIVE EFFORT

If the reproductive value of juvenile increases: **reproductive effort increases**



REPRODUCTIVE EFFORT IN A METAPOPOPULATION



Only juveniles
disperse

Juvenile survival
decreases with the
density of adults
and other juveniles

Island model of
dispersal

REPRODUCTIVE EFFORT AND DISPERSAL

If individuals disperse only when they are juvenile (as in common lizards)

Young individuals having dispersed colonize and reproduce in patches with low density

High reproductive value of juveniles

As they get older, density increases as recolonization proceeds

Low reproductive value of juveniles

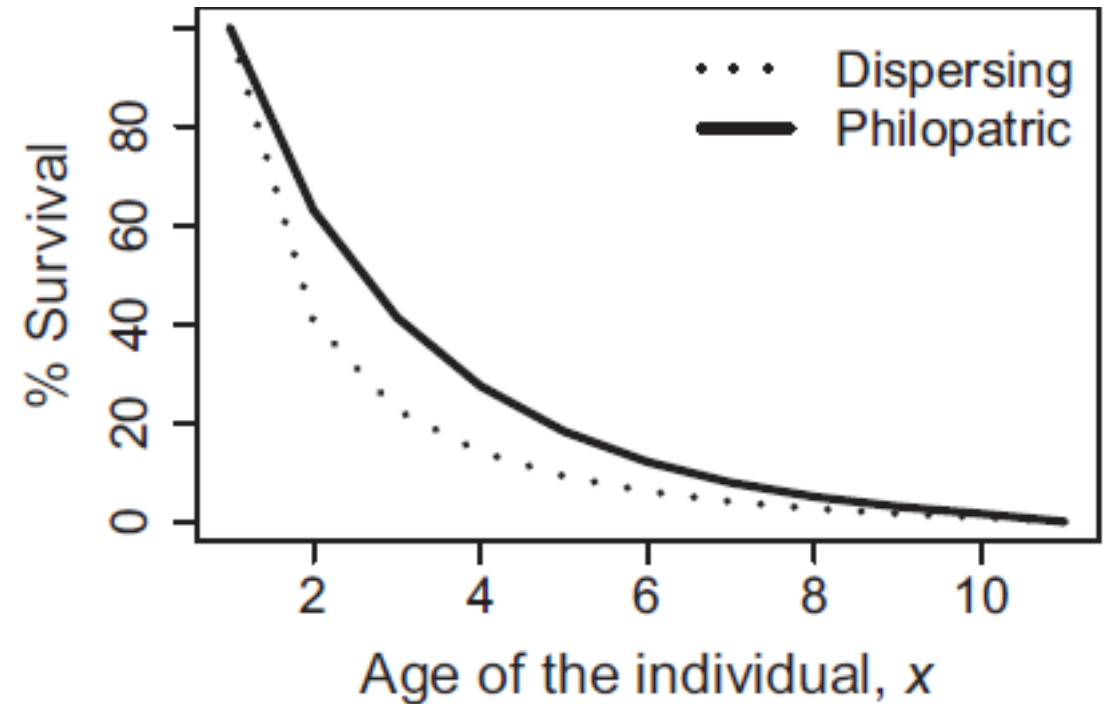
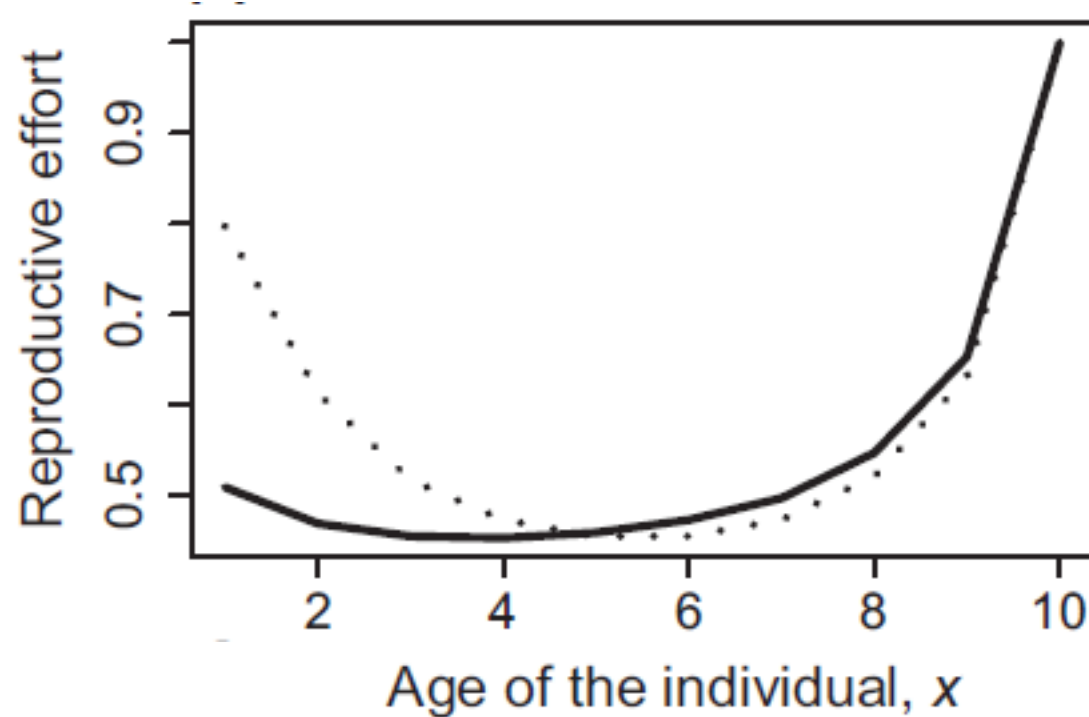
Young and old philopatric individuals reproduce in occupied patches with high density

Low reproductive value of juveniles

REPRODUCTIVE EFFORT AND DISPERSAL

Theoretical predictions in a metapopulation

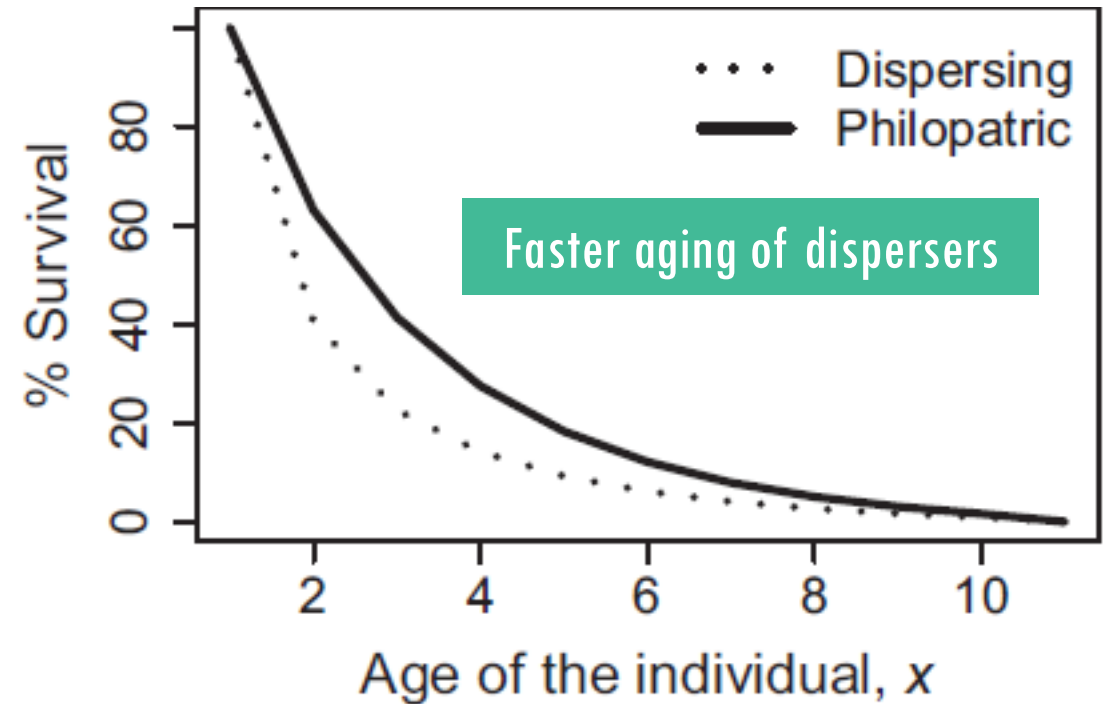
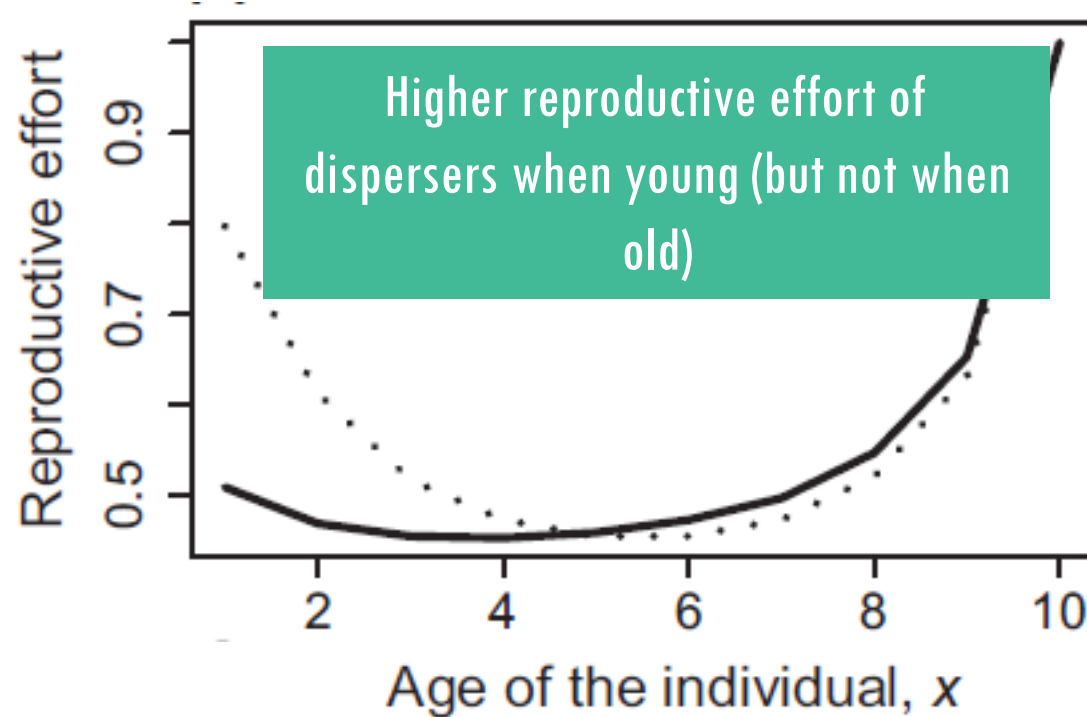
Cotto et al. 2014



REPRODUCTIVE EFFORT AND DISPERSAL

Theoretical predictions in a metapopulation

Cotto et al. 2014



REPRODUCTIVE EFFORT AND DISPERSAL

Disperser and philopatric individuals do not have the same optimal life history because they live in different environments

Life histories are not necessarily optimized!

AGING AS A FAILURE TO ADAPT

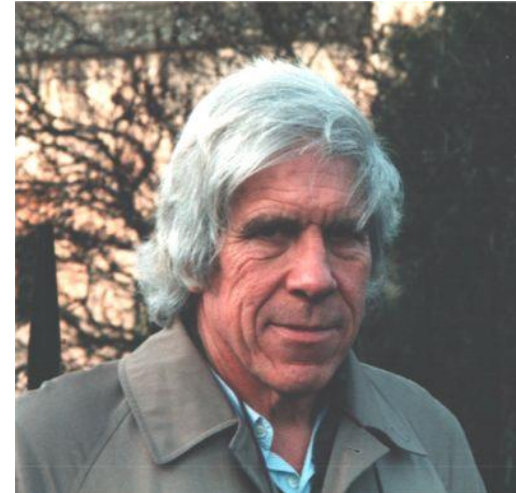
The moulding of senescence by natural selection

Hamilton 1966

Population growth rate measures fitness

Mutations with age-specific effects

Force of selection acting on such mutations



senescence is an inevitable outcome
of evolution

... cannot be avoided by any
conceivable organism

AGING AS A FAILURE TO ADAPT

Force of selection on age specific survival

Hamilton 1966

$$H_p(x) \equiv \frac{\partial r}{\partial \ln p_x} = \frac{\sum_{y=x+1}^{+\infty} l_y m_y e^{-ry}}{T}$$

Survival to age y

Age-specific fecundity

Contribution of individuals older than x

Survival from age x to x+1

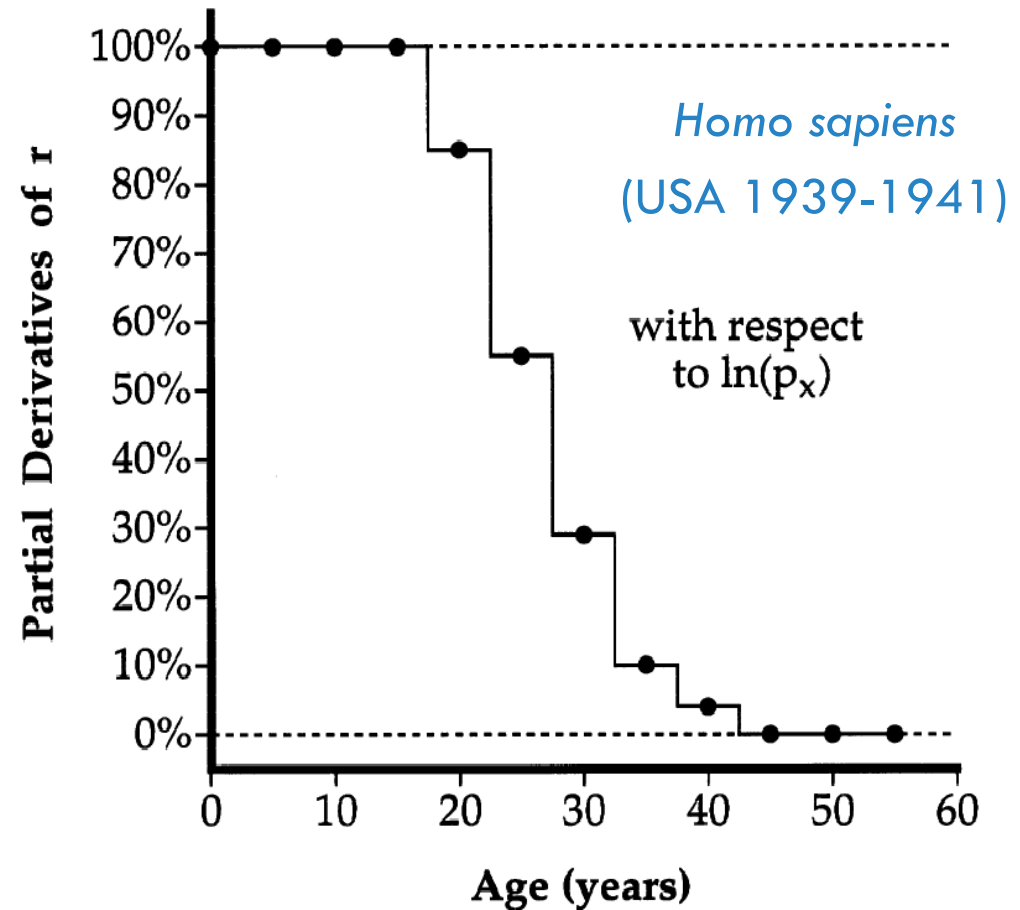
Generation time

Always decline with age!

AGING AS A FAILURE TO ADAPT

Force of selection on age specific survival

Charlesworth &
Williamson 1975



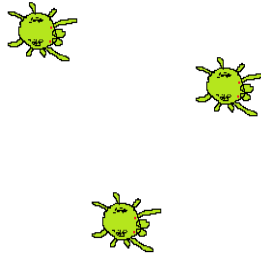
DISPERSAL CONSTRAIN ADAPTATION IN HETEROGENEOUS HABITATS

Cotto & Ronce 2014

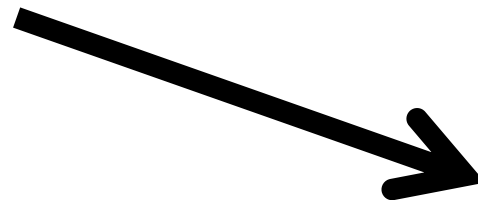
Immigration from a source with a different phenotype



Abundant host plant



Rare host plant with different optimal phenotype

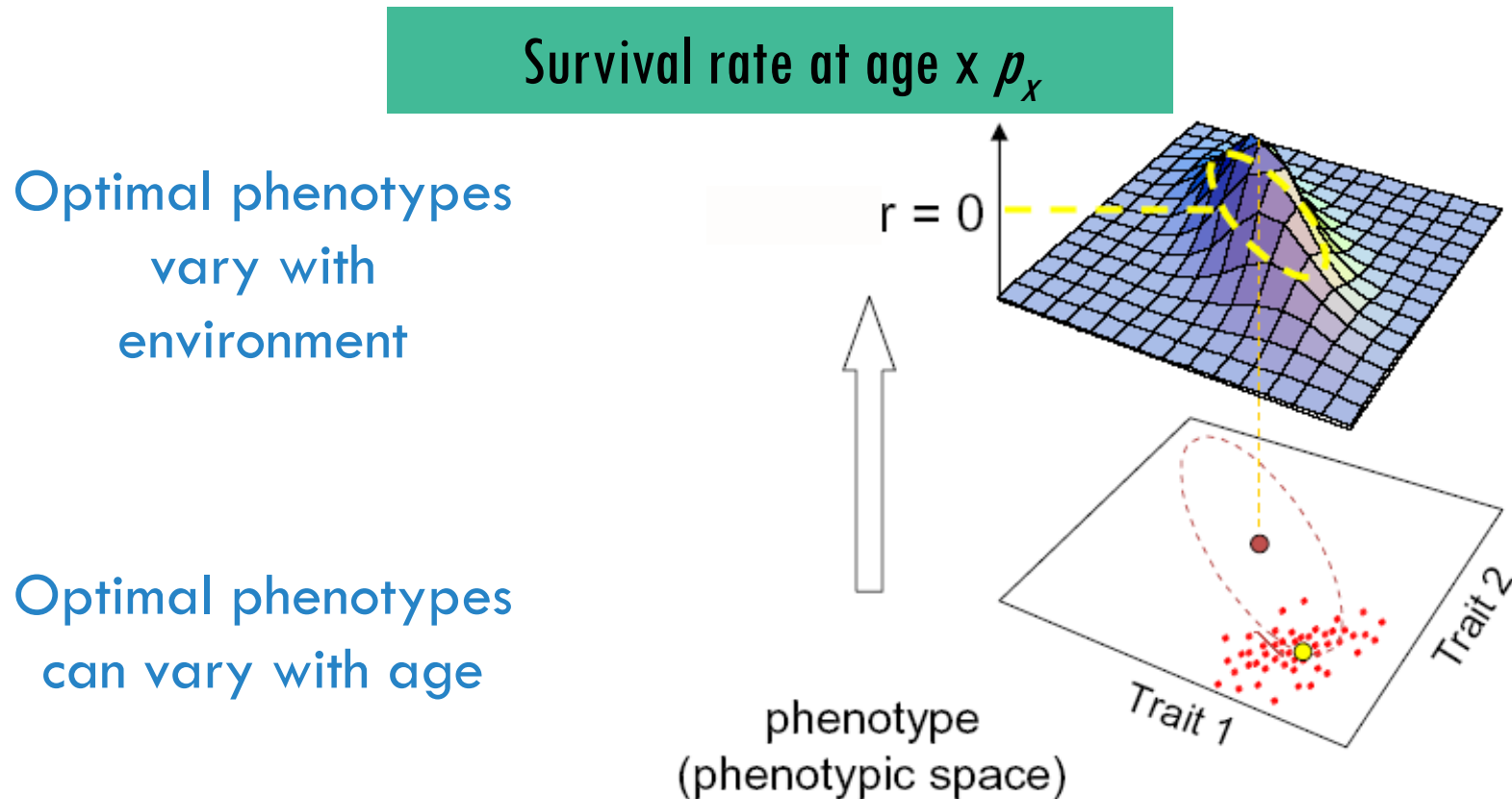


One-way gene flow



DISPERSAL CONSTRAIN ADAPTATION IN HETEROGENEOUS HABITATS

Cotto & Ronce 2014



DISPERSAL CONSTRAIN ADAPTATION IN HETEROGENEOUS HABITATS

Cotto & Ronce 2014

Maladaptation = lag to optimal phenotype

Mean phenotype — optimal phenotype

Immigrant phenotype

$$\frac{\bar{z} - \theta}{V} = m \frac{\bar{z}_I - \theta}{mV + (1 - m)G_x H_x}$$

Proportion of immigrants

Strength of selection on age-specific mortality

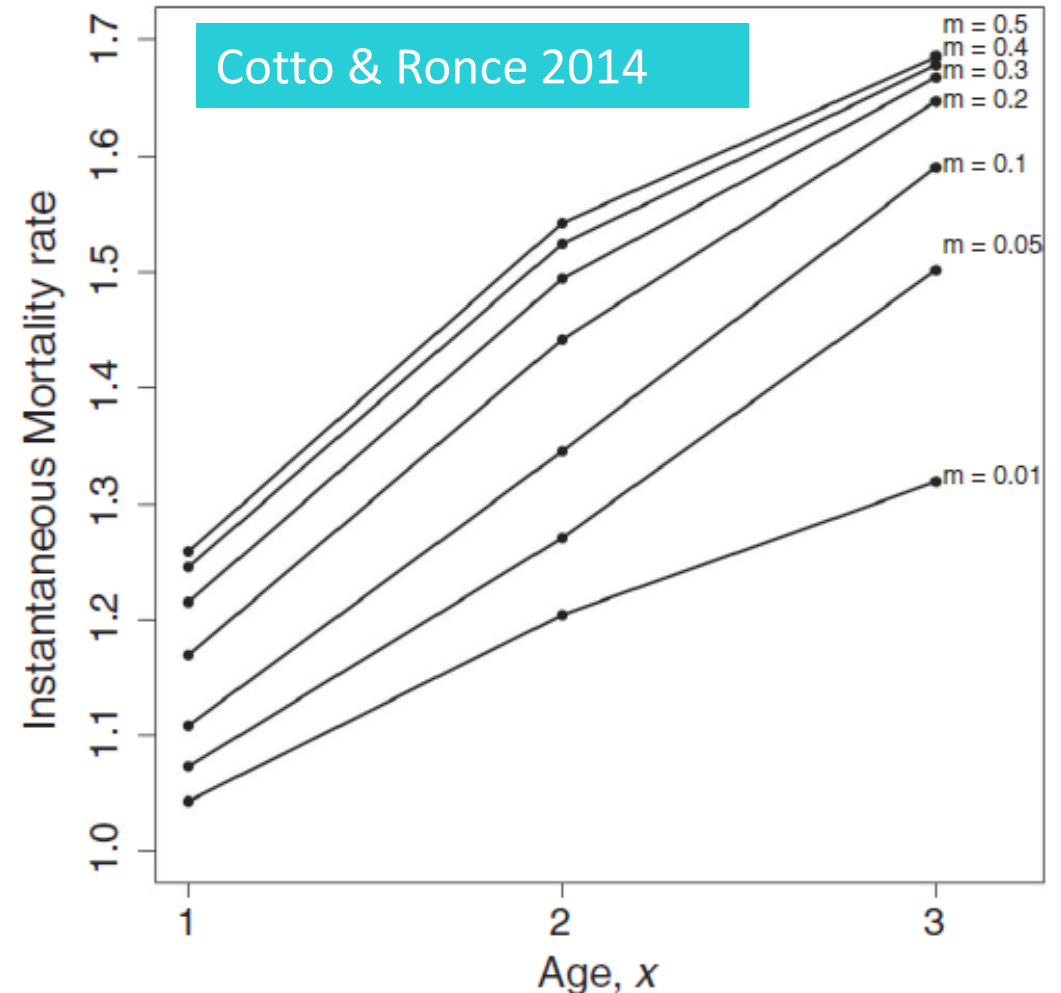
Higher maladaptation for traits expressed at later ages

DISPERSAL ACCELERATES AGING IN HETEROGENEOUS HABITATS

Mortality increases with increasing dispersal from the source for all age classes

Late mortality increases faster when dispersal increases

Faster aging with gene flow in heterogenous environments



DISPERSAL AND AGING

Dispersing individuals may not express the same life history than other individuals:
cost of dispersal or specific adaptation to their lifestyle?

Dispersal modifies the evolution of life history in the whole population: can facilitate or constrain adaptation, or change selection pressures

Conversely, life history traits can affect dispersal evolution

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Jean Clobert



Olivier Cotto



Manuel Massot



Isabelle
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