

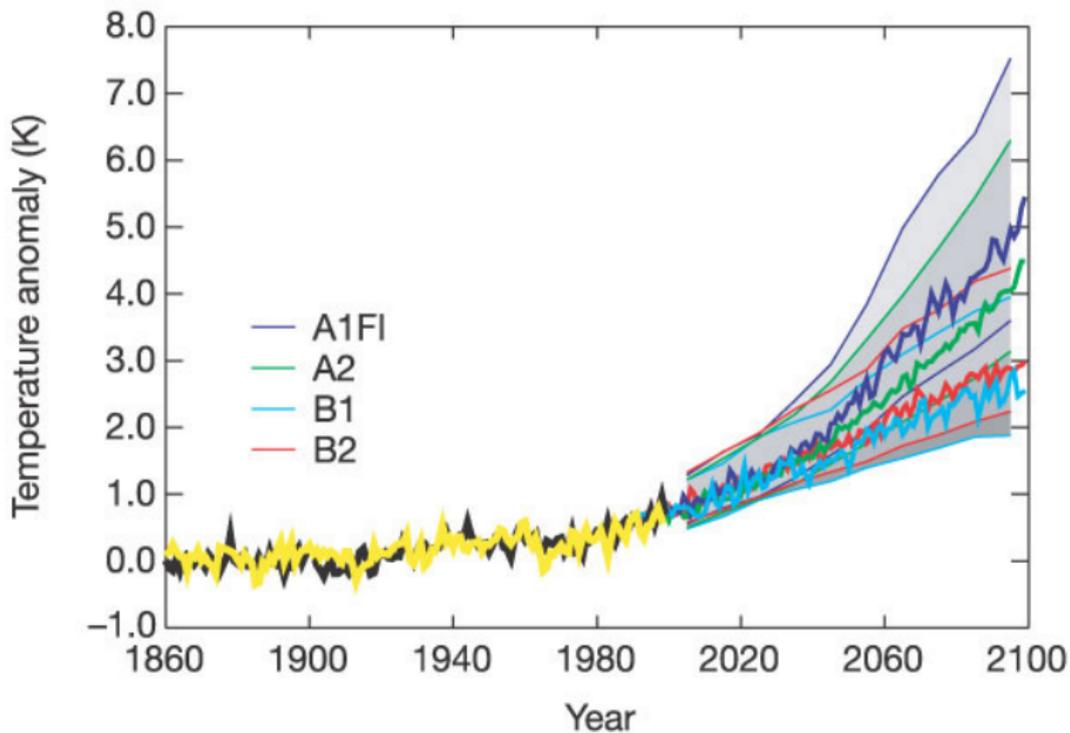
How does pollen dispersal affect species range shift and adaptation under climate change?

Robin Aguilée, Gaël Raoul, François Rousset and Ophélie Ronce

Université Paul Sabatier, Janvier 2016

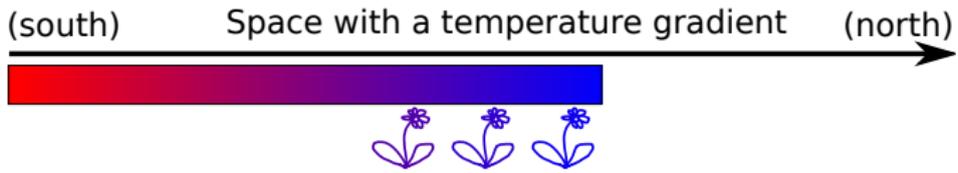


Fast climate change forecasted

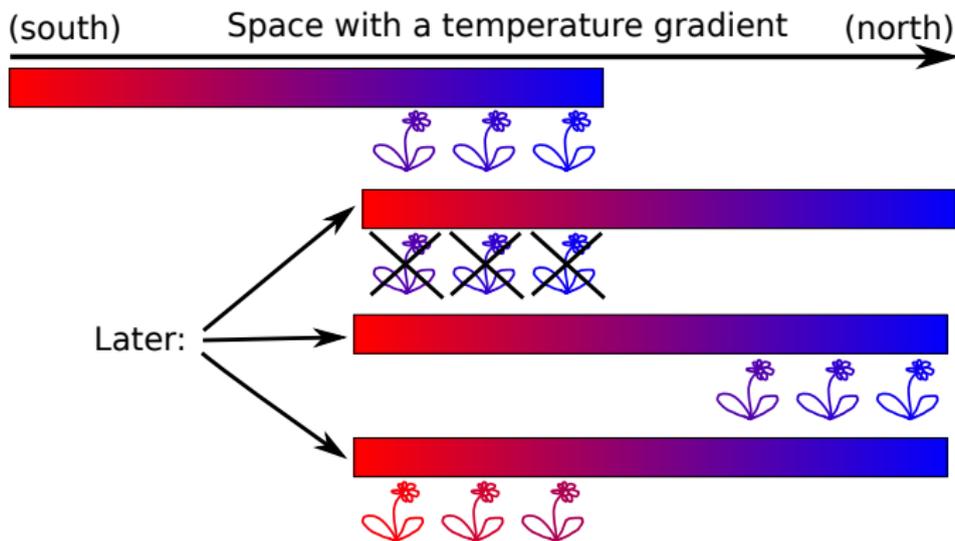


(from Stott & Kettleborough, 2002)

How to escape from extinction under climate change?



How to escape from extinction under climate change?



- 1 Spatial range shift via dispersal
- 2 Climatic niche shift via *in situ* adaptation

Effects of dispersal and feedbacks

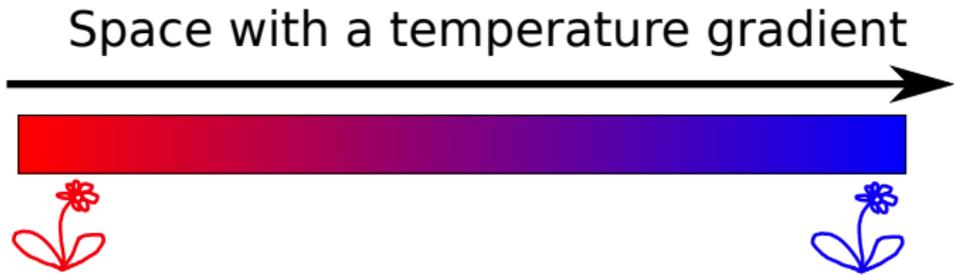
Holt & Gaines (1992), Holt (1996a,b), Holt (1997), Ronce & Kirkpatrick (2001), Holt et al. (2003)

Dispersal

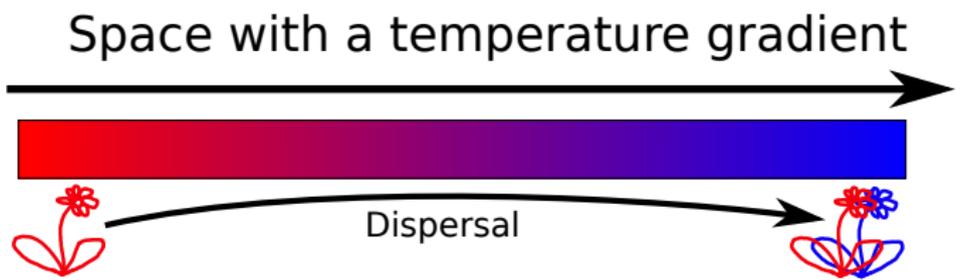
Demography

Adaptation

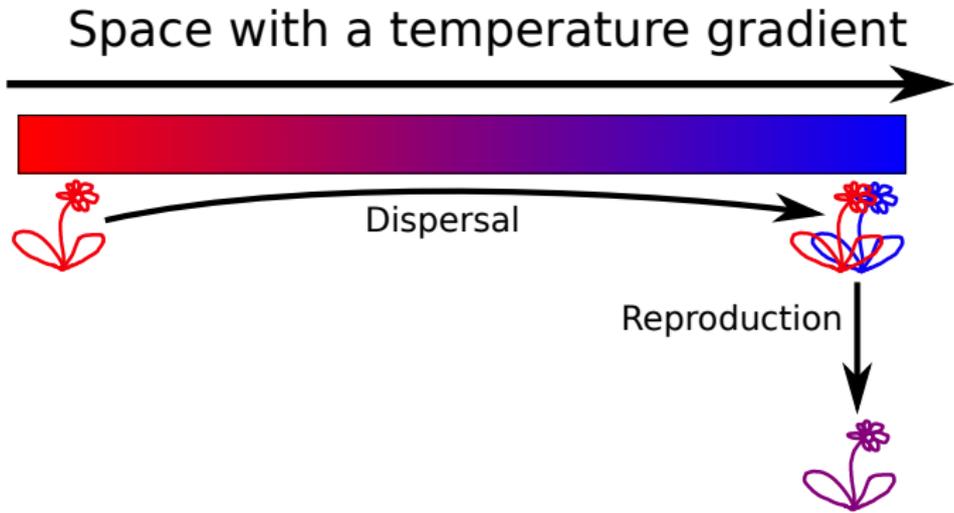
Effects of dispersal and feedbacks



Effects of dispersal and feedbacks

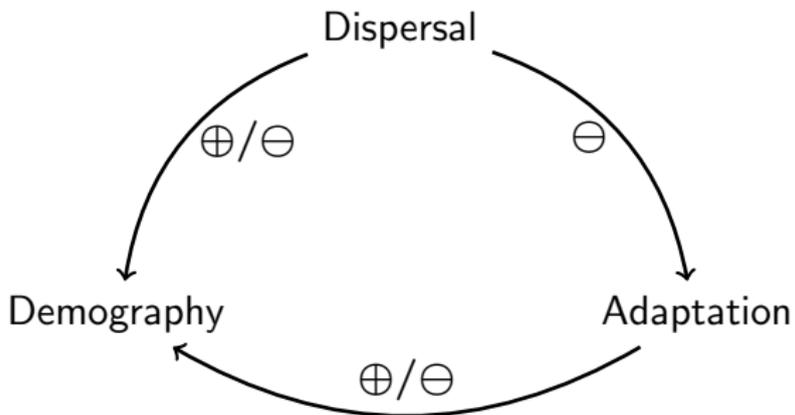


Effects of dispersal and feedbacks



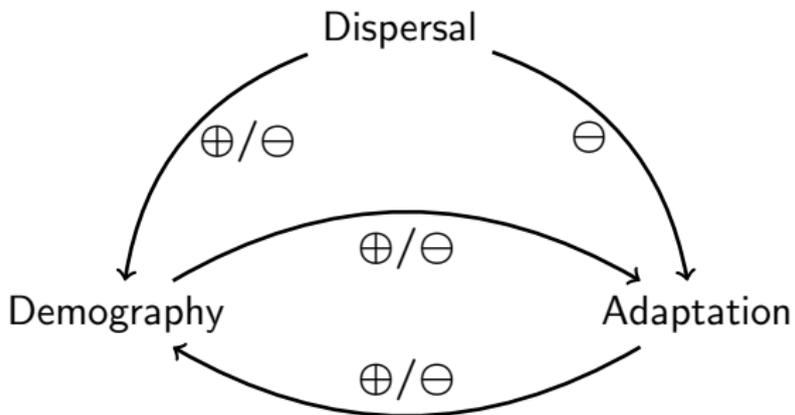
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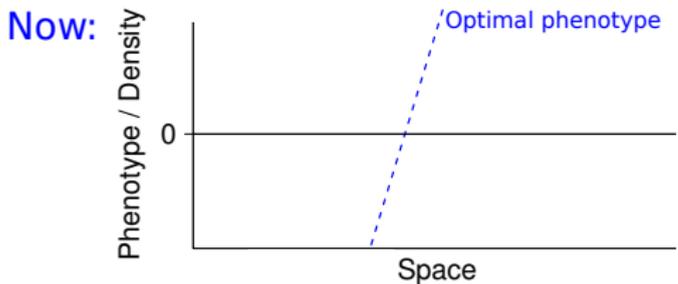
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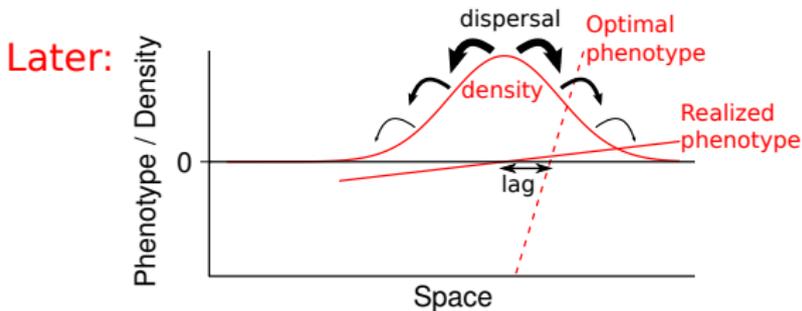
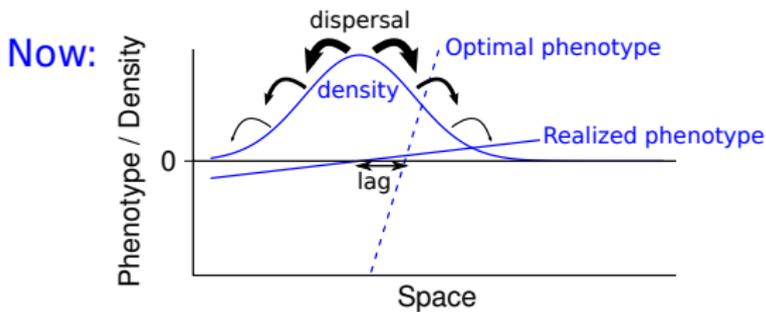
Response to climate shift in **animals**: **spatial** range shift

Pease et al. (1989), Kirkpatrick & Barton (1997), Barton (2001), Polechová et al. (2009),
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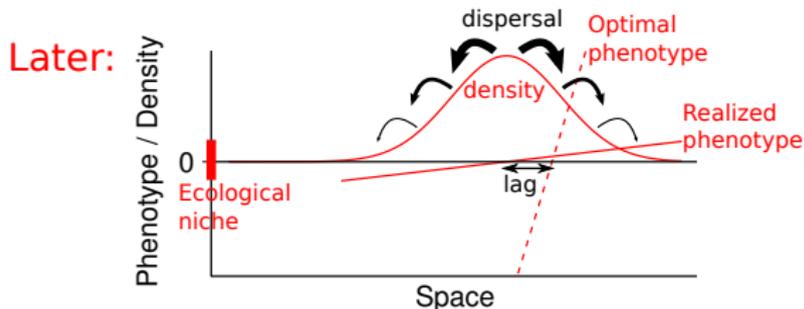
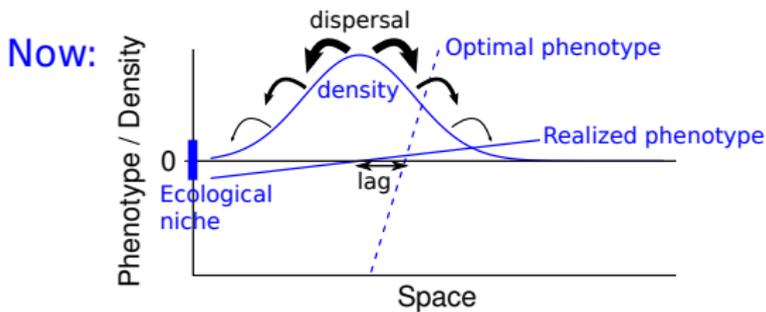
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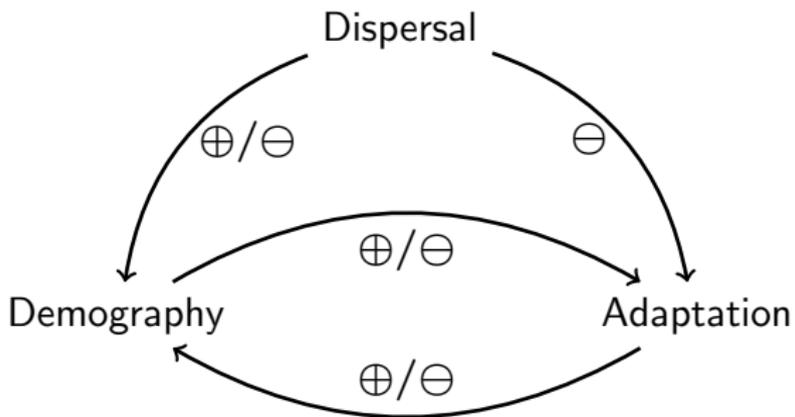
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Spatial range shift only (same speed as climate)

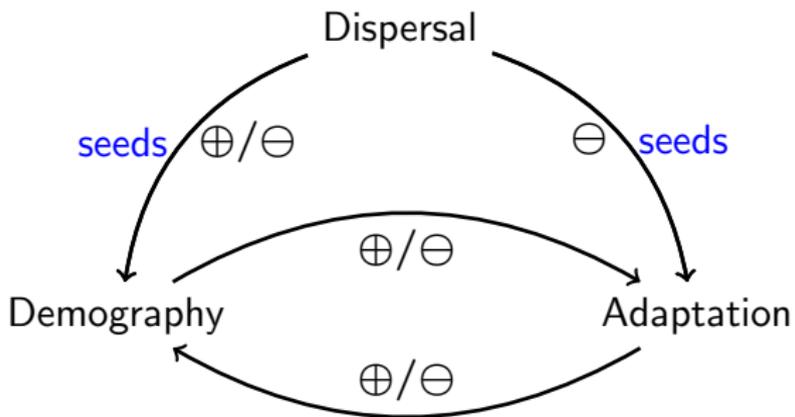
Response to climate change with **pollen** dispersal?

Hu & He (2006), Lopez et al. (2008), Aguilée et al. (2013)



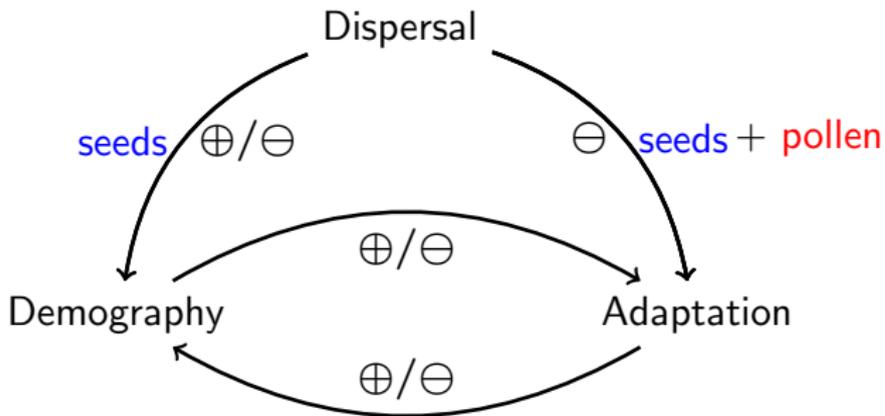
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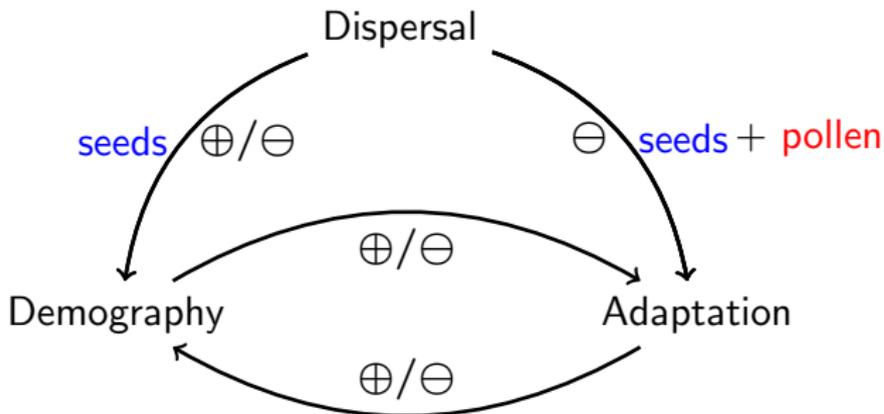
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Response to climate change with pollen dispersal?

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Questions:

- Will a **plant** species shift its **spatial** range or its **climatic** niche?
- How **pollen** does affect the **maximal sustainable rate** of climate change?

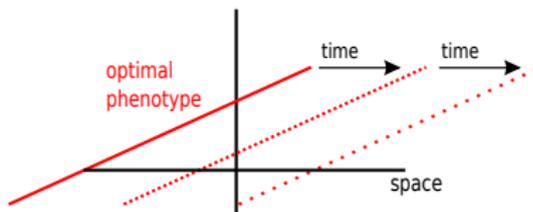
Outline of the model

A quantitative genetic model for population size $n(x, t)$ and mean phenotype $\bar{z}(x, t)$ with:

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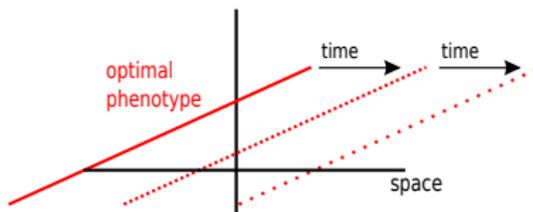
- Linear spatial gradient $\theta(x, t)$ with slope b shifting in time at speed v



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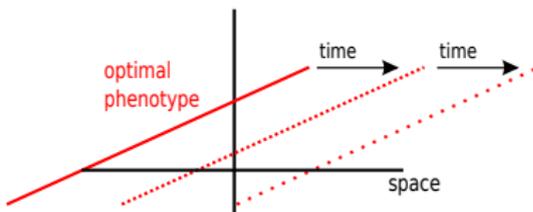


- Seed dispersal σ_s^2 and pollen dispersal σ_p^2 (Gaussian kernel)

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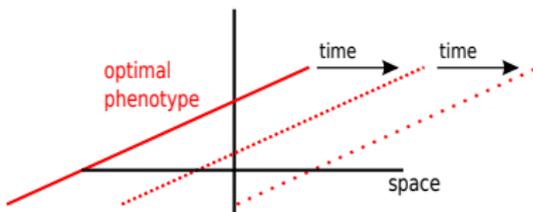


- Seed dispersal σ_s^2 and pollen dispersal σ_p^2 (Gaussian kernel)
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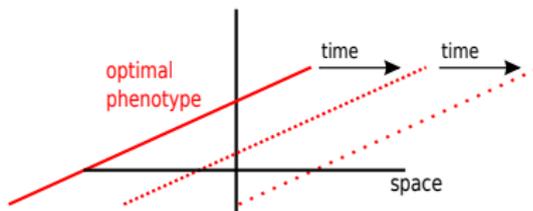


- Seed dispersal σ_s^2 and pollen dispersal σ_p^2 (Gaussian kernel)
- Pollen is not limiting
- Feedbacks between demography and adaptation

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- Seed dispersal σ_s^2 and pollen dispersal σ_p^2 (Gaussian kernel)
- Pollen is not limiting
- Feedbacks between demography and adaptation

Two strong assumptions:

- Global density dependence
- Constant genetic variance V_g

Change in population size $n(x, t)$ and mean phenotype $\bar{z}(x, t)$

Following Pease et al. (1989), Kirkpatrick & Barton (1997), Polechová et al. (2009), Duputié et al. (2012):

$\partial_t n$ = effect of dispersal + effect of adaptation

$\partial_t \bar{z}$ = effect of dispersal + effect of demography

Effect of dispersal on population size $n(x, t)$

Random walk for **seed** only (pollen not limiting)

Effect of dispersal on population size $n(x, t)$

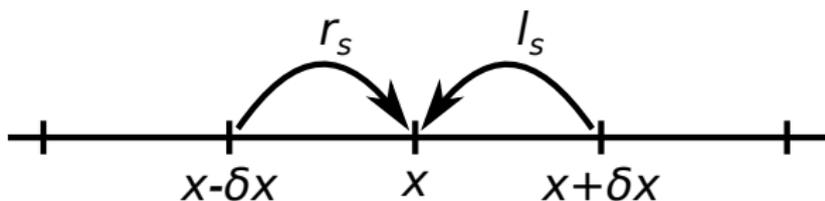
Random walk for **seed** only (pollen not limiting)

$f(x, t) = \mathbb{P}(\text{a given seed is at location } x \text{ at time } t)$

$l_s = \mathbb{P}(\text{seed moves left})$

$r_s = \mathbb{P}(\text{seed moves right})$

$\delta t = \text{small time interval}$



Effect of dispersal on population size $n(x, t)$

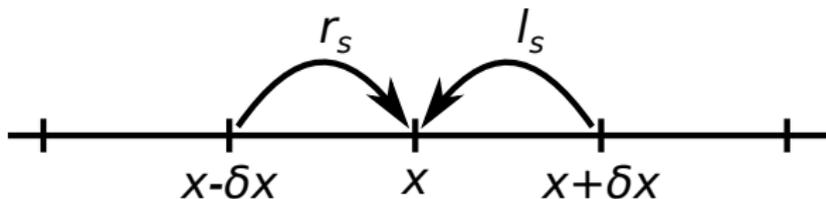
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$$f(x, t + \delta t) = r_s f(x - \delta x, t) + l_s f(x + \delta x, t) + (1 - r_s - l_s) f(x, t)$$

Effect of dispersal on population size $n(x, t)$

Random walk for **seed** only (pollen not limiting)

Using Taylor approximation:

$$\begin{aligned} f(x, t + \delta t) = & \\ & r_s \left(f(x, t) - \delta x \partial_x f(x, t) + \frac{(\delta x)^2}{2} \partial_{x,x} f(x, t) + o(\delta x)^3 \right) \\ & + l_s \left(f(x, t) + \delta x \partial_x f(x, t) + \frac{(\delta x)^2}{2} \partial_{x,x} f(x, t) + o(\delta x)^3 \right) \\ & + (1 - r_s - l_s) f(x, t) \end{aligned}$$

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Assuming unbiased dispersal ($l_s = r_s = m_s$):

$$\frac{f(x, t + \delta t) - f(x, t)}{\delta t} = m_s \frac{(\delta x)^2}{\delta t} \partial_{x,x} f(x, t) + \frac{o(\delta x)^3}{\delta t}$$

Effect of dispersal on population size $n(x, t)$

Random walk for **seed** only (pollen not limiting)

Taking the limit when $\delta x \rightarrow 0$ and $\delta t \rightarrow 0$:

$$\partial_t f(x, t) = \frac{\sigma_s^2}{2} \partial_{x,x} f(x, t)$$

where $\sigma_s^2 = \lim_{\delta x \rightarrow 0, \delta t \rightarrow 0} 2m_s \frac{(\delta x)^2}{\delta t}$

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Same reasoning true for all seeds, thus:

$$\partial_t n(x, t) = \frac{\sigma_s^2}{2} \partial_{x,x} n(x, t)$$

Effect of dispersal on mean phenotype $\bar{z}(x, t)$

Random walk for **seed and pollen**

$g(x, t)$ = phenotype of a new born individual at t in x

$l_p = \mathbb{P}(\text{a pollen grain moves left})$

$r_p = \mathbb{P}(\text{a pollen grain moves right})$

Effect of dispersal on mean phenotype $\bar{z}(x, t)$

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$g(x, t)$ = phenotype of a new born individual at t in x

$l_p = \mathbb{P}(\text{a pollen grain moves left})$

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A new born individual in x can originate from:

- a seed dispersing from $x - \delta x$; phenotype = $g(x - \delta x, t)$
- a seed dispersing from $x + \delta x$; phenotype = $g(x + \delta x, t)$

Effect of dispersal on mean phenotype $\bar{z}(x, t)$

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A new born individual in x can originate from:

- a seed dispersing from $x - \delta x$; phenotype = $g(x - \delta x, t)$
- a seed dispersing from $x + \delta x$; phenotype = $g(x + \delta x, t)$
- an ovule in x fertilized by pollen dispersing from $x - \delta x$;
phenotype = $\frac{g(x - \delta x, t) + g(x, t)}{2}$
- an ovule in x fertilized by pollen dispersing from $x + \delta x$;
phenotype = $\frac{g(x + \delta x, t) + g(x, t)}{2}$

Effect of dispersal on mean phenotype $\bar{z}(x, t)$

Random walk for **seed and pollen**

Weighting each event by local population density:

$g(x, t + \delta t) =$

$$\frac{r_s g(x - \delta x, t) n(x - \delta x, t) + l_s g(x + \delta x, t) n(x + \delta x, t) + r_p \frac{g(x - \delta x, t) + g(x, t)}{2} n(x - \delta x, t) + l_p \frac{g(x + \delta x, t) + g(x, t)}{2} n(x + \delta x, t) + (1 - r_s - l_s - r_p - l_p) g(x, t) n(x, t)}{r_s n(x - \delta x, t) + l_s n(x + \delta x, t) + r_p n(x - \delta x, t) + l_p n(x + \delta x, t) + (1 - r_s - l_s - r_p - l_p) n(x, t)}$$

Effect of dispersal on mean phenotype $\bar{z}(x, t)$

Random walk for **seed and pollen**

Assuming unbiased dispersal ($l_s = r_s = m_s$ and $l_p = r_p = m_p$) and denoting $m_t = m_s + \frac{m_p}{2}$:

$$g(x, t + \delta t) - g(x, t) =$$

$$\frac{m_t((g(x - \delta x, t) - g(x, t))n(x - \delta x) + (g(x + \delta x, t) - g(x, t))n(x + \delta x))}{(m_s + m_p)(n(x - \delta x, t) + n(x + \delta x, t)) + (1 - 2m_s - 2m_p)n(x, t)}$$

Effect of dispersal on mean phenotype $\bar{z}(x, t)$

Random walk for **seed and pollen**

Using Taylor approximation of g and n :

$$\frac{g(x, t + \delta t) - g(x, t)}{\delta t} =$$

$$\frac{m_t \frac{(\delta x)^2}{\delta t} \partial_{x,x} g(x, t) n(x, t) + 2m_t \frac{(\delta x)^2}{\delta t} \partial_x g(x, t) \partial_x n(x, t) + o(\delta x)^3}{(m_s + m_p)(n(x - \delta x, t) + n(x + \delta x, t)) + (1 - 2m_s - 2m_p)n(x, t)}$$

Effect of dispersal on mean phenotype $\bar{z}(x, t)$

Random walk for seed and pollen

Taking the limit when $\delta x \rightarrow 0$ and $\delta t \rightarrow 0$:

$$\partial_t g(x, t) = \frac{\sigma_t^2}{2} \partial_{x,x} g(x, t) + \sigma_t^2 \partial_x g(x, t) \partial_x \log(n(x, t))$$

where $\sigma_t^2 = \sigma_s^2 + \frac{1}{2}\sigma_p^2$ and $\sigma_p^2 = \lim_{\delta x \rightarrow 0, \delta t \rightarrow 0} 2m_p \frac{(\delta x)^2}{\delta t}$

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Same reasoning true for all births, thus:

$$\partial_t \bar{z}(x, t) = \frac{\sigma_t^2}{2} \partial_{x,x} \bar{z}(x, t) + \sigma_t^2 \partial_x \bar{z}(x, t) \partial_x \log(n(x, t))$$

Effect of adaptation on population size $n(x, t)$

$$\partial_t n(x, t) = n(x, t) \bar{r}(x, t, \bar{z})$$

where $\bar{r}(x, t, \bar{z})$ is the mean growth rate

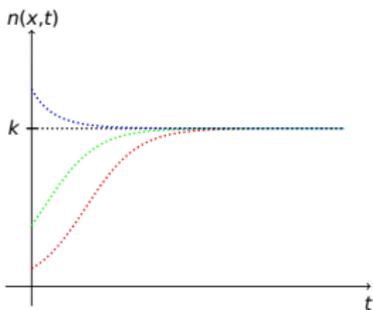
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where $\bar{r}(x, t, \bar{z})$ is the mean growth rate

$$\bar{r}(x, t, \bar{z}) = r_0 \left(1 - \frac{n(x, t)}{k} \right)$$

Density-dependent
growth rate



Effect of adaptation on population size $n(x, t)$

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where $\bar{r}(x, t, \bar{z})$ is the mean growth rate

$$\bar{r}(x, t, \bar{z}) = r_0 \left(1 - \frac{\lambda}{k} \right)$$

Density-dependent
growth rate

Global density-
dependance,

$$\lambda = \int n(x', t) dx'$$

Effect of adaptation on population size $n(x, t)$

$$\partial_t n(x, t) = n(x, t) \bar{r}(x, t, \bar{z})$$

where $\bar{r}(x, t, \bar{z})$ is the mean growth rate

$$\bar{r}(x, t, \bar{z}) = r_0 \left(1 - \frac{\lambda}{k} \right) - \frac{(\bar{z}(x, t) - \theta(x, t))^2}{2V_s}$$

Density-dependent
growth rate

Global density-
dependence,

$$\lambda = \int n(x', t) dx'$$

Evolutionary load,
i.e. maladaptation

$$\theta(x, t) = b(x - vt)$$

Effect of adaptation on population size $n(x, t)$

$$\partial_t n(x, t) = n(x, t) \bar{r}(x, t, \bar{z})$$

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$$\bar{r}(x, t, \bar{z}) = r_0 \left(1 - \frac{\lambda}{k} \right) - \frac{(\bar{z}(x, t) - \theta(x, t))^2}{2V_s} - \frac{V_p}{2V_s}$$

Density-dependent
growth rate

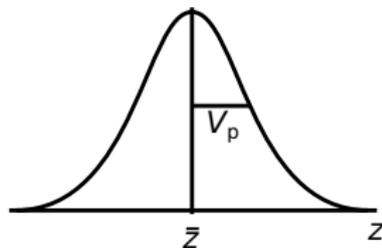
Global density-
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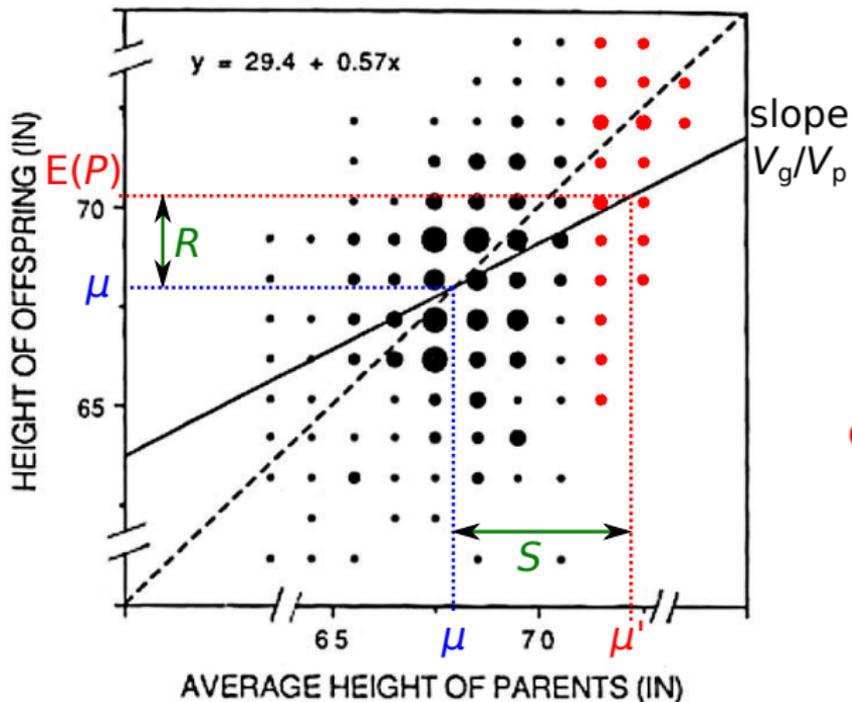
Evolutionary load,
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$$\theta(x, t) = b(x - vt)$$

Phenotypic load



Effect of demography on mean phenotype $\bar{z}(x, t)$



$$R = \frac{V_g}{V_p} S$$

 \Rightarrow

$$\partial_t \bar{z}(x, t) = V_g \partial_{\bar{z}} \bar{r}(x, t, \bar{z})$$

Constant genetic variance

Change in population size $n(x, t)$

Following Pease et al. (1989), Kirkpatrick & Barton (1997), Polechová et al. (2009), Duputié et al. (2012):

$$\partial_t n =$$

Change in population size $n(x, t)$

Following Pease et al. (1989), Kirkpatrick & Barton (1997), Polechová et al. (2009), Duputié et al. (2012):

$$\partial_t n = \frac{\sigma_s^2}{2} \partial_{x,x} n$$

- Seed dispersal (diffusion)

Change in population size $n(x, t)$

Following Pease et al. (1989), Kirkpatrick & Barton (1997), Polechová et al. (2009), Duputié et al. (2012):

$$\partial_t n = \frac{\sigma_s^2}{2} \partial_{x,x} n + n\bar{r}$$

- Seed dispersal (diffusion)
- Population growth

with

$$\bar{r} = r_0 \left(1 - \frac{\lambda}{k} \right) - \frac{(\bar{z} - \theta)^2}{2V_s} - \frac{V_p}{2V_s}$$

Density
dependence

Evolutionary load

Phenotypic load

Change in mean phenotype $\bar{z}(x, t)$

Following Pease et al. (1989), Kirkpatrick & Barton (1997), Polechová et al. (2009), Duputié et al. (2012):

$$\partial_t \bar{z} =$$

Change in mean phenotype $\bar{z}(x, t)$

Following Pease et al. (1989), Kirkpatrick & Barton (1997), Polechová et al. (2009), Duputié et al. (2012):

$$\partial_t \bar{z} = \frac{\sigma_t^2}{2} \partial_{x,x} \bar{z} + \sigma_t^2 \partial_x \bar{z} \partial_x \log(n)$$

- Seed and pollen diffusion
- Seed and pollen asymmetrical dispersal

Total dispersal: $\sigma_t^2 = \sigma_s^2 + \frac{1}{2}\sigma_p^2$

Change in mean phenotype $\bar{z}(x, t)$

Following Pease et al. (1989), Kirkpatrick & Barton (1997), Polechová et al. (2009), Duputié et al. (2012):

$$\partial_t \bar{z} = \frac{\sigma_t^2}{2} \partial_{x,x} \bar{z} + \sigma_t^2 \partial_x \bar{z} \partial_x \log(n) + V_g \partial_{\bar{z}} \bar{r}$$

- Seed and pollen diffusion
- Seed and pollen asymmetrical dispersal
- Response to selection

Total dispersal: $\sigma_t^2 = \sigma_s^2 + \frac{1}{2}\sigma_p^2$

Rescaled equations

Following Kirkpatrick & Barton (1997):

$$R_0 = r_0 - \frac{V_p}{2V_s}$$

$$X = \frac{\sqrt{2R_0}}{\sigma_s} x$$

$$T = R_0 t$$

$$K = k \frac{R_0}{r_0}$$

$$\Lambda = \frac{\lambda}{K}$$

$$Z = \frac{\bar{z}}{\sqrt{R_0 V_s}}$$

$$N = \frac{n}{K}$$

Rescaled equations

After rescaling, only 4 parameters:

- $\gamma = \frac{\frac{1}{2}\sigma_p^2}{\sigma_t^2}$ = contribution of pollen to dispersal
- $V = v \frac{\sqrt{2}}{\sigma_s \sqrt{R_0}}$ speed of climate change
- $A = \frac{V_g}{R_0 V_s}$ adaptive potential
- $B = b \frac{\sigma_s}{R_0 \sqrt{2V_s}}$ slope of the optimal gradient

$$\partial_T N = \partial_{X,X} N + NR$$

$$\partial_T Z = \frac{1}{1-\gamma} \partial_{X,X} Z + \frac{2}{1-\gamma} \partial_X Z \partial_X \log(N) - A \partial_Z R$$

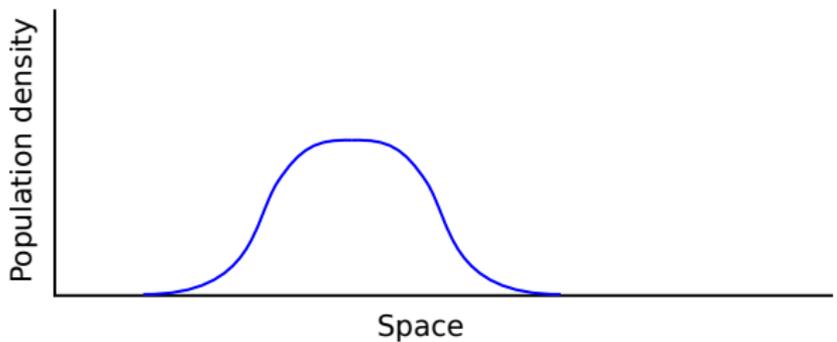
with $R = 1 - \Lambda - \frac{1}{2}(Z - \Theta)^2$ and $\Theta = B(X - VT)$

The 3 solutions of the model

- Extinction of the population

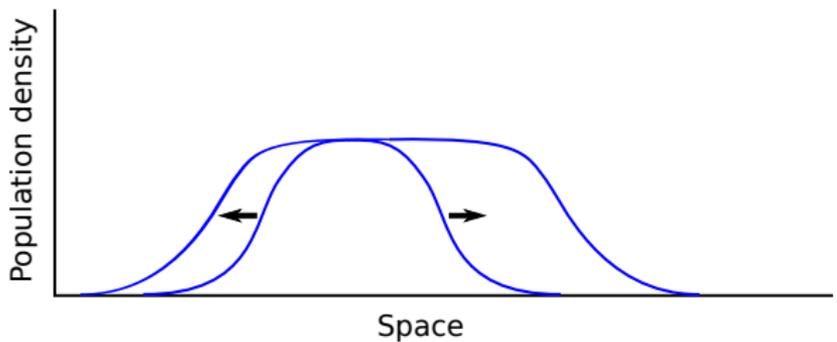
The 3 solutions of the model

- Extinction of the population
- Invasion of the whole space



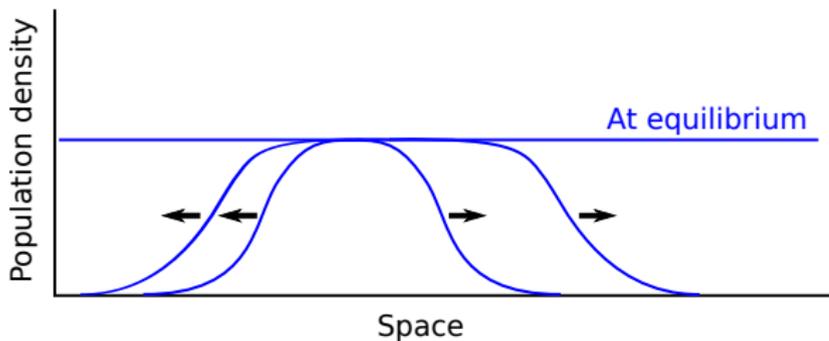
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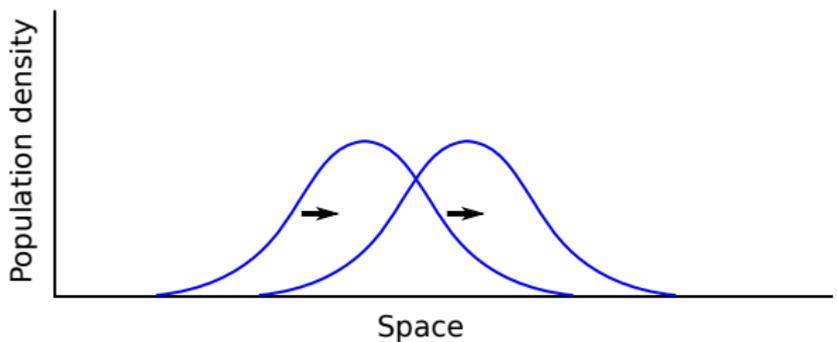
The 3 solutions of the model

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The 3 solutions of the model

- Extinction of the population
- Invasion of the whole space
- A travelling wave



With pollen: spatial range shift **and** climatic niche shift

Let's assume there is a solution with spatial range shift **and** climatic niche shift:

$$N(X, T) = N_0 \exp \left(-\frac{(X - CT - L_n)^2}{2V_n} \right)$$

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Spatial range shift at speed C

$$Z(X, T) = S(X - CT - L_n) + DT$$

Ecological niche shift at speed D

With pollen: spatial range shift **and** climatic niche shift

Such solution indeed exists with:

$$S = \text{sign}(B) \frac{A}{\sqrt{2}} (1 - \gamma)$$

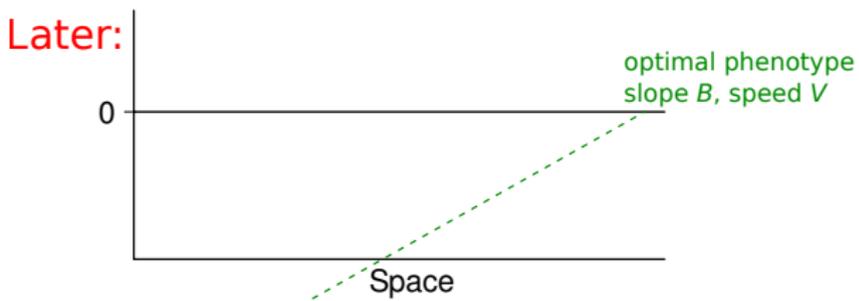
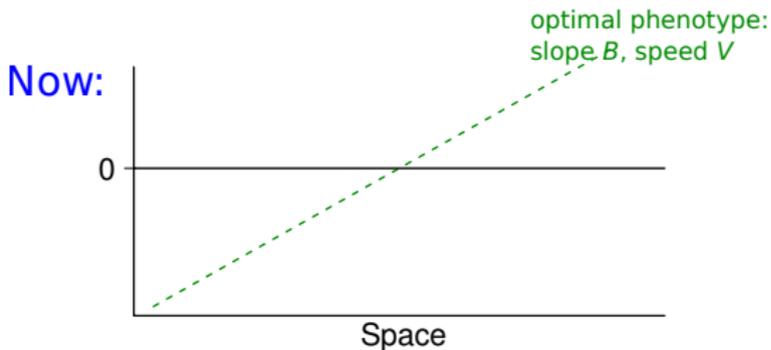
$$V_n = \frac{A}{|B|\sqrt{2} - A(1 - \gamma)}$$

$$C = \frac{A}{1 + \frac{A}{|B|\sqrt{2}}\gamma}$$

$$L_n = -\frac{A}{|B|\sqrt{2} + A\gamma}$$

$$D = -\frac{ABV\gamma}{|B|\sqrt{2} + A\gamma}$$

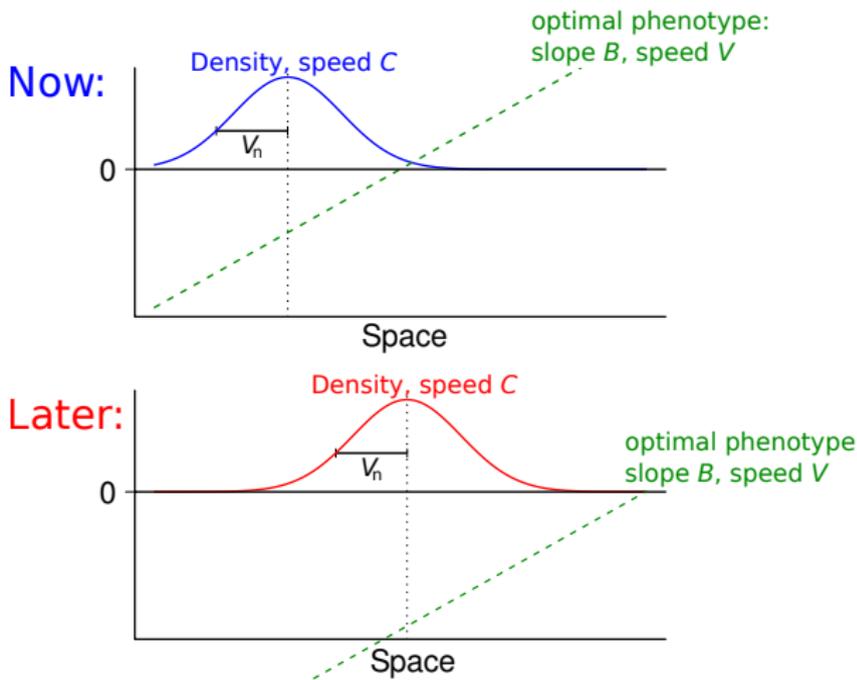
With pollen: spatial range shift **and** climatic niche shift



With pollen: spatial range shift **and** climatic niche shift

V_n = size of the range

C = speed of spatial range shift:
different from climate



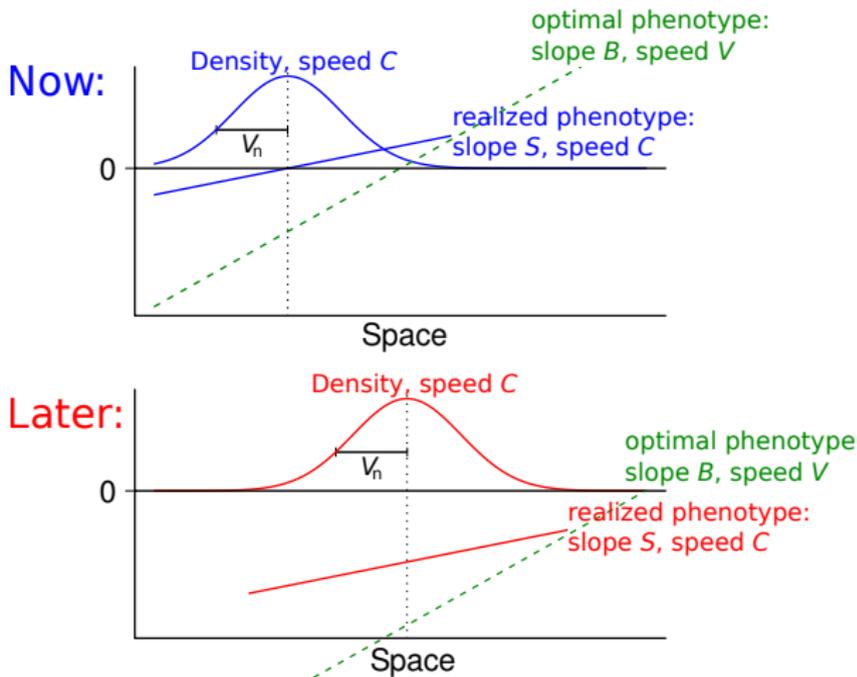
⇒ spatial range shift

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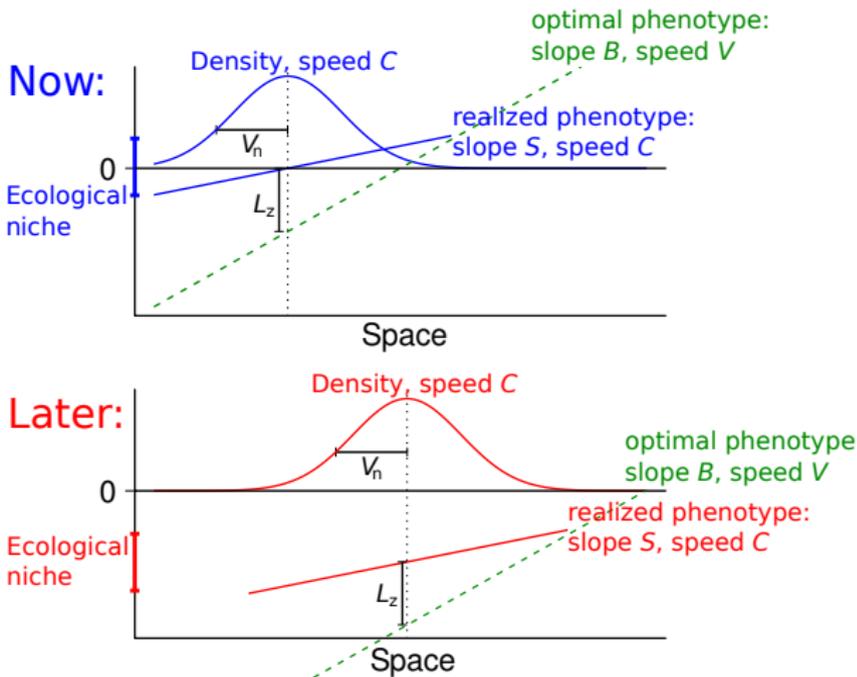
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⇒ spatial range shift **and** ecological niche shift

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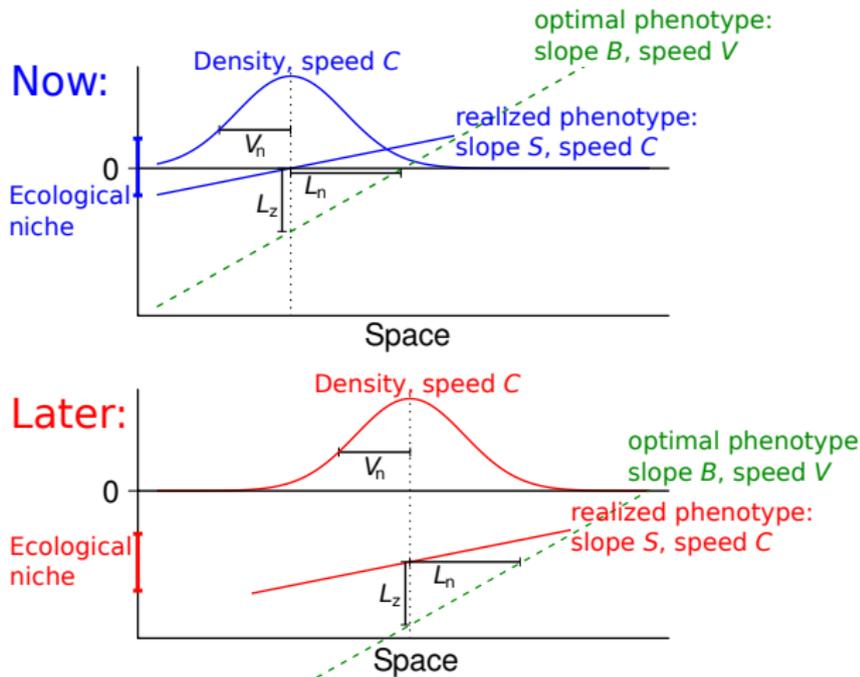
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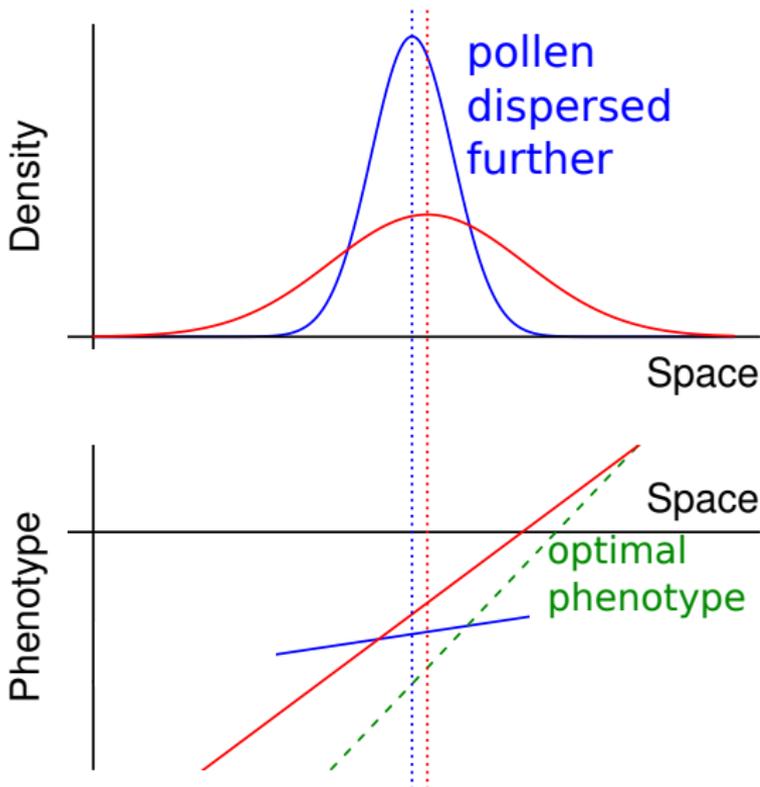
L_n = spatial lag



⇒ spatial range shift **and** ecological niche shift

Effect of pollen (γ) on the features of the travelling wave

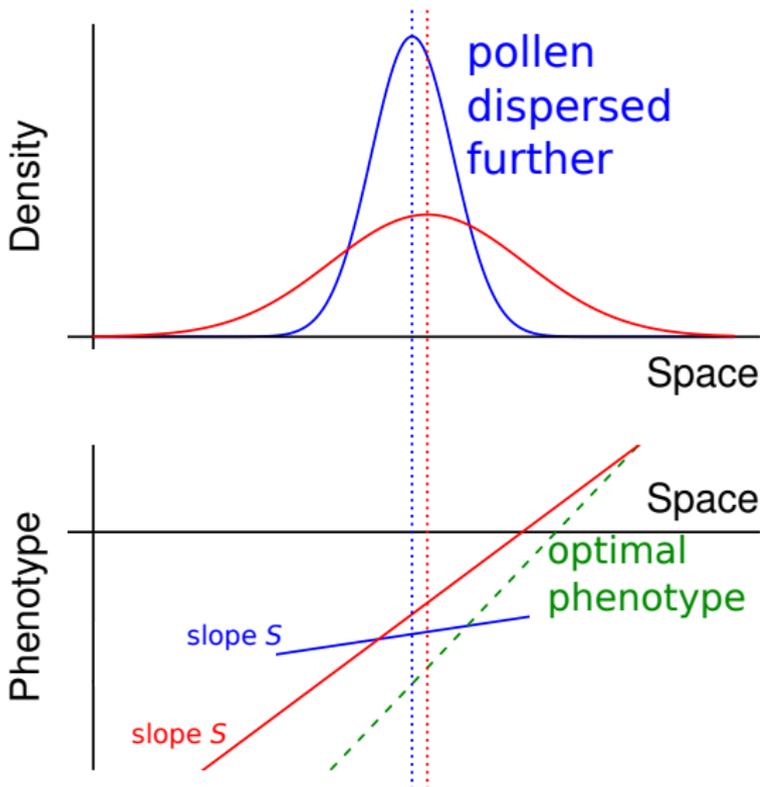
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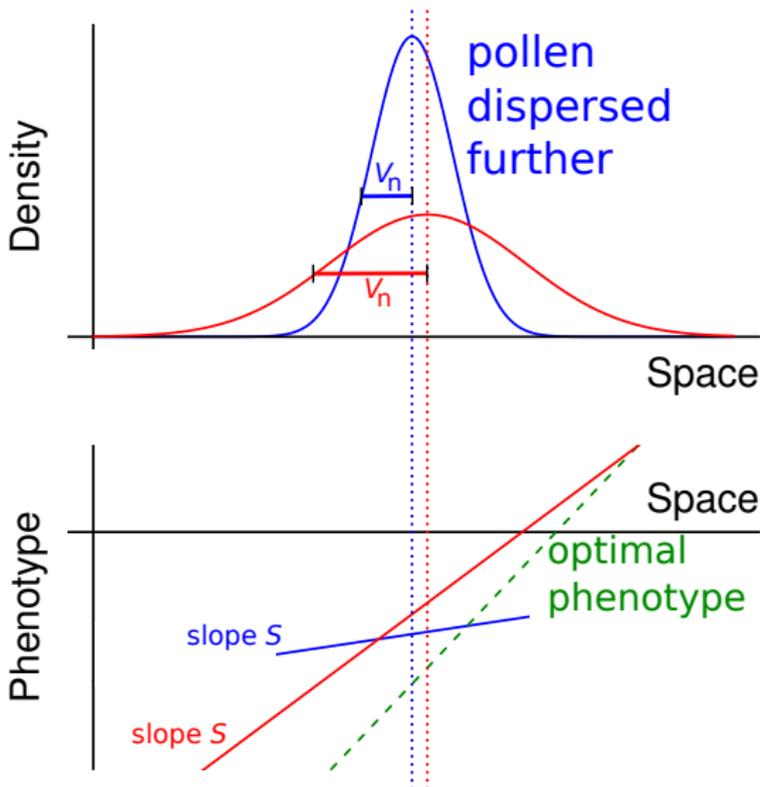
- Flatter phenotypic cline ($|S|$)



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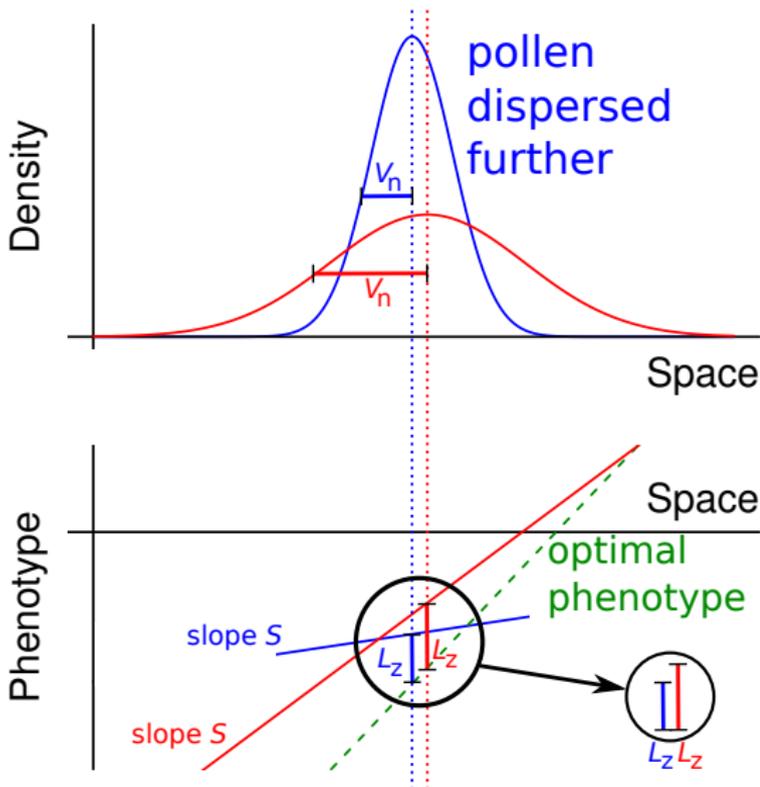
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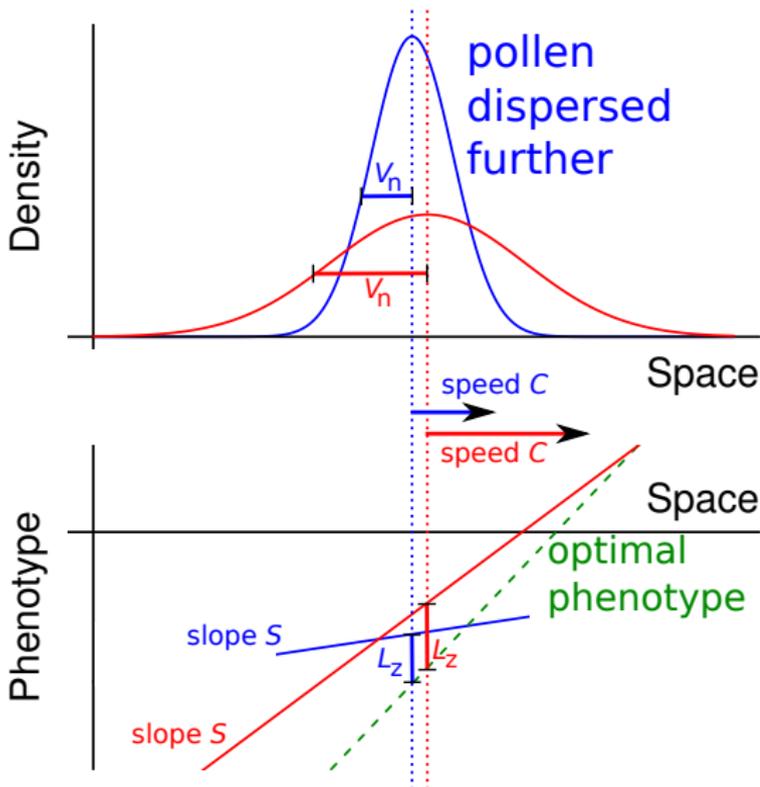
- **Flatter** phenotypic cline ($|S|$)
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- **Better** adaptation at the core ($|L_z|$)



Effect of pollen (γ) on the features of the travelling wave

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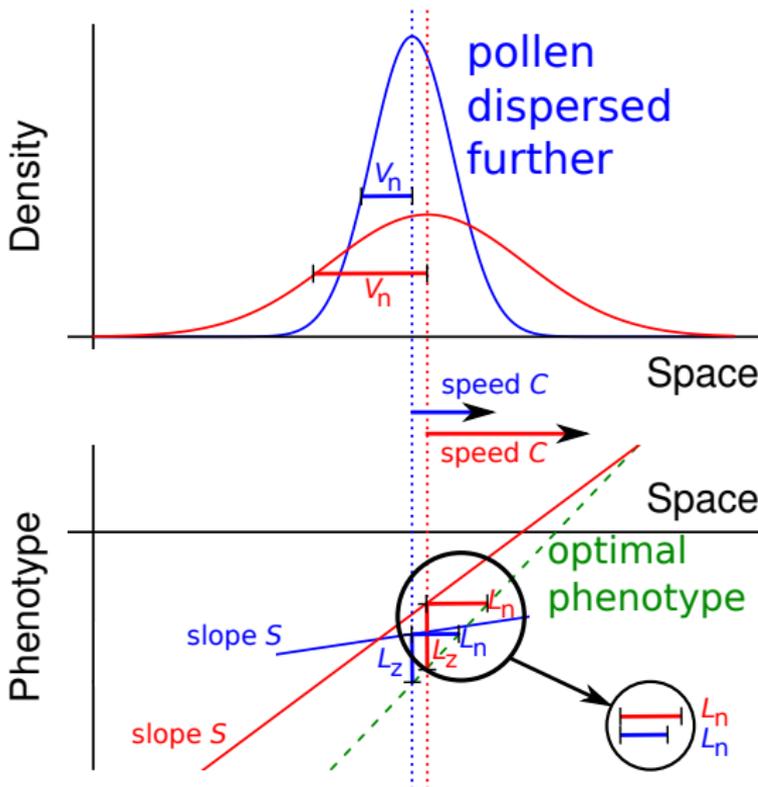
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- Slower wave (C)
- Closer track of the optimum ($|L_n|$)



Maximal **sustainable** rate of climate change

Sustainable climate change if $\Lambda = 1 - \frac{1}{V_n} - \frac{L_z^2}{2} > 0$, i.e. if:

$$V < V^{\text{crit}} = 2 \left(1 + \frac{A}{|B|\sqrt{2}} \gamma \right) \sqrt{1 - \frac{|B|\sqrt{2}}{2} + \frac{A}{2}(1 - \gamma)}$$

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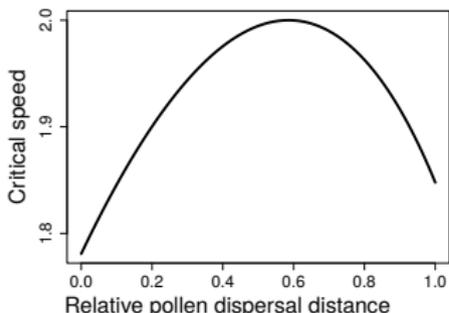
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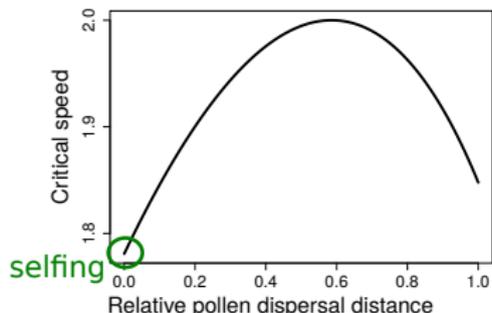


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Pollen dispersal may allow to persist under **faster** climate changes than without pollen dispersal

Robustness of the results

Two strong assumptions to relax:

- 1 Density dependence: global → local
- 2 Genetic variance: constant → evolving

With **local** density dependence: methods

Global density dependence

$$\bar{r}(x, t, \bar{z}) = r_0 \left(1 - \frac{\lambda}{k} \right) - \frac{(\bar{z} - \theta)^2}{2V_s} - \frac{V_p}{2V_s}$$

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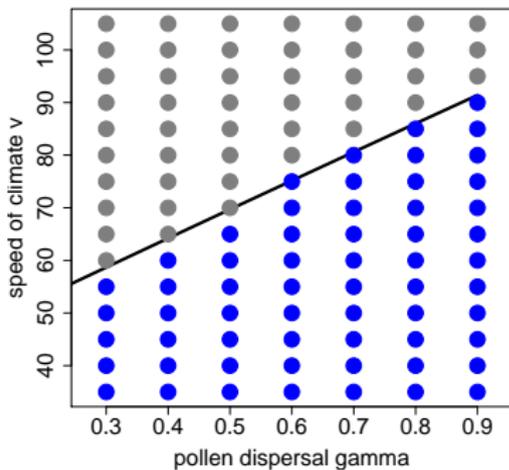
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- Resolution of the equations with **numerical** integration

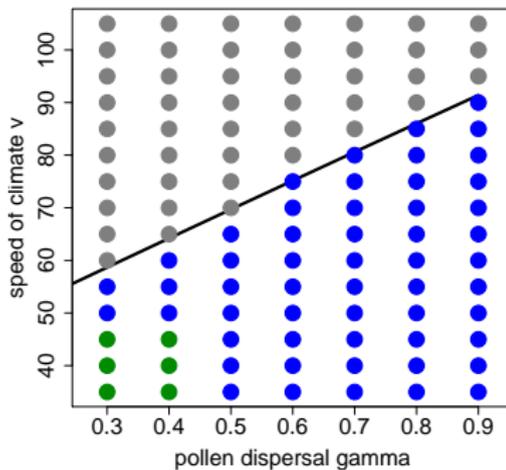
With local density dependence: results are **robust**

Maximal sustainable rate of climate change:

Global density dependence



Local density dependence



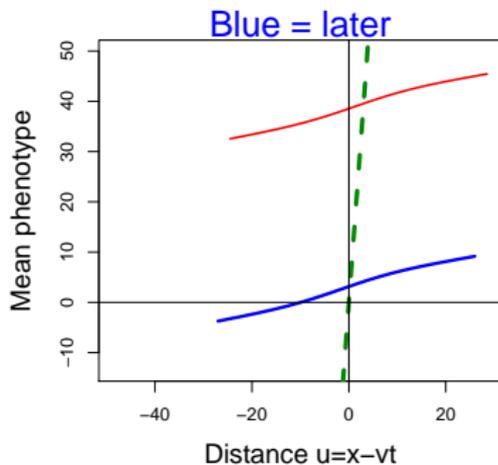
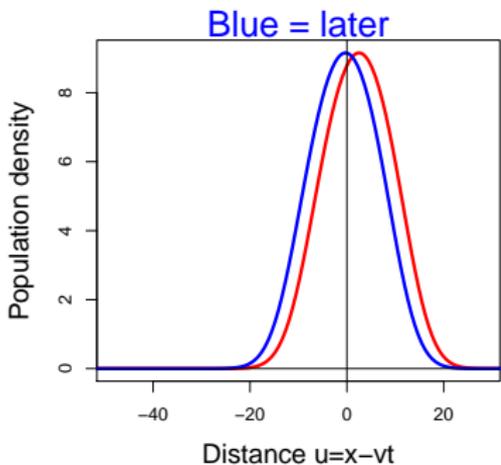
Blue = Travelling wave

Gray = Extinction

Green = Invasion of the whole space

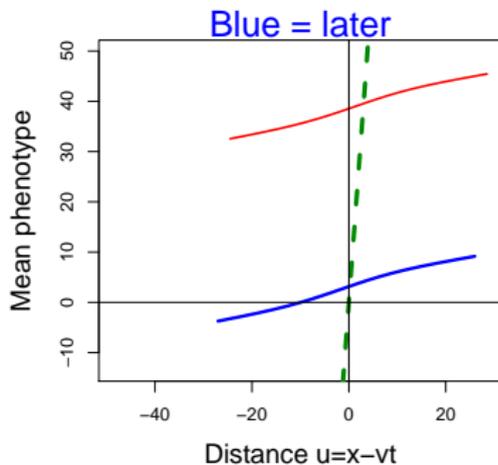
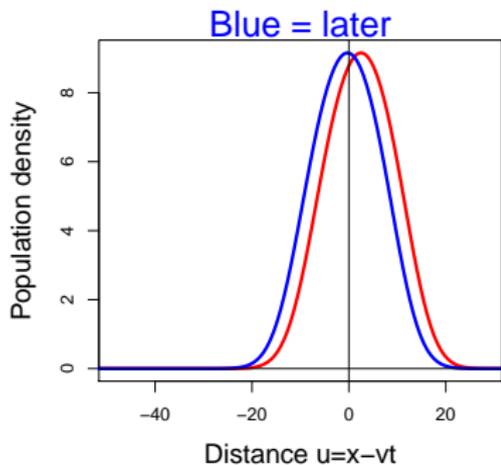
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A travelling wave with spatial range shift and ecological niche shift:



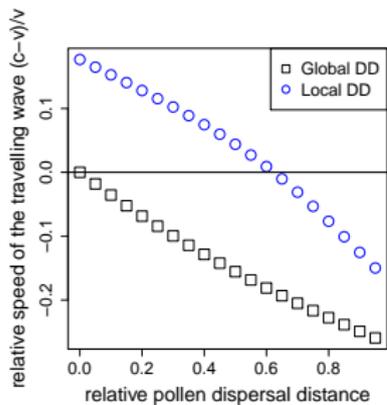
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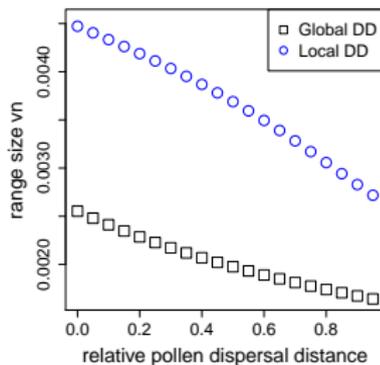
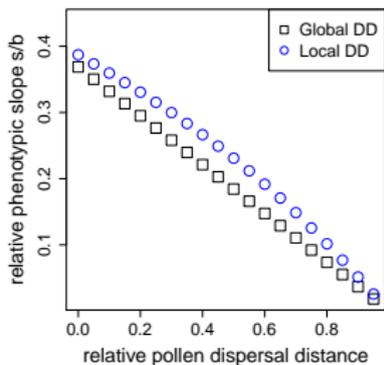
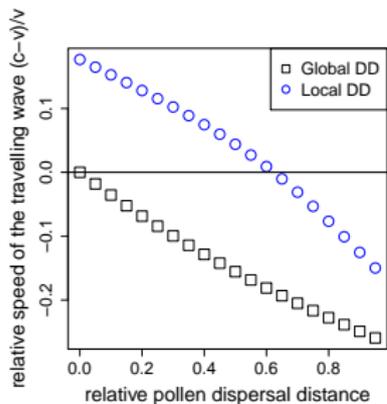
Possibly asymmetrical travelling wave (more individuals at the leading edge)

With local density dependence: results are **robust**



- Faster travelling wave
- Pollen still decreases the speed of the travelling wave (and magnifies the climatic niche shift)

With local density dependence: results are **robust**



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- Quite **small** quantitative effect

With **evolving** genetic variance: methods

- **Genotype** centered model,

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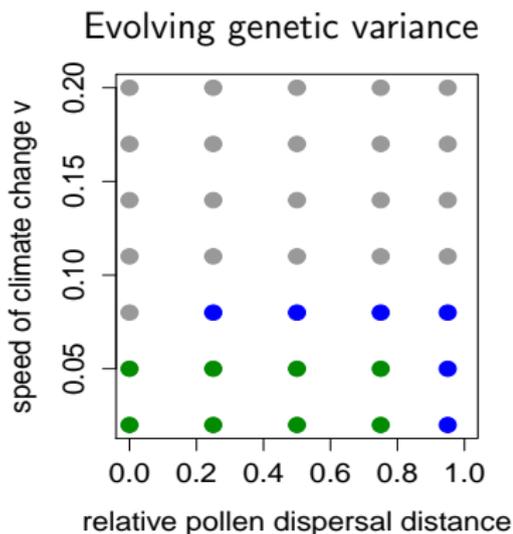
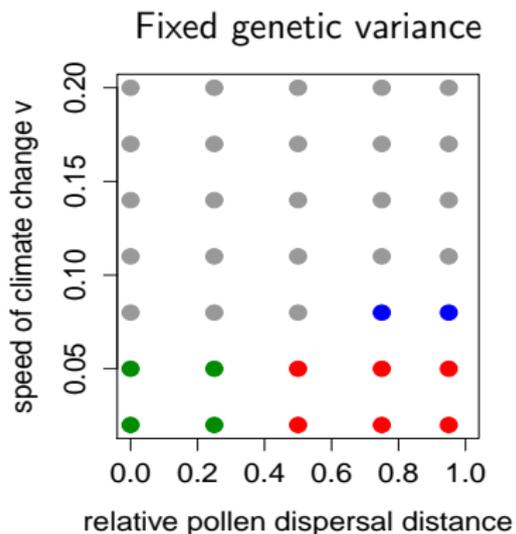
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$$\partial_t n(x, t, \mathbf{g}) = \text{dispersal} + \text{births} + \text{deaths}$$

- **Explicit** model of genes inheritance
- Local density dependence
- Numerical resolution
- Parameters value as estimated for Sitka spruce

With evolving genetic variance: results are **robust**

Maximal sustainable rate of climate change:



Gray = Extinction

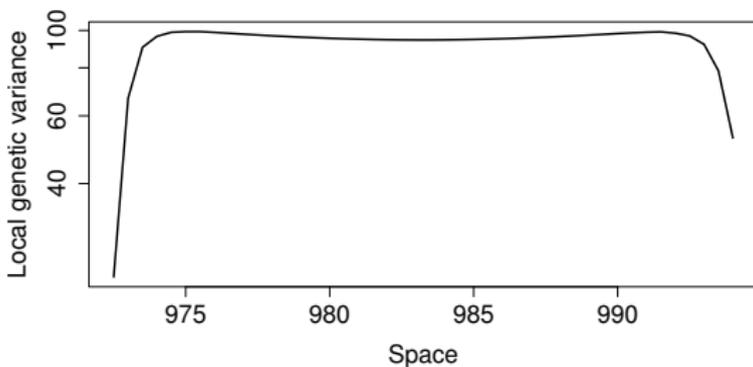
Blue = Travelling wave

Green = Invasion of the whole space

Red = Travelling wave or Invasion of the whole space

With evolving genetic variance: results are **robust**

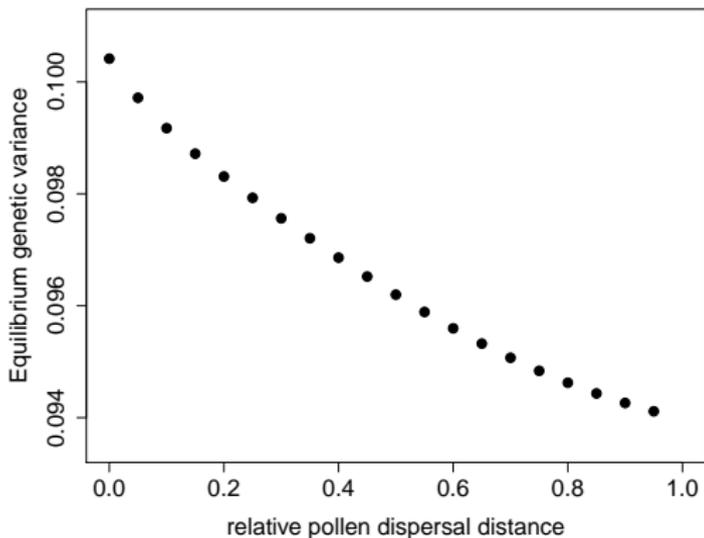
An **equilibrium** genetic variance is reached:



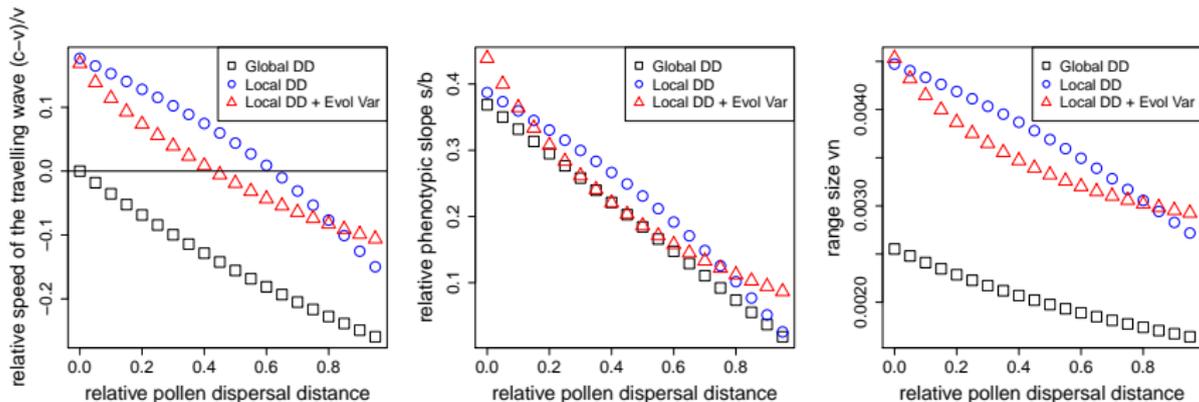
- Lower genetic variance at the very edges
- Slightly lower genetic variance at the core

With evolving genetic variance: results are **robust**

The equilibrium genetic variance **slightly** decreases with the relative pollen dispersal distance:



With evolving genetic variance: results are **robust**



- Qualitative effect of pollen dispersal unchanged
- Quantitative effect quite **small**

Take Home Messages (for biologists)

- Genetic effect of pollen dispersal and feedbacks with demography: worsens adaptation at the margins but **improves adaptation** at the core

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- Pollen dispersal slows the spatial range shift and **magnifies** the climatic niche shift
- Pollen dispersal may allow to persist under **faster** climate changes
- Conclusions **robust** to the strongest assumptions of the model

Take Home Messages (for mathematicians)

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- Don't you want to work with me?