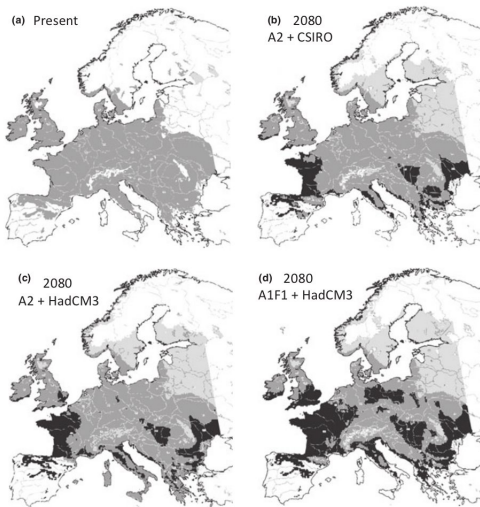


# Dynamique d'aires de répartition d'espèces

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# evolution of species' range



1

1. Thuiller, Glob. Change Biol. 9 (2003).

# Consequences for the forestry industry

**We found that by 2100—depending on the interest rate and climate scenario applied—this loss varies between 14 and 50% (mean: 28% for an interest rate of 2%) of the present value of forest land in Europe, excluding Russia, and may total several hundred billion Euros.**

2

What should be done :

- Change the culture strategy ?
- Change the crop species ?
- How can micro-scale properties be taken into account ?
- ...

# SAFRAN data

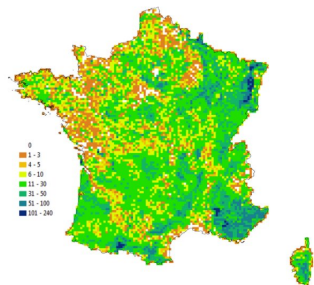


Figure 1.7 : Nombre de points IFN par maille SAFRAN

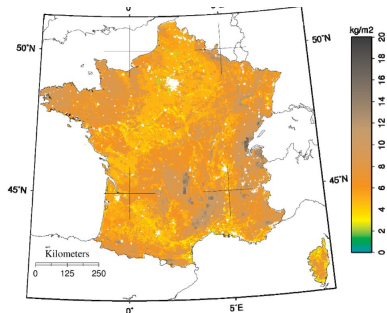
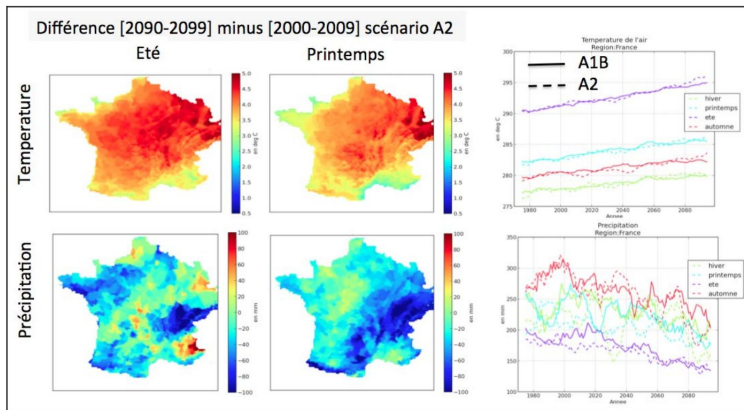


Figure 1.9 : Carte des stocks de carbone organique sur les premiers 30cm de sol.

3

# Climate predictions



**Figure 2.2 :** Distribution spatiale des différences de température et de précipitations pour l'été (Juin, Juillet, Aout) et le printemps (Mars, avril, mai) entre la période 2090-2099 et la période 2000-2009. A gauche sont reporté les évolutions en moyenne sur la France des températures et précipitations pour les 4 saisons.

4

## On-going projects

- ANR project Evorange (Ophélie Ronce, ISEM) : try to improve field data and prediction models to assess the effect of climate change on species' range.
- Software PHENOFIT (Isabelle Chuine, CEFÉ) : a software to characterize the effect of environmental conditions on a species, and simulate the (quantitative) effect of a given climatic scenario.  
Theoretical tool : climate envelope modeling.
- GIS Climat Environnement Société

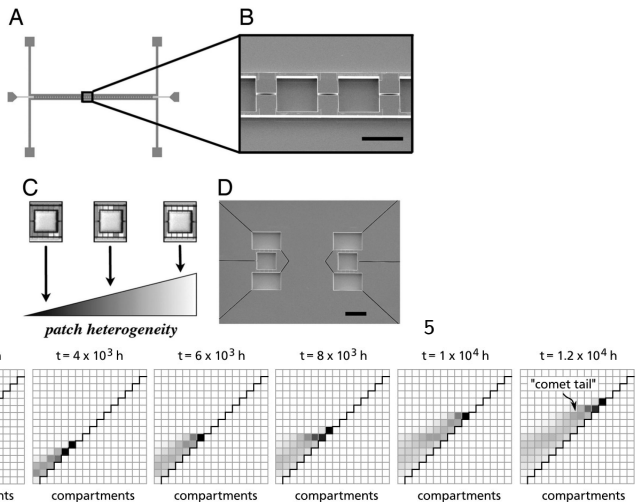
- 1 Asexual populations submitted to climate change
- 2 Sexual populations submitted to climate change

# Collaborators

- Matthieu Alfaro (University of Montpellier),
- Henri Berestycki (EHESS),
- + Ophélie Ronce (ISEM, University of Montpellier) for biological aspects.



# Experimental settings



5. Keymer et al., PNAS, 2006.

6. Hermsen et al., PNAS, 2012.

# Experimental settings



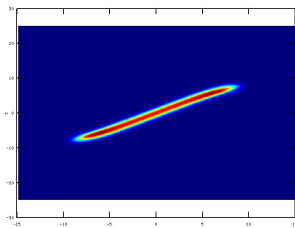
7

7. Andrew Gonzalez lab, Mc Gill University.

## Model for asexual populations

We consider a population  $n(t, x, y)$ , where  $t \geq 0$  is the time,  $x \in \mathbb{R}$  is a space variable, and  $y \in \mathbb{R}$  is a phenotypic trait (or breeding value). The evolution of  $n$  is given by the following model :

$$\partial_t n(t, x, y) - \Delta_x n(t, x, y) - \Delta_y n(t, x, y) = \left( r(t, x, y) - \int_{\mathbb{R}} n(t, x, y') dy' \right) n(t, x, y).$$

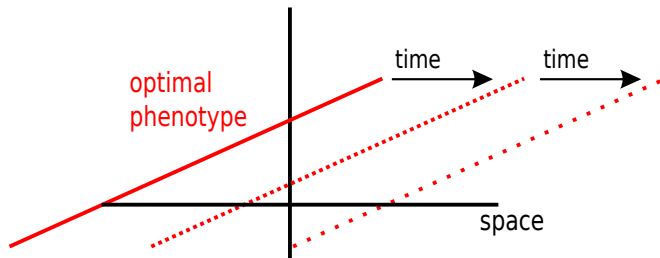


# Climate change

We consider a climate change of (spatial) speed  $c$  :

$$\partial_t n(t, x, y) - \Delta_x n(t, x, y) - \Delta_y n(t, x, y) = \left( r(x - ct, y) - \int_{\mathbb{R}} n(t, x, y') dy' \right) n(t, x, y).$$

A typical example would be  $r(x - ct, y) = 1 - (y - B(x - ct))^2 - \alpha y^2$ , for some  $\alpha > 0$ .



## Principal eigenvalue problem

we can define  $\lambda_\infty \in \mathbb{R}$  and  $\Gamma_\infty$  as the solution of the principal eigenvalue problem

$$\begin{cases} -\partial_{xx}\Gamma_\infty(x, y) - \partial_{yy}\Gamma_\infty(x, y) - r(x, y)\Gamma_\infty(x, y) = \lambda_\infty\Gamma_\infty(x, y) \\ \Gamma_\infty(x, y) > 0, \quad \|\Gamma_\infty\|_\infty = 1. \end{cases}$$

In the example above, we can explicitly compute, when  $\alpha = 0$  :

$$\lambda_\infty = \sqrt{A(1 + B^2)} - 1, \quad \Gamma_\infty = \exp\left(-\sqrt{\frac{A}{1 + B^2}}(y - Bx)^2\right).$$

# Extinction or survival

$$c^* := \begin{cases} 2\sqrt{-\lambda_\infty} & \text{if } \lambda_\infty < 0 \\ -\infty & \text{if } \lambda_\infty \geq 0 \end{cases}$$

## Proposition

If  $c^* < c$ , and  $\sup_{x \in \mathbb{R}} \int_{\mathbb{R}} n_0(x, y) dy < \infty$ . Then,

$$\|n(t, \cdot, \cdot)\|_\infty \rightarrow_{t \rightarrow \infty} 0,$$

If  $0 \leq c < c^*$ , then for any non-negative solution  $n \neq 0$ , there exists a non-negative function  $h \neq 0$  such that

$$n(t, x + ct, y) \geq h(x, y) \text{ for all } t \geq 1, x \in \mathbb{R}, y \in \mathbb{R}.$$

## Scheme of the proof 1 : Estimations on the tails

$$\partial_t n(t, x, y) - \Delta_x n(t, x, y) - \Delta_y n(t, x, y) = \left( r(x - ct, y) - \int_{\mathbb{R}} n(t, x, y') dy' \right) n(t, x, y).$$

**Lemma** (Exponential decay of tails)

Assume that  $r(x, y) \leq -\delta < 0$  for  $(x, y)$  large enough. If moreover  $0 \leq n_0(x, y) \leq C_0 e^{-\mu_0(|x|+|y|)}$ , then there exist  $C > 0$  and  $\mu > 0$  such that

$$0 \leq n(t, x, y) \leq C e^{-\mu(|x-ct|+|y|)},$$

for all  $t \geq 0$ ,  $x \in \mathbb{R}$ ,  $y \in \mathbb{R}$ .

## Scheme of the proof 2 : extinction case

$n$  satisfies :

$$(\partial_t - \Delta_x - \Delta_y) n(t, x, y) \leq r(x - ct, y) n(t, x, y),$$

and then, with  $\tilde{n} := e^{\frac{c(x+ct)}{2}} n(t, x + ct, y)$ ,

$$(\partial_t - \Delta_x - \Delta_y) \tilde{n}(t, x, y) \leq \left( r(x, y) - \frac{c^2}{4} \right) \tilde{n}(t, x, y),$$

We notice that  $\bar{n}(t, x, y) := Me^{(-\lambda_\infty - \frac{c^2}{4})t} \Gamma_\infty(x, y)$  is a solution of the above equation, which, combined to the tail estimates, provides the result (if  $n^0$  is gentle enough).

We see here how  $c^* = 2\sqrt{-\lambda_\infty}$  comes into play...



## Scheme of the proof 3 : survival case

- We consider the problem on a compact set :  $n$  satisfies

$$\begin{aligned} & (\partial_t - \Delta_x - \Delta_y) n(t, x, y) \\ &= \left( r(x - ct, y) - \int_{-R}^R n(t, x, y') dy' + o(R) \right) n(t, x, y), \end{aligned}$$

for  $t \geq 0$  and  $(x - ct, y) \in B_R(0)$ .

- We use the Harnack inequality to estimate the non-local term :

$$\sup_{(x-ct, y) \in B_R(0)} n(t, x, y) \leq C \inf_{(x-ct, y) \in B_R(0)} n(t + 1, x, y),$$

and then,

$$\max_{(x-ct) \in B_R(0)} \int_{-R}^R n(t + 1, x, y') dy' \leq 2CR e^{\max r} n(t, x_0, y_0) \text{ for any } (x_0 - ct, y_0) \in B_R(0).$$

## Scheme of the proof 4 : survival case

- we have shown that  $n$  satisfies, for  $t \geq 0$  and  $(x - ct, y) \in B_R(0)$

$$(\partial_t - \Delta_x - \Delta_y) n = (r(x - ct, y) - Cn(t, x, y) + o(R)) n.$$

- Just as in the extinction part, we introduce  $\tilde{n} := e^{\frac{c(x+ct)}{2}} n(t, x + ct, y)$ , that satisfies

$$(\partial_t - \Delta_x - \Delta_y) \tilde{n} = \left( r(x, y) - \frac{c^2}{4} - C\tilde{n}(t, x, y) + o(R) \right) \tilde{n}.$$

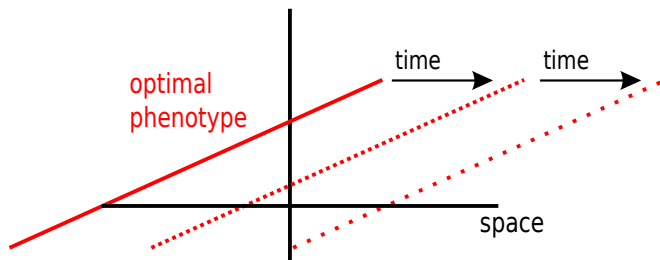
- We notice that  $\bar{n}(t, x, y) := Me^{(-\lambda_\infty - \frac{c^2}{4})t} \Gamma_R(x, y)$  is a sub-solution of the above equation provided  $M > 0$  is chosen small enough. Thus,  $\bar{n}(t, \cdot, \cdot) \leq \tilde{n}(t, \cdot, \cdot)$  for all  $t \geq 0$ , which proves the result.

## Unconfined case

We consider a climate change of (spatial) speed  $c$  :

$$\partial_t n(t, x, y) - \Delta_x n(t, x, y) - \Delta_y n(t, x, y) = \left( r(x - ct, y) - \int_{\mathbb{R}} n(t, x, y') dy' \right) n(t, x, y).$$

A second example is  $r(x - ct, y) = 1 - (y - B(x - ct))^2 - \alpha y^2$ , for  $\alpha > 0$ .



## Unconfined case

Assume  $r(x, y) = \tilde{r}(y - Bx)$ .

$$c^{**} := \begin{cases} 2\sqrt{-\lambda_\infty \frac{1+B^2}{B^2}} & \text{if } \lambda_\infty < 0 \\ -\infty & \text{if } \lambda_\infty \geq 0 \end{cases}$$

### Proposition

If  $c^{**} < c$ , and  $\sup_{x \in \mathbb{R}} \int_{\mathbb{R}} n_0(x, y) dy < \infty$ . Then,

$$\|n(t, \cdot, \cdot)\|_\infty \xrightarrow{t \rightarrow \infty} 0,$$

If  $0 \leq c < c^*$ , then the population propagates to the left at a speed  $\omega_x^-$ , and to the right at a speed  $\omega_x^+$ , where

$$\omega_x^\pm = \pm \sqrt{-\frac{4\lambda_\infty}{1+B^2} - \frac{B^2}{(1+B^2)^2} c^2} + \frac{B^2}{1+B^2} c.$$

## Unconfined case

Remarks :

- $\omega_+ > 0$  can be less or greater than  $c$ , the speed of the climate.
- $\omega_-$  can be either positive or negative (linked to the survival of the population in one given location),
- the minimal trait present in the population decreases. The maximal trait can either increase or decrease.
- $c^* = 2\sqrt{-\lambda_\infty} < c^{**} = 2\sqrt{-\lambda_\infty \frac{1+B^2}{B^2}}$ . Indeed,  $c > c^*$  in the unconfined case is equivalent to  $\omega_x^- < 0$ .

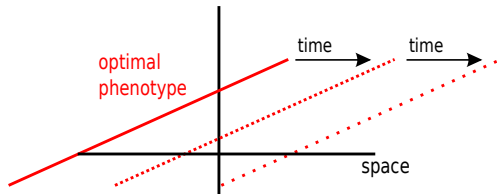
## Mixed case

We consider a climate change of (spatial) speed  $c$  :

$$\partial_t n(t, x, y) - \Delta_x n(t, x, y) - \Delta_y n(t, x, y) = \left( r(x - ct, y) - \int_{\mathbb{R}} n(t, x, y') dy' \right) n(t, x, y).$$

A third (and last) example is

$r(x - ct, y) = 1 - A(y + B(x - ct))^2 1_{x-ct \leq 0} - Ay^2 1_{x-ct \geq 0} - \alpha y_+^2$ , for  $\alpha > 0$  small.



## Mixed case

Our goals here :

- understand better the interplay between  $c^*$  and  $c^{**}$ ,
- investigate the robustness of the biological implications of the results above.

Assumption :  $r(x, y)$  such that  $r(x, y) = r_u(x, y)$  for  $x < 0$ , where  $r_u$  satisfies the conditions of the unconfined case, while for  $x > 0$ ,  $r(x, y)$  satisfies the conditions of the confined case.

Definition :  $c^*$  as before, and  $\widetilde{c}^{**}$  as  $c^{**}$ , but defined with  $r_u$ .

# Mixed case

## Proposition

- ① if  $\max(c^*, \widetilde{c}^{**}) < c$ , then

$$\sup_{x \in \mathbb{R}} \int_{\mathbb{R}} n(t, x, y) dy \xrightarrow{t \rightarrow \infty} 0.$$

- ② if  $\widetilde{c}^{**} < c < c^*$ , and  $n_0$  is compactly supported, The population survives and follows the climate shift, but does not succeed to propagate.
- ③ if  $c^* < c < \widetilde{c}^{**}$ , then the population survives, but does not succeed to follow the climate
- ④ if  $c < \min(c^*, \widetilde{c}^{**})$ , then the population survives. It propagates at speed  $c$  to the right, and at speed  $\widetilde{\omega}_x^-$  to the left.



## Mixed case

Given the dynamics of a population's range, is it possible to infer robustness of the population to an increase of the climate shift speed ?

- $c^*$  is not necessarily smaller than  $\widetilde{c}^{**}$  : a species that succeed to follow the climate change is not necessary far from extinction.

In the example :  $c^* < \widetilde{c}^{**}$  if and only if  $(1 + B^2)^{3/2} - B^2 < \frac{1}{\sqrt{A}}$ .

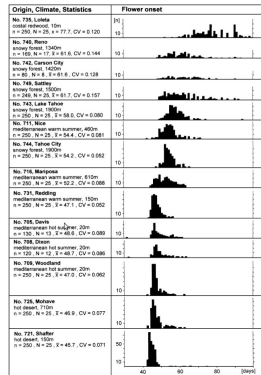
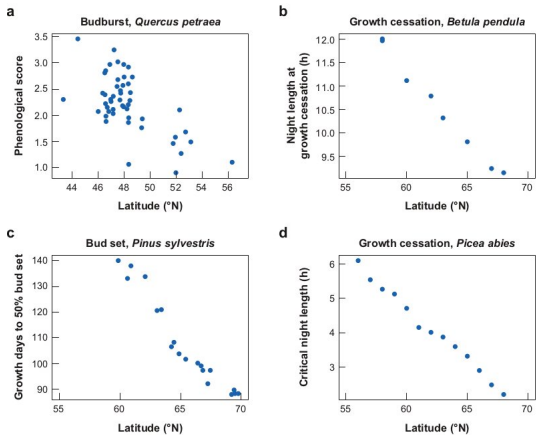
- A species with a range that increases in size (even rapidly) may not be far from extinction.

- 1 Asexual populations submitted to climate change
- 2 Sexual populations submitted to climate change

# Collaborators

- Robin Aguilée (LEDB, University of Toulouse),
- Ophélie Ronce (ISEM, University of Montpellier),
- François Rousset (ISEM, University of Montpellier).

## Phenotypic gradients



8. O.Savolainen, T. Pyhajarvi, T. Knurr, Annu. Rev. Ecol. Evol. Syst. 2007.  
9. Neuffer et al., Molecular Ecology, 1999.

## Existing models

C.P. Pease, R. Lande, J.J. Bull, Ecology, 1989.

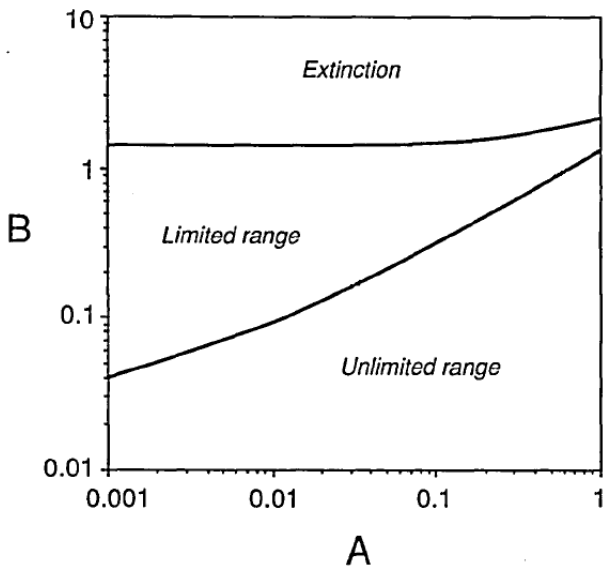
$N(t, x)$  : population density,  $Z(t, x)$  : mean phenotypic trait.

$$\begin{cases} \partial_t N - \Delta_x N = \left(1 - \frac{1}{2}(y - Bx)^2 - \int N(t, y) dy\right) N, \\ \partial_t Z - \Delta_x Z = 2 \frac{\partial_x N}{N} \partial_x Z + A(Bx - Z). \end{cases}$$

M. Kirkpatrick, N. Barton, American Naturalist, 1997.

$$\begin{cases} \partial_t N - \Delta_x N = \left(1 - \frac{1}{2}(y - Bx)^2 - N\right) N, \\ \partial_t Z - \Delta_x Z = 2 \frac{\partial_x N}{N} \partial_x Z + A(Bx - Z). \end{cases}$$

# Dynamics of the population



## An infinitesimal model (see Sepideh Mirrahimi, G.R.)

We consider a population  $n(t, x, y)$ , where  $t \geq 0$  is the time,  $x \in \mathbb{R}$  is a space variable, and  $y \in \mathbb{R}$  is a phenotypic trait (or breeding value). Then, the evolution of  $n$  is given by the following model :

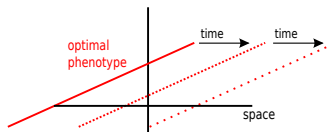
$$\begin{aligned} & \partial_t n(t, x, y) - \Delta_x n(t, x, y) \\ &= - \left[ (C - (1 + A/2)) + (y - Bx)^2 + \int n(t, x, y') dy' \right] n(t, x, y) \\ & \quad + C \int \int \frac{n(t, x, y_*) n(t, x, y'_*)}{\int n(t, x, w) dw} K(y, y_*, y'_*) dy_* dy'_*, \end{aligned}$$

Parameters :  $A, B, C$ . If  $C$  becomes large, we formally recover the model of Kirkpatrick and Barton.

# Pollen + climate change

We want to investigate the effect of the pollen on a population facing a climate change :

- Climate change :



- Pollen : the male gametes disperse much more than the seeds.



# Model

We consider a tree population  $n(t, x, y)$ , and the pollen population  $p(t, x, y)$  :

$$\begin{aligned} & \partial_t n(t, x, y) - \frac{\sigma^2}{2} \Delta_x n(t, x, y) \\ &= - \left[ \eta + \frac{1}{2V_s} (y - b(x - vt))^2 + \frac{r_{max}}{K} \int n(t, x, y') dy' \right] n(t, x, y) \\ & \quad + (r_{max} + \eta) \int \int \frac{n(t, x, y_*) p(t, x, y'_*)}{\int n(t, x, w) dw} K(y, y_*, y'_*) dy_* dy'_*. \end{aligned}$$

with  $p(t, x, y) = K *_{x'} n(t, x, y) \sim n(t, x, y) + \kappa \Delta n(t, x, y)$ .

# Moment equation

Then, with similar arguments as above, we get :

$$\partial_t N - \Delta_x N = \left[ 1 - \frac{1}{2}(Z - B(x - Vt))^2 - N \right] N,$$

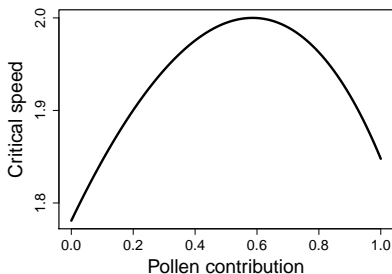
$$\partial_t Z - \frac{1}{1-\gamma} \Delta_x Z = \frac{2}{1-\gamma} \frac{\partial_x N}{N} \partial_x Z + A(B(x - Vt) - Z),$$

where  $\gamma := \frac{\frac{1}{2}\sigma_p^2}{\sigma_t^2} \in (0, 1)$  is the contribution of pollen to dispersal.

## Consequence : Critical speed of climate change

Sustainable climate change if  $1 - \frac{1}{V_n} - \frac{L^2}{2} > 0$ , that is if the speed of the climate change is below :

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



## Consequence : Optimal pollen dispersal

The optimal critical speed is obtained for  $\gamma_{opt} = \frac{2}{3} - \frac{1}{A} (|B|\sqrt{2} - \frac{4}{3})$ . It is then best to :

- disperse pollen a lot when  $|B| < \frac{4-A}{3\sqrt{2}}$ ,
- not disperse pollen when  $|B| > \frac{\sqrt{2}}{3}(2 + A)$ ,
- disperse at an intermediate rate for an intermediate gradient of the optimal phenotypic trait  $B$ .

# Numerical simulations

These computation had to be checked numerically.

- Pease et al model : OK,
- Kirkpatrick Barton model : OK for a part of the parameter space,
- Individual-based simulations with explicit loci : would require too much time,
- Kinetic model : OK.

Why is it interesting : The phenotypic variance is not fixed, the linkage equilibrium is not assumed.

Thank you for your attention !