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A population facing climate change: joint influences of Allee effects and environmental boundary geometry

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Abstract As a result of climate change, many populations have to modify their range to follow the suitable areas—their "climate envelope"—often risking extinction. During this migration process, they may face absolute boundaries to dispersal because of external environmental factors. Consequently, not only the position, but also the shape of the climate envelope can be modified. We use a reaction-diffusion model to analyse the effects on population persistence of simultaneous changes in the position and shape of the climate envelope. When the growth term is of logistic type, we show that extinction and persistence are principally conditioned by the species mobility and the speed of climate change, but not by the shape of the climate envelope. However, with a growth term taking an Allee effect into account, we find a high sensitivity to variations in the shape of the climate envelope. In this case, the species which have a high mobility, although they could more easily follow the migration of the climate envelope, would be at risk of extinction when encountering a local narrowing of the boundary geometry. This effect can be attenuated by a progressive opening at the exit of the narrowing into the available space, even though this leads temporarily to a diminished area of the climate envelope.

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Introduction

Over the last century, the global temperature has increased by about 0.7°C, with an even faster warming trend, in the past 50 years, of about 0.13°C per decade (IPCC 2007). The consequences of this warming on fauna and flora are already visible and well documented (see e.g., Walther et al. 2002). In particular, poleward and upward shifts of many species ranges have been recorded and are most likely linked to climate change (Parmesan and Yohe 2003; Parmesan 2006).

The variations in the Earth's climate are in fact highly spatially heterogeneous (IPCC 2007). Thus, depending on the region, species may be subject to greater or lesser changes in climate. Some species can adapt, whereas others, and especially range-restricted species, risk extinction. A recent study based on the species–area relationships by Thomas et al. (2004) predicted the extinction of between 15 and 37% of species in the next 50 years due to climate change in sample regions covering 20% of the Earth's terrestrial surface.

For the next century, climate projections indeed predict a mean increase in temperature of 1.8°C for minimum scenarios to 4°C for maximum expected scenarios.

Recently, some authors proposed mathematical models for analysing the factors that influence the persistence of a population facing a climate change. They used the notion of "climate envelope," corresponding to the environmental conditions under which a population can persist. They assumed that the conditions defining this envelope did not

change with time, while the envelope location moved according to climate change (Thomas et al. 2004). Keeping 0.9°C/100 km as the poleward temperature gradient, the above-mentioned temperature increases should imply poleward translations of the climate envelope at speeds of 2−4.5 km year^{-1}.

A one-dimensional reaction-diffusion model has been proposed by H. Berestycki et al. (unpublished data). Results have been obtained, especially regarding the links between population persistence and species mobility. Indeed, if individuals have too low a rate of movement, then the population cannot follow the climate envelope and thus becomes extinct. On the other hand, if the individuals have a very high rate of movement, they disperse outside the climate envelope and thus the population also becomes extinct. Other related works, based on one-dimensional reaction-diffusion models, can be found in Potapov and Lewis (2004), Deasi and Nelson (2005), Pachepsky et al. (2005) and Lutscher et al. (2006).

The model that we consider here is derived from the classical Fisher population dynamics model (Fisher 1937; Kolmogorov et al. 1937). In a two-dimensional bounded environment Ω, the corresponding equation is:

$$\frac{\partial u}{\partial t} = D\nabla^2 u + ug(t,x,u), \quad t \in [0,+\infty), \quad x \in \Omega \subset \mathbb{R}^2. \tag{1}$$

The one-dimensional model considered by H. Berestycki et al. (unpublished data) is a particular case of model (1), with a logistic growth function $ug(t,x,u)$. Indeed, the authors assumed the per capita growth rate g to decrease with the population density u for all fixed x and t.

Other types of growth functions are of interest, especially those accounting for an Allee effect. An Allee effect occurs when the per capita growth rate reaches its peak at a strictly positive population density. At low densities, the per capita growth rate may then become negative (strong Allee effect). The Allee effect is known in many species (see Allee 1938; Dennis 1989; Veit and Lewis 1996) and results from several processes which can co-occur (Berec et al. 2007), such as diminished chances of finding mates at low densities (McCarthy 1997; Robinet et al. 2007b), fitness decreases due to consanguinity or decreased visitation rates by pollinators for some plant species (Groom 1998). It is commonly accepted that populations subject to an Allee effect are more extinction prone (Stephens and Sutherland 1999).

In reaction-diffusion models, Allee effects are generally modelled by equations of bistable type (Fife 1979; Turchin 1998; Shi and Shivaji 2006). Mathematical analyses involving these equations have demonstrated important effects of the domain's geometry, especially in studies of travelling wave solutions. These solutions generally describe the invasion of a constant state, for instance where no individuals are present, by another constant state (typically the carrying capacity), at a constant speed, and with a constant profile (see Aronson and Weinberger 1978). Berestycki and Hamel (2006) have proved that in an infinite environment with hard obstacles, that is otherwise homogeneous, travelling wave solutions of bistable equations may exist or not, depending on the shape of the obstacles. Similarly, in an infinite homogeneous square cylinder, Chapuisat and Grenier (2005) proved that travelling wave solutions may not exist if the cylinder's diameter is suddenly increased somewhere. See also Matano et al. (2006) for another related work. In parallel, Keitt et al. (2001), while studying invasion dynamics in spatially discrete environments, showed that an Allee effect can cause an invasion to fail and can therefore be a key factor that determines the limits of species ranges. In one-dimensional models, an Allee effect has also been shown to slow down invasions (Hurford et al. 2006) or even to stop or reverse invasions in the presence of predators (Owen and Lewis 2001) or pathogens (Hilker et al. 2005). In a study by Tobin et al. (2007), empirical evidence has also been given regarding the fact that geographical regions with higher Allee thresholds are associated with lower speeds of invasion.

The aim of this work is to study, for the simple two-dimensional reaction-diffusion model (1), how the population size variation during a shift in the climate envelope depends on the shift speed, the geometry of the environmental boundary, and on the population mobility and growth characteristics.

The first section is dedicated to the precise mathematical formulation of the model. Two types of growth functions are considered, a logistic one, and one taking account of an Allee effect; both cases are dependent on the climate envelope's position. We define three domain types, corresponding to three kinds of geometry of the environmental boundaries. Domain **1** is a straight rectangle, and domain **2** is the union of two rectangles of the same width joined by a narrow corridor. The comparison between domains **1** and **2** enables an analysis of the effects of a local narrowing of the habitat on population persistence. As suggested by the work of Chapuisat and Grenier (2005) and Berestycki and Hamel (2006), in the case with an Allee effect, extinction phenomena may not be caused directly by the reduction in climate envelope due to the narrowing of the domain in the corridor, but by its too sudden increase at the exit of the corridor. This is why we introduced domains of type **3**, which correspond to two rectangles of the same width joined by a narrow corridor, which gradually opens over a trapezoidal region of length h [the case $h = 0$ corresponds to domain **2**].

Results of numerical computations of the population size over 30 years are presented and analysed, under different hypotheses relating to growth rate, mobility, speed of climate change, and domain's shape. These results are further discussed in the last section of this paper.

Formulation of the model

The population dynamics is modelled by the following reaction-diffusion equation:

$$\frac{\partial u}{\partial t} = D\nabla^2 u + ug(t,x,u), \quad t \in [0,+\infty), \quad x \in \Omega \subset \mathbb{R}^2.$$

Here, $u = u(t,x)$ corresponds to the population density at time t and position $x = (x_1, x_2)$. The number $D > 0$ measures the species mobility, and ∇^2 stands for the spatial dispersion operator $\nabla^2 u = \frac{\partial^2 u}{\partial x_1^2} + \frac{\partial^2 u}{\partial x_2^2}$. The set Ω is a bounded subdomain of $\mathbb{R}^2$. We assume reflecting boundary conditions (also called no-flux or Neumann boundary conditions):

$$\frac{\partial u}{\partial n}(t,x) = 0, \quad \text{for} \quad x \in \partial\Omega,$$

where $\partial\Omega$ is the domain's boundary and $n = n(x)$ corresponds to the outward normal to this boundary. Thus, the boundary of the domain Ω, or equivalently the environmental boundary, constitutes an absolute barrier that the individuals cannot cross.

Growth functions

The function g corresponds to the per capita growth rate of the considered species. In our model, it can be of two main types, g_l or g_a. The first case corresponds to a logistic-like growth rate, depending on the position of the climate envelope:

$$\begin{cases} g_l(t,x,u) = r^+\left(1 - \frac{u}{K}\right), & \text{if } x \in \mathcal{C}(t), \\ g_l(t,x,u) = r^+\left(1 - \frac{u}{K}\right) - r^-, & \text{if } x \notin \mathcal{C}(t). \end{cases} \quad (2)$$

The set $\mathcal{C}(t) \subset \Omega$ corresponds to the climate envelope at time t, the real number $r^+ > 0$ is the intrinsic growth rate of the species inside the climate envelope, K corresponds to the carrying capacity inside the climate envelope, and r^- corresponds to the drop in intrinsic growth rate outside the climate envelope.

In the second case, a strong Allee effect is modelled. For fixed values of t and x, the function $g_a(t,x,u)$ does not attain its maximum at $u = 0$, and furthermore $g_a(t,x,0) < 0$ for all $t > 0$, $x \in \Omega$. The typical form of the per capita growth term taking account of an Allee effect is

$$g_a = r\left(1 - \frac{u}{k}\right)\left(\frac{u - c}{k}\right),$$

where r is a growth term, k is the environment's carrying capacity and c is the Allee threshold (see e.g., Lewis and Kareiva 1993; Keitt et al. 2001). For the comparison with the logistic case (2) to stand, we choose r and k such that $g_a(t,x,K) = g_l(t,x,K) = 0$ for all $x \in \mathcal{C}(t)$ and

$$\max_{u\in(0,K),x\in\mathcal{C}(t)} g_a(t,x,u) = \max_{u\in(0,K),x\in\mathcal{C}(t)} g_l(t,x,u) = r^+.$$

Moreover, we impose an "Allee threshold" c equal to ρK, for $\rho \in (0,1)$, which means that $g_a(t,x,u) < 0$ as soon as $u < \rho K$, and for all $x \in \Omega$. Such conditions yield $k = K$ and $r = \frac{4r^+}{(1-\rho)^2}$. As in the logistic case, we assume that g_a drops by r^- outside the climate envelope. Finally, we obtain,

$$\begin{cases} g_a(t,x,u) = r^+\frac{4}{(1-\rho)^2}\left(1 - \frac{u}{K}\right)\left(\frac{u}{K} - \rho\right) & \text{if } x \in \mathcal{C}(t), \\ g_a(t,x,u) = r^+\frac{4}{(1-\rho)^2}\left(1 - \frac{u}{K}\right)\left(\frac{u}{K} - \rho\right) - r^- & \text{if } x \notin \mathcal{C}(t). \end{cases}$$
$$(3)$$

The profiles of the growth functions ug_l and ug_a are depicted in Fig. 1, for x inside and outside the climate envelope.

Fig. 1 **a** Profile of the growth rate $u \mapsto ug_l(t,x,u)$ inside the climate envelope ($x \in \mathcal{C}(t)$, *solid line*), and outside the climate envelope ($x \notin \mathcal{C}(t)$ *dashed line*) in the logistic case. **b** Profile of the growth rate u $g_a(t,x,u)$ inside the climate envelope (*solid line*), and outside the climate envelope (*dashed line*), in the case with strong Allee effect. We have set $r^+ = 1$, $r^- = 2$, $K = 10$, and $\rho = 0.25$
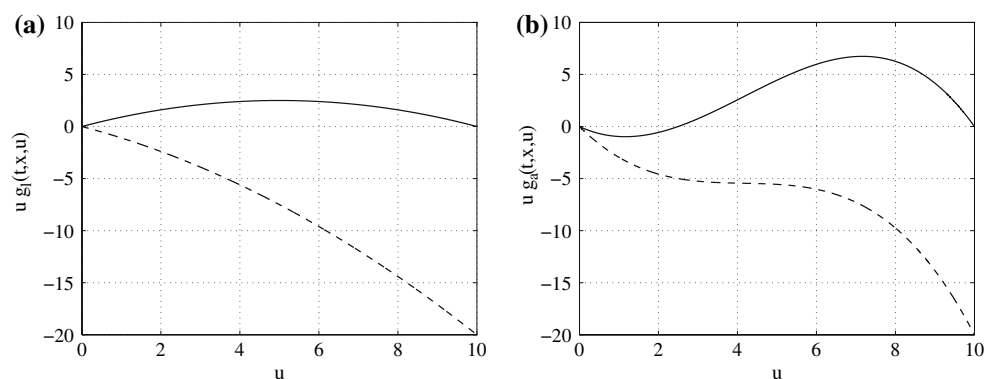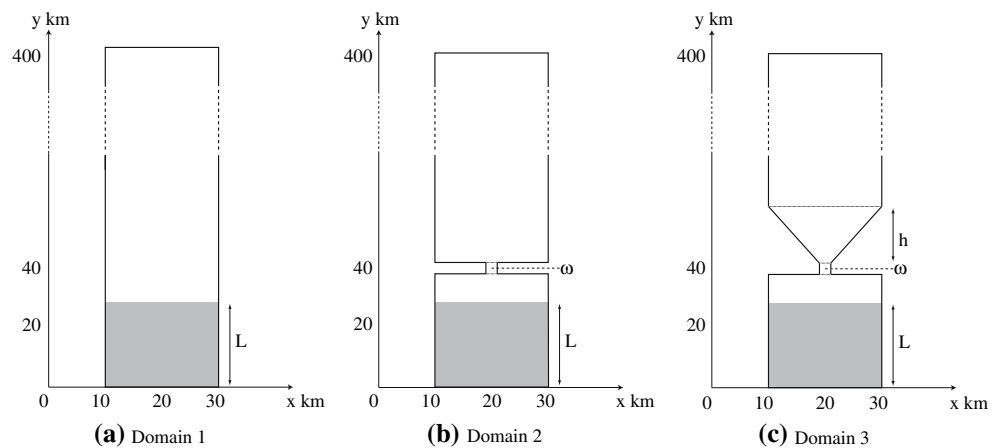
Fig. 2 Three types of domains
Ω. The *shaded area* corresponds
to the climate envelope $\mathcal{C}(0)$ at
$t = 0$; it is represented here with
a length $L = 30$ km. The
narrow passage ω of domains **2**
and **3** is separated at the
entrance and exit by *thin dotted
lines* and is followed by a
trapezoidal region of height h in
domain **3**

(a) Domain 1 **(b)** Domain 2 **(c)** Domain 3

Throughout this paper, we make the hypothesis $r^+ < r^-$.

Remark 1 In both cases, the environment's carrying
capacity is equal to K inside the climate envelope. However,
outside the envelope, the carrying capacity in the logistic
case would be $K\left(1 - \frac{r^-}{r^+}\right)$ for $r^+ \geq r^-$. However, it is not
defined when $r^+ < r^-$. Indeed, in this last situation, the
equation $u g_l(t,x,u) = 0$ has no positive solution. Similarly, in
the case with an Allee effect, the equation $u g_a(t,x,u) = 0$ has
no positive solution outside the climate envelope as soon as r^+
$< r^-$, since $\max_{u \in (0,K), x \in \mathcal{C}(t)} g_a(t,x,u) = \max_{u \in (0,K), x \in \mathcal{C}(t)}$
$g_l(t,x,u) = r^+$. This means that the environment is not
suitable for persistence outside the climate envelope.

As explained in the introduction, we assume that the cli-
mate envelope $\mathcal{C}(t) \subset \Omega$ moves poleward, according to the
climate change. Assuming we are in the Northern hemi-
sphere, we consider this move to be of constant speed $v > 0$,
in the second variable direction (to the "north"). Further-
more, we assume $\mathcal{C}(t)$ to be of constant thickness $L > 0$:

$$\mathcal{C}(t) := \{x = (x_1, x_2) \in \Omega, \quad \text{such that} \quad x_2 \in [vt, L + vt]\}.$$

Remark 2 In this framework, the spreading speed of the
population, if it survives, is constrained by the speed at
which the climate envelope moves. Let us recall that, in an
homogeneous one-dimensional environment, with a
logistic growth rate $u r^+(1 - u/K)$, the spreading speed is
$c_l^* = 2\sqrt{r^+ D}$ (see e.g., Aronson and Weinberger 1978). In
such an homogeneous environment, but with the growth
rate, $4u r^+/(1 - \rho)^2(1 - u/K)(u/K - \rho)$, taking account of an
Allee effect, the spreading speed becomes $c_a^* =$
$2\sqrt{r^+ D}\sqrt{2}(1/2 - \rho)/(1 - \rho)$ (see Lewis and Kareiva
1993). We observe that $c_a^* < c_l^*$, and that c_a^* decreases
with ρ. Thus, the spreading speed is slowed down by the
Allee effect. The case $\rho = 0$ corresponds to a weak Allee
effect: the per capita growth rate does not exhibit a
maximum at $u = 0$, but remains positive at low densities.
In that case, $c_a^*[\rho = 0] = c_l^*/\sqrt{2}$. The cases where $\rho \geq 1/2$,

corresponding to a very strong Allee effect, lead to
population extinction (see Lewis and Kareiva 1993).

Geometry of the environmental boundary

We work in bounded domains Ω of $\mathbb{R}^2$ of three different
types:

1 A straight rectangle.
2 The union of two rectangles of same width by a
   narrow passage ω.
3 The union of two rectangles of same width by a
   narrow passage ω followed by a trapezoidal region of
   height h.

These three domain types and their position relative to
the origin are depicted in Fig. 2.

The domains are assumed to have a width of 20 km [on
the larger parts, for domains **2** and **3**]. In domains **2** and **3**,
the "southern" rectangles are assumed to have a length of
40 km. The width of the passage ω is assumed to be 2 km,
and its length 4 km. The "northern" environmental
boundaries are situated far enough (400 km away from the
"southern" boundaries), so that they have no influence on
the population. The climate envelope is assumed to have a
latitudinal range $L = 30$ km.

Initial condition

We assume that the population was at equilibrium and that
the climate envelope was stationary before the considered
period starting at a time $t = 0$. This means that the initial
condition $u(0,x)$ is a positive solution to the stationary
equation:

$$-D \nabla^2 p = p\, g(0,x,p), \quad x \in \Omega \subset \mathbb{R}^2, \tag{4}$$

with $\frac{\partial p}{\partial n}(x) = 0$ over $\partial\Omega$. We place ourselves under the
appropriate conditions for the existence of such positive

stationary solutions in the logistic and Allee effect cases (see the Appendix for more details).

Results

Using a second-order finite elements method, we computed the solution $u(t,x)$ of the model (1) with the growth functions and initial conditions discussed above. We focus here on the population size,

$$P(t) := \int_\Omega u(t,x)\mathrm{d}x,$$

which was computed over 30 years in various situations.

Unless otherwise mentioned, we set $r^+ = 1$ year^{-1} for the intrinsic growth rate coefficient inside the climate envelope, and we assumed that the per capita growth rate was decreased by two outside the climate envelope: $r^- = 2$ year^{-1}. We assumed that $K = 10$ individuals/km^2. In our computations, the diffusion coefficient D varied between 1 km^2 year^{-1}, corresponding to populations with low mobility, e.g., some insect species, and 50 km^2 year^{-1}, corresponding to populations with high mobility (Shigesada and Kawasaki 1997, for some observed values of D, for different species). We first chose $\rho = 0.25$, so that the Allee threshold ρK is 2.5 individuals/km^2. The speeds v used for the climate-envelope shift varied between 1 and 6 km year^{-1}.

Population size over time

In order to get a first insight into the general behaviour of the population size $P(t)$ for $t \in [0,30]$, we first computed it

with the fixed values $v = 2.5$ km year^{-1} and $D = 10$ km^2 year^{-1}. The results are presented in Fig. 3.

First notice that, as expected with our choice of growth functions, the initial population sizes, $P(0)$, are almost the same for both growth functions (2) and (3): 5,800 and 6,000 respectively in the logistic case and Allee effect case. A slight transient increase or decrease in $P(t)$, probably due to the initial effect of the southern boundary, vanishes after 5 years.

In domain **1**, for both growth functions (2) and (3), after this short period of 5 years, the population sizes remain stable around their initial values.

In contrast, the populations react very differently in domain **2** depending on the type of growth rate. In the logistic case (Fig. 3a), the population size recovers its initial value after a transient decrease that lasts as long as the corridor is included in the climate envelope. In the case with an Allee effect (Fig. 3b), the population size declines to 0 after 20 years.

The behaviour of the population with an Allee effect in domain **3**, with $h = 25$ km (Fig. 3b), leads, as in domain **2** with logistic growth, to the recovery of the initial level of population.

As a preliminary conclusion to this first step, the fate of the population is driven by the interaction between environmental parameters (v and the type of domain) and biological parameters (D, r^+, r^-, K, ρ, and the type of growth function).

Intertwined effects of mobility and environmental parameters

We computed the "final" population size $P(30)$, for the range of parameters $(v,D) \in (1,6) \times (1,50)$. We define the

Fig. 3 Computation of population sizes $P(t)$ as a function of time t. **a** Case of the logistic growth rate $ug_l(t,x,u)$, in domain **1** (*solid line*) and in domain **2** (*dashed line*). **b** Case of the growth rate $ug_a(t,x,u)$ with an Allee effect, in domains **1** (*solid line*), **2** (*dashed line*) and **3** (*dotted line*). For these computations, we fixed $D = 10$, $v = 2.5$, $r^+ = 1$, $r^- = 2$, $K = 10$, $\rho = 0.25$ and $h = 25$
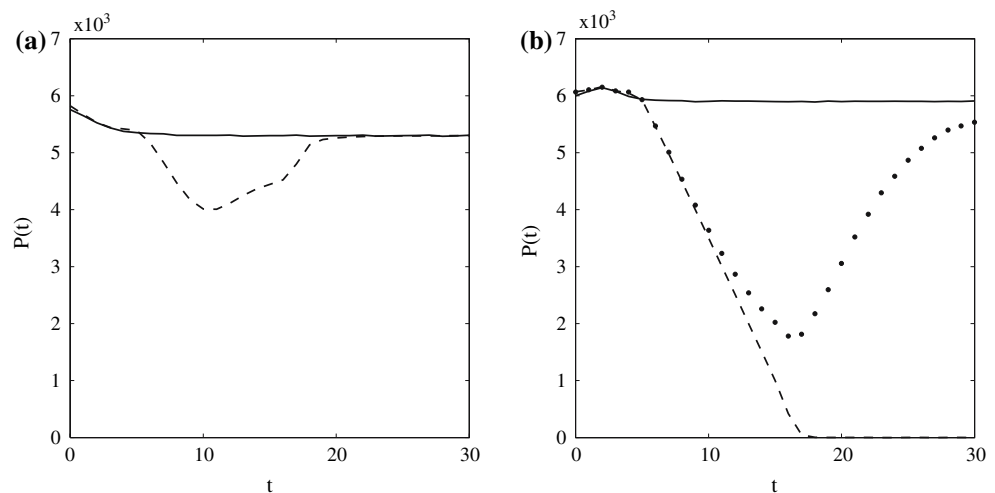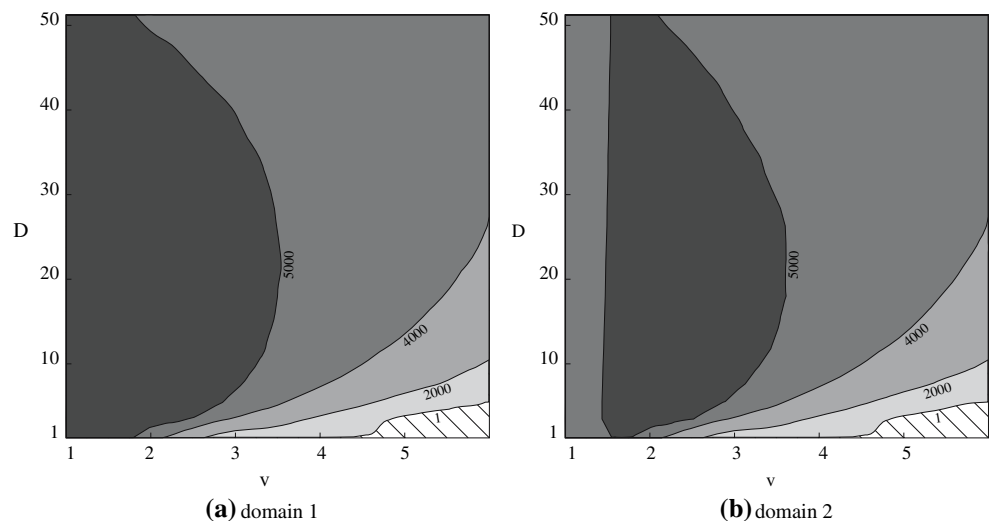
Fig. 4 Logistic growth rate $ug_l(t,x,u)$. Contour lines of $P(30)$ as a function of the speed of climate change v and of the diffusion coefficient D, in domains **1** (**a**) and **2** (**b**). The *hatched areas* correspond to the extinction regions. We fixed $r^+ = 1$, $r^- = 2$ and $K = 10$

(a) domain 1

(b) domain 2

"extinction region" as the portion of the parameter space leading to $P(30) < 1$.

Logistic case

The extinction region is very similar in domains **1** and **2** (Fig. 4), and corresponds to high values of v and low D values. In those cases, the population mobility (D) is not sufficient to follow the climate envelope (moving at speed v). In domain **1**, for each value of D, $P(30)$ decreases with respect to v, while in domain **2**, $P(30)$ decreases with v for $v \geq 1.5$ (whenever $v < 1.5$, the climate envelope has not totally crossed the corridor ω at $t = 30$). As has already been proved in the one-dimensional case (H. Berestycki et al., unpublished data), and for the same reasons as described in the Introduction section, we observe here that population sizes $P(30)$ are not monotonically linked with the parameter D.

Case with Allee effect

In domain **1** (Fig. 5a), $P(30)$ decreases with respect to v and increases with D. The extinction region again corresponds to high values of v and low D values. However, the extinction region is wider than in the logistic case. In domain **2** (Fig. 5b), the population does not survive as soon as $v > 1.8$. The extinction region is therefore very wide compared to the one of domain **1**.

In contrast to the logistic case, a marked difference between the fate of populations in domains **1** and **2** does exist. This reflects the sensitivity to environmental boundary geometry of populations subject to an Allee effect. In domain **3**, with $h = 25$, where the opening at the exit of the corridor is more progressive than in domain **2**,

we observe that the extinction region is reduced (Fig. 5c). It remains, however, larger than in domain **1**, especially for large values of D.

## Allee effect and boundary geometry

Effect of gradual boundary change at the exit of the corridor

We have seen in the case of a population subject to an Allee effect that domain **3**, with $h = 25$, gives a greater chance of population persistence than domain **2** (which corresponds to domain **3**, with $h = 0$). Let us fix $v = 2.5$, and see how persistence depends on h and D. The results of the computation of $P(30)$ for $(h,D) \in [0,30] \times (1,50)$ are presented in Fig. 6.

For each value of D, $P(30)$ increases with h; thus higher h values provide a greater chance for population persistence. Furthermore, for cases where $D \geq 3$, we observe that we can define a real number h^* such that the population goes to extinction if $h < h^*$, and the population survives if $h > h^*$. Remarkably, h^* defines two types of geometry, characterised by the progressiveness of the opening at the exit of the corridor ω, which lead to extinction or survival, respectively. For most values of D ($D \geq 5$), h^* increases linearly with D. For small values of D ($D < 3$), extinction occurs independently of the value h, which simply means that, as in domain **1**, the population cannot follow the climate-envelope shift.

These results indicate that the increased extinction risk in domain **2**, compared to domain **1**, may not be caused by the shrinking of the climate envelope and its fragmentation in two parts, but by the lack of progressiveness of the opening at the exit of the corridor.

Fig. 5 Case with Allee effect. **a, b, c** Contour lines of $P(30)$ as a function of v and D in domains **1**, **2** and **3**, respectively. The *hatched areas* correspond to the extinction regions. For these computations, we fixed $r^+ = 1$, $r^- = 2$, $K = 10$, $\rho = 0.25$ and $h = 25$

(a) domain 1

(b) domain 2

(c) domain 3
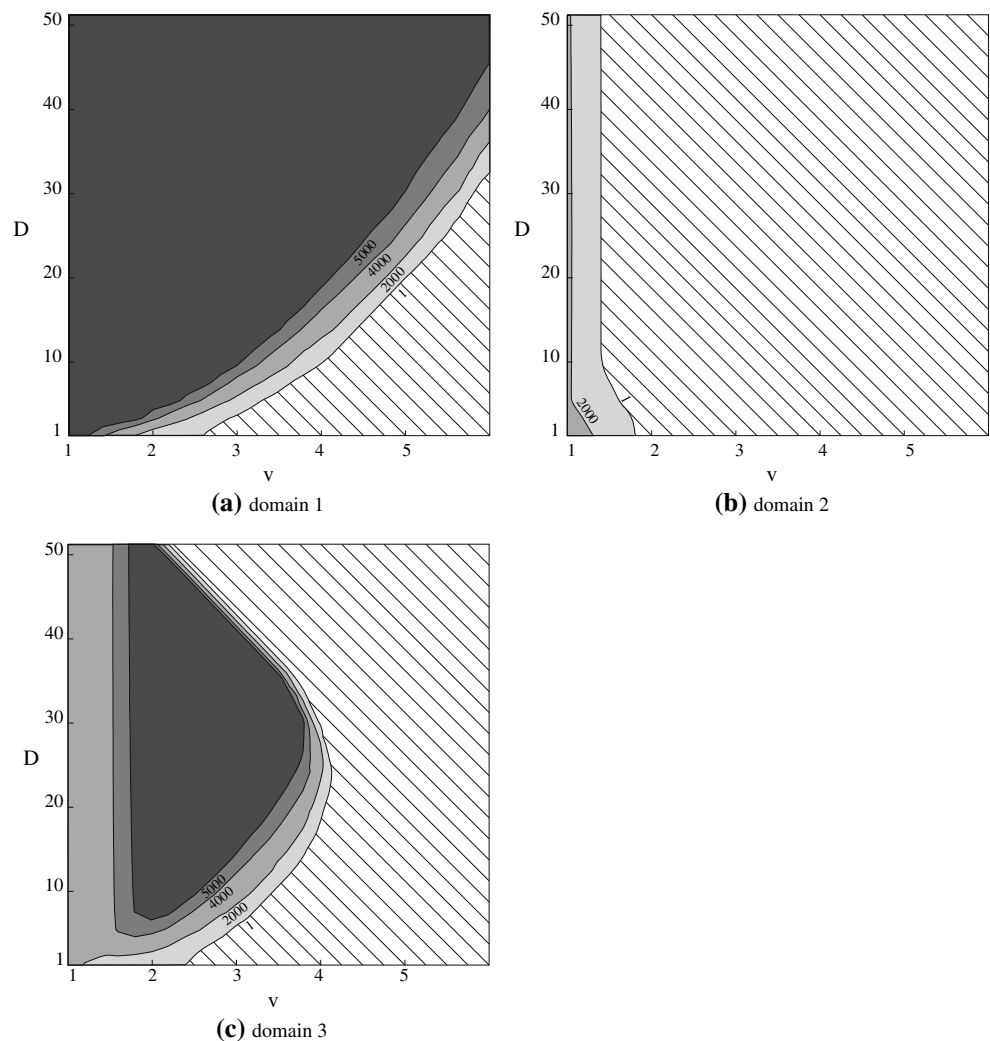
Population density at the exit of the corridor governs the fate of the population

Let us focus on what happens at the exit of the corridor ω. We considered the region $\Omega_1 = \Omega \cap \{y \in (44, 48)\}$, corresponding to the 4 km following the corridor. We computed the number $P_1(t) = \int_{\Omega_1} u(t, x) dx$ of individuals in this region, and the population density $u(t,c)$ at the "centre" $\mathbf{x}_c$ of Ω_1 of coordinates (10;46). We compared domains **2** and **3**, with the fixed parameters values $v = 2.5$, $D = 10$, $\rho = 0.25$, and $h = 25$ (which is larger than $h^* = 10$ in this case; see Fig. 6). The results are presented in Fig. 7.

We observe that, at the beginning of the invasion of Ω_1, for $t \in [4,7]$, the populations $P_1(t)$ are almost identical in the two domains. Thus, the boundary geometry after the corridor has no effect on the number of individuals which first invade the region Ω_1. On the contrary, during the same period of time, the population density at $\mathbf{x}_c$, which is situated at the exit of the corridor, remains lower in domain **2**, and never reaches the

Allee threshold $\rho K = 2.5$. Thus, in domain **2**, the dispersion of the few invaders into an open wide space, after the corridor, leads to a low population density, and therefore to a negative value of the per capita growth rate $g_a(t,x,u)$ (it would be false for a logistic growth function). The higher density in domain **3** for $h > h^*$ results from the progressiveness of the domain width offered to population development. Even if the individuals are scarce in Ω_1, the population density at $\mathbf{x}_c$ exceeds the Allee threshold at $t = 7$. That makes the population increase, leading to survival (survival can indeed be observed in Fig. 5c). Thus, the fate of the population seems to depend on whether or not the population density at the exit of the corridor reaches the Allee threshold.

This leads us to analyse the effect of the Allee threshold. For the same values $v = 2.5$ and $D = 10$, the function $\rho \mapsto h^*$ is presented in Fig. 8. For small values of ρ ($\rho \le 0.16$), we observe that $h^* = 0$, i.e., the population even survives in domain **2**. Then, h^* increases with ρ. For higher values of ρ, the population never persists, at least when
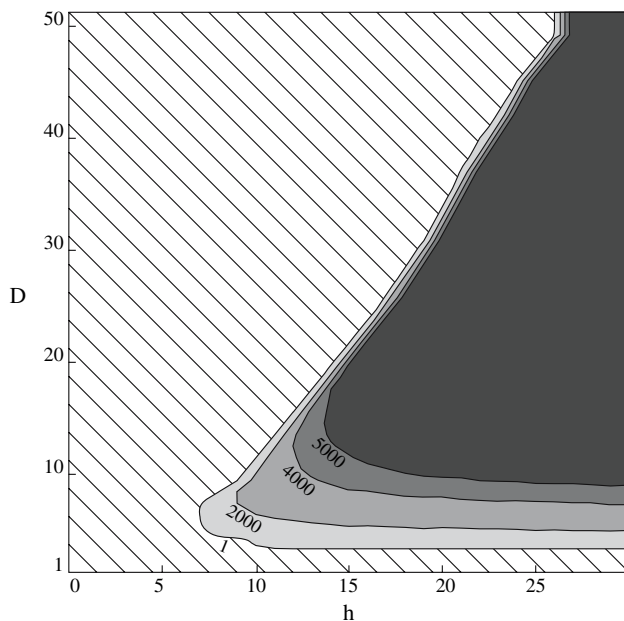
Fig. 6 Case with Allee effect. Contour lines of $P(30)$ in domain **3**, as a function of D and of the height h of the trapezoidal region. The *hatched area* corresponds to the extinction region. The other parameters values were $r^+ = 1$, $r^- = 2$, $K = 10$, $\rho = 0.25$ and $v = 2.5$
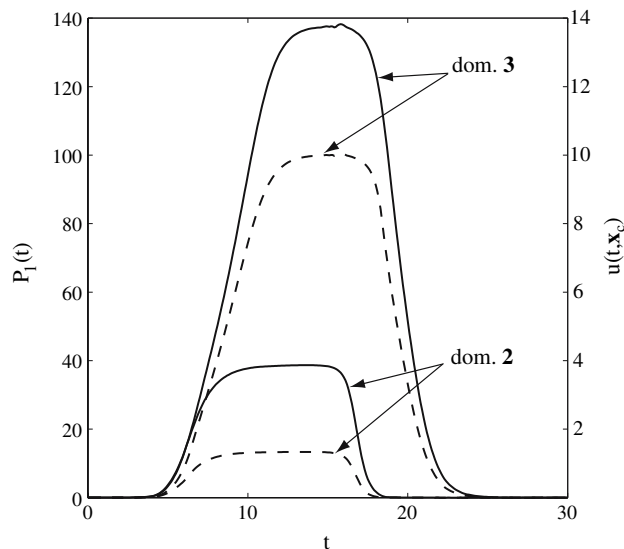

Fig. 7 Case with Allee effect. *Solid lines*: Number of individuals $P_1(t)$ in the region $\Omega_1 = \Omega \cap \{y \in (44, 48)\}$, corresponding to the 4 km following the corridor, in domains **2** and **3**. *Dashed lines*: Population density $u(t,c)$ at the "centre" $\mathbf{x}_c = (10;46)$ of Ω_1. For this computation, we fixed $D = 10$, $r^+ = 1$, $r^- = 2$, $K = 10$, $\rho = 0.25$ and $v = 2.5$

$h \leq 30$ (see also the end of Remark 2). Finally, the stronger the Allee effect, the more progressive must be the opening at the exit of the corridor ω.

On the contrary, the degree of hostility outside $\mathcal{C}(t)$, quantified by r^-, does not seem to affect h^* much. Indeed,
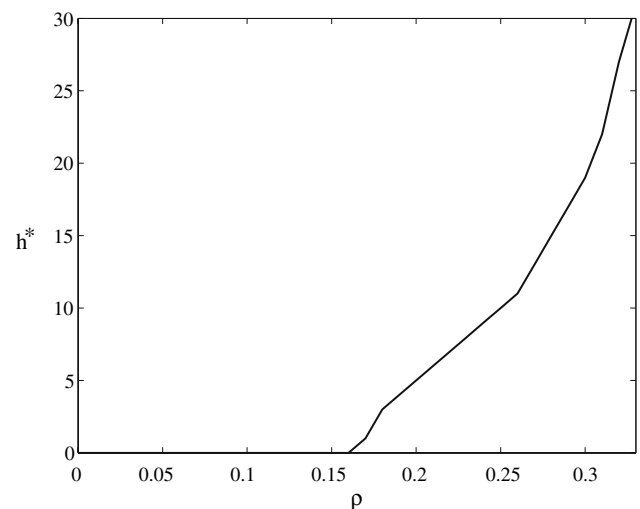

Fig. 8 Case with Allee effect. Minimum value h^* of h required for persistence, in terms of the parameter ρ. The other parameter values were $D = 10$, $r^+ = 1$, $r^- = 2$, $K = 10$ and $v = 2.5$

computing h^*, for $v = 2.5$, $D = 10$ and $\rho = 0.25$, we always obtained $h^* = 10$, for $r^- \in (1,2)$ (remember that, in this work, it is assumed that $r^- > r^+$, see Remark 1).

Discussion

Using a two-dimensional reaction-diffusion model, we have studied the fate of populations with different mobility and growth characteristics facing environmental change—a shift of their climate envelope, the shape of which can be modified by environmental boundary geometry.

The growth functions we considered were of two types, logistic, with a per capita growth rate modelled by (2) or taking account of a strong Allee effect (3). Boundary geometry diversity has been summarised into three schematic domain shapes (Fig. 2).

In the logistic case, the other biological parameters being fixed, the response (survival or extinction) to a climate envelope shift at speed v is simply determined by the mobility of the population, which is measured by the diffusion parameter D. The minimum required mobility for survival increases with the speed v. This response is independent of the environmental boundary geometry. This clearly appeared when comparing domains **1** and **2**. In fact, we conjecture that it is true for any local perturbation of the boundary (it could be proved using the methods of Berestycki and Rossi 2007).

In the case with an Allee effect, we observed a more complex pattern of interactions among biological and environmental parameters. In the straight domain **1**, the result was similar to the logistic case, the higher the speed at which the climate envelope shifted, the higher the

required mobility for survival. Additionally, the required mobility, at any v, is always higher than in the logistic case.

Facing a local narrowing of the environment, as in domain **2**, in contrast to the logistic case, the chances of survival dramatically decrease in the presence of an Allee effect. In that case, high mobility is not sufficient to face climate envelope shifting at high speeds. Indeed, the population density drop at the exit of the corridor exhibits the sensitivity of this type of populations to low densities. This drop can be attenuated by a progressive opening of the available space at the exit of the corridor, as in domain **3**. Even though this geometry temporarily leads to a diminished area of the climate envelope, it finally results in higher chances of survival. The opening has to be all the more progressive when the Allee threshold and the species mobility are high.

Thus, a population subject to an Allee effect should have a mobility which is neither too low, in order to be able to follow the climate envelope, nor too high, in order to overcome various changes in the shape of the climate envelope. For this reason, species whose mobility is increasingly dependent on their density should be more robust to climate change (see Okubo and Levin 2002, for a survey of reaction-diffusion models with density-dependent dispersal terms). On the other hand, under the environmental changes considered in this paper, populations with negatively density-dependent dispersal, such as in the model proposed by King and McCabe (2003) for the dispersal of early Palaeoindian people in North America, should have high probabilities of extinction, if an Allee effect is assumed.

The reflective boundary conditions that we used throughout this paper mean that individuals encountering the environmental boundary are reflected inside the domain. These boundary conditions can be encountered in many real-world situations, corresponding to cliffs, rivers or coasts (Shigesada and Kawasaki 1997; Jaeger and Fahrig 2004). Other boundary conditions could have been considered. With Robin boundary conditions, for instance, some of the individuals cross the boundary. These boundary conditions are written as $\partial u/\partial n + \varepsilon u = 0$ (see e.g., Cantrell and Cosner 2003, for some details on this type of boundary condition). Preliminary numerical computations have shown that our results still hold in such a case, at least for small positive values of ε, corresponding to a few individuals crossing the environmental boundary.

It was stated in Parmesan (2006), on the basis of empirical studies, that range-restricted species, like polar and mountain-top species, are at high risk of extinction induced by warming. Our study suggests that some other species may fail to expand poleward and that their capacity to expand is linked to the geometry of the geographical limits. Apart from laboratory tests under controlled conditions, the diversity of arrangements of the Alpine valleys could allow us to see whether the results of this paper can be observed in natural conditions. Indeed, insects such as the pine processionary moth, whose present range expansion is undoubtedly related to climate change (Robinet et al. 2007a), may allow us to test statistically the relationships between insect progression and the geometry of the Alpine corridors.

In this paper, a southern retraction of the climate envelope was assumed. This can be directly linked, for some species, to the fact that they are sensitive to high temperatures. This can also be caused indirectly by competition with other species whose ranges are shifting to the north. For some species, however, this retraction does not occur, leading to an expansion of the species range. This could be easily integrated in our model, by setting

$$\mathcal{C}(t) := \{x = (x_1, x_2) \in \Omega, \quad \text{such that} \quad x_2 \in [0, L + vt]\}.$$

In this case, comparable results should be obtained, with stagnation instead of extinction.

Appendix: initial conditions

When the growth rate is of logistic type, with $g = g_l$ satisfying (2), a sufficient condition for the existence of a positive solution p_l of (4) can be derived by finding an appropriate sub-solution for (4) (see e.g., Amann 1976); indeed, the constant K is readily a super-solution. With our choices of Ω, $\mathcal{C}(0)$ and boundary conditions, for a small enough $\alpha > 0$, the function

$$\phi(x, y) = \alpha \sin\left(\frac{\pi}{2} + \frac{\pi y}{2L}\right) \quad \text{for } y < L,$$
$$\text{and } \phi(x, y) = 0 \quad \text{for } y \geq L,$$

is such a sub-solution, as soon as $\frac{D\pi^2}{4L^2} < r^+$. Under this condition, the function p_l is then the unique positive and bounded solution of (4); it can be proved as in Berestycki et al. (2005). In the logistic case, we assume that $u(0, x) = p_l$.

In case (3) with an Allee effect, the condition for the existence of a solution of (4), with $g = g_a$ is more complex, and multiple solutions may exist. However, the

existence of a positive and bounded solution of (4) is still granted when $\mathcal{C}(0)$ contains a sufficiently large ball B_R. Indeed, for a large enough R, there exists a positive solution ψ for (4) on B_R, with Dirichlet boundary conditions (Berestycki and Lions 1980). The function ψ, extended by 0 outside B_R, is then a sub-solution of (4); the constant K is again a super-solution. This implies the existence of a solution p_a of (4) on Ω. We can assume in this case that $u(0,x) = p_a$.

For our computations, p_l was obtained by numerically solving (4) using a second-order finite elements method with triangular mesh elements. In the case with an Allee effect, p_a was computed as the limit of the solution $w(T,x)$, as $T \to +\infty$ of the initial-value problem

$$\frac{\partial w}{\partial t} - D\nabla^2 w = w\, g(0,x,w), \quad t > 0, \quad x \in \Omega,$$

with $w(0,x) = 2K$ and $\frac{\partial w}{\partial n}(t,x) = 0$ over $\partial\Omega$. The solution $w(T,x)$ was also obtained thanks to a finite elements method. The convergence of $w(T,x)$ to a positive equilibrium as $T \to +\infty$ ensures that the condition for the existence of p_a is fulfilled.

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