The effect of climate shift on a species submitted to dispersion, evolution, growth and nonlocal competition

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Abstract

We consider a population structured by a space variable and a phenotypical trait, submitted to dispersion, mutations, growth and nonlocal competition. We introduce the climate shift due to *Global Warming* and discuss the dynamics of the population by studying the long time behavior of the solution of the Cauchy problem. We consider three sets of assumptions on the growth function. In the so-called *confined case* we determine a critical climate change speed for the extinction or survival of the population, the latter case taking place by "strictly following the climate shift". In the so-called *environmental gradient case*, or *unconfined case*, we additionally determine the propagation speed of the population when it survives: thanks to a combination of migration and evolution, it can here be different from the speed of the climate shift. Finally, we consider *mixed scenarios*, that are complex situations, where the growth function satisfies the conditions of the confined case on the right, and the conditions of the unconfined case on the left.

The main difficulty comes from the nonlocal competition term that prevents the use of classical methods based on comparison arguments. This difficulty is overcome thanks to estimates on the tails of the solution, and a careful application of the parabolic Harnack inequality.

Key Words: structured population, nonlocal reaction-diffusion equation, propagation, parabolic Harnack inequality.

AMS Subject Classifications: 35Q92, 45K05, 35B40.

1 Introduction

In this article, we are interested in the long time dynamics of the solution $n = n(t, x, y)$ to the following nonlocal parabolic problem

$$\begin{cases} \partial_t n(t,x,y) - \partial_{xx} n(t,x,y) - \partial_{yy} n(t,x,y) \\ \qquad = \left(r(x-ct,y) - \int_{\mathbb{R}} K(t,x,y,y') n(t,x,y')\, dy' \right) n(t,x,y) & \text{for } (t,x,y) \in \mathbb{R}_+ \times \mathbb{R}^2, \\ n(0,x,y) = n_0(x,y) & \text{for } (x,y) \in \mathbb{R}^2. \end{cases} \quad (1)$$

This models describes the dynamics of a population which, at each time $t \geq 0$, is structured by a space variable $x \in \mathbb{R}$, and a phenotypic trait $y \in \mathbb{R}$. The population is submitted to four essential processes: spatial dispersion, mutations, growth and competition. It also has to face the climate shift induced by *Global Warming*. The spatial dispersion and the mutations are modelled by diffusion operators. We assume that the growth rate of the population, if the competition is neglected, depends initially ($t = 0$) on both the location x and the phenotypic trait y, through the given function r. The effect of climate shift is simply to shift those conditions in space, at a given and forced speed c (without loss of generality, we will always consider $c \geq 0$). Hence, the growth rate is given by $r(x-ct, y)$, which is typically negative outside a strip centred on the line $y - B(x - ct) = 0$ (see the *environmental gradient case* below, and notice that we also study other situations). This corresponds to a population living in an environmental gradient: to survive at time t and location x, an individual must have a trait close to the optimal trait $y_{opt}(t, x) = B(x-ct)$ which is shifted by the climate (one may think of x being the latitude). Finally, we consider a logistic regulation of the population density that is local in the spatial variable x and nonlocal in the phenotypic trait y. In other words, we consider that there exists an intra-specific competition (for e.g. food) at each location, which may depend on the traits of the competitors.

Our aim is to determine conditions that imply extinction of the population and the ones that imply its survival, or even its propagation. The model (1) can be seen as a reaction-diffusion equation with a monostable reaction term. Solutions of such equation typically propagate in space at a linear speed, that can often be explicitly determined. In some models, such as the Fisher-KPP equation [18], [24], it is actually possible to push the analysis beyond the propagation speed: one can for instance describe the convergence of the population to a travelling wave, see [12, 13]. The analysis of (1) is however much more involved, in particular because of the nonlocal competition term it contains. We will then focus our analysis on the qualitative properties of the solutions, based on the notion of spreading introduced in [4].

In [5], a model has been introduced to study the effect of *Global Warming* on a species, when evolutionary phenomena are neglected, that is when all individuals are assumed to be identical (see also [30], [10, 11]). Among more detailed results, it is shown that there exists a critical speed c^* such that the population survives if and only if the climate change occurs at a speed slower than c^*. However, it is well documented that species adapt to local conditions, see e.g. [32], and in particular to the local temperatures. Two closely related models taking into account this heterogeneity of the population have been proposed in [28] and [23] (see e.g. [29], [26], [15] for recent results). The models of [28], [23] describe the evolution of the population size and its mean phenotypic trait, and can be derived formally from a structured population model similar to (1), provided the population reproduces sexually (see [26]). Such simplified models do not exist for asexual populations, so that one has to consider (1) in this latter case. In this framework, let us mention the construction of travelling waves [2] for equation (1), and [7] for a related but different model, when there is no climate shift ($c = 0$). Notice also that the model (1) can be derived as a limit of stochastic models of finite populations [14].

The well-posedness of a Cauchy problem very similar to (1), but on a bounded domain, has been studied in [31, Theorem I.1], under reasonable assumptions on the coefficients. We believe a similar argument could be used here to show the existence of a unique solution $n_R = n_R(t, x, y)$, for $(x, y) \in$

$[-R,R]^2$. The existence and uniqueness of solutions to (1) could then be obtained through a limit $R \to \infty$, thanks to the estimates on the tails of the solutions obtained in Lemma 2.4. We have however chosen to focus on the qualitative properties of the solutions in this article.

Typically, we expect the existence of a critical value $c^* > 0$ for the forced speed c of the climate shift: the population goes extinct (in the sense that it can not adapt or migrate fast enough to survive the climate shift) when $c \geq c^*$ and survives, by following the climate shift and/or thanks to an adaptation of the individuals to the changing climate, when $0 \leq c < c^*$. To confirm these scenarios, we shall study the long time behavior of a global nonnegative solution $n(t,x,y)$ of the Cauchy problem (1).

The main difficulty in the mathematical analysis of (1) is to handle the nonlocal competition term. When the competition term is replaced by a local (in x and y) density regulation, many techniques based on the comparison principle — such as some monotone iterative schemes or the sliding method — can be used to get, among other things, monotonicity properties of the solution. Since integro-differential equations with a nonlocal competition term do not satisfy the comparison principle, it is unlikely that such techniques apply here. Problem (1) shares this difficulty with the nonlocal Fisher-KPP equation

$$\partial_t n(t,x) - \partial_{xx} n(t,x) = \left(1 - \int_{\mathbb{R}} \phi(x-y) n(t,y)\, dy\right) n(t,x), \tag{2}$$

which describes a population structured by a spatial variable only, and submitted to nonlocal competition modelized by the kernel ϕ. As far as equation (2) is concerned, let us mention the possible destabilization of the steady state $u \equiv 1$ by some kernels [19], the construction of travelling waves [8], additional properties of these waves [17], [1], and a spreading speed result [22]. We also refer to [3], [21] for the construction of travelling waves for a bistable nonlocal equation, for an epidemiological system with mutations respectively.

In this paper we investigate three main types of problems giving rise to qualitatively different behaviors. These correspond to different assumptions about the region where the growth function r is positive. We now define these various cases and state some of the main results we obtain for each one of them.

1.1 The confined case

In the *confined case*, the growth function can be positive only in a bounded (favorable) region of the (x,y) plane. The precise assumption is as follows.

Assumption 1.1 (Confined case)**.** *For all $\delta > 0$, there is $R > 0$ such that*

$$r(x,y) \leq -\delta \quad \textit{for almost all } (x,y) \textit{ such that } |x| + |y| \geq R.$$

Simple but meaningful examples of such growth functions are given by

$$r_\varepsilon(x,y) := 1 - A(y - Bx)^2 - \varepsilon x^2, \tag{3}$$

for some $A > 0$, $B > 0$ and $\varepsilon > 0$. At every spatial location $x \in \mathbb{R}$, the optimal phenotypic trait (i.e. the phenotypic trait that provides the highest growth rate) is $y_{opt} = Bx$, and the constant B represents the linear variation on this optimal trait in space. The constant A characterizes the quadratic decrease of the growth rate r away from the optimal phenotypic trait. Finally, the constant ε describes how the optimal growth rate varies in space: we assume that an individual originating from a given region can adapt to warmer temperatures induced by the climate shift, but will not, nevertheless, be as successful as it was originally (in the sense that its growth decreases). In Figure 1 (left), we represent the function r given by (3) with $A = 4$, $B = \frac{1}{5}$, and $\varepsilon = \frac{1}{15}$.

The main results in this case are given in Proposition 3.1, Proposition 3.3 and in Theorem 3.4. Essentially these state that there is a *critical speed* c^* such that when the climate change speed c is such that $c < c^*$, then the population persists by keeping pace with the climate change, whereas when $c > c^*$, the population becomes extinct as time goes to infinity. We obtain the critical speed from an explicit (generalized) eigenvalue problem. We explain these notions in subsection 2.1.

1.2 The environmental gradient case

In ecology, an *environmental gradient* refers to a gradual change in various factors in space that determine the favored phenotypic traits. Environmental gradients can be related to factors such as altitude, temperature, and other environment characteristics. In our framework this case is defined by the following condition.

Assumption 1.2 (Environmental gradient case, or unconfined case)**.** *We assume that* $r(x,y) = \bar{r}(y - Bx)$ *for some* $B > 0$ *and some function* $\bar{r} \in L^\infty_{loc}(\mathbb{R})$ *such that, for all* $\delta > 0$*, there is a* $R > 0$ *such that*

$$\bar{r}(z) \leq -\delta \ \text{ for almost all } z \text{ such that } |z| \geq R.$$

Note that in this case, without climate change, the favourable region, where $r(x,y)$ can be positive, spans an unbounded slab, in sharp contrast with the confined case where it is bounded. An instructive example of function satisfying the environmental gradient case is given by

$$r(x,y) := 1 - A(y - Bx)^2, \tag{4}$$

for some $A > 0$ and $B > 0$ which have the same interpretations as in (3): at every spatial location $x \in \mathbb{R}$, the optimal phenotypic trait is $y_{opt} = Bx$, B represents the linear variation on this optimal trait in space, while A characterizes the quadratic decrease of the growth rate r away from the optimal phenotypic trait. Note however that the optimal growth rate is now constant in space. In Figure 1 (center), we represent the function r given by (4) with $A = 4$ and $B = \frac{1}{2}$.

The main results in this case are given in Proposition 4.5 and Theorem 4.2. As in the confined case, there is a critical speed c^{**} for the climate shift — obtained from a generalized eigenvalue problem, and even explicitly computable in some simple situations, see formula (51)— which separates extinction from survival/invasion. Nevertheless, let us emphasize on a main difference with the confined case: the population does not necessarily keep pace with the climate but may persist thanks to a combination of migration and evolution, see Remark 4.4. To shed light on this phenomenon, in Theorem 4.2 we further identify the propagation speed of a population in an environmental gradient when $c < c^{**}$, which we believe to be important for further investigations.

1.3 The mixed case

Finally, we introduce here a more complex situation, that combines the two previous cases. We call it the *mixed case*. It is defined by the following condition.

Assumption 1.3 (Mixed case)**.** *We have*

$$r(x,y) = \mathbf{1}_{\mathbb{R}_- \times \mathbb{R}}(x,y) r_u(x,y) + \mathbf{1}_{\mathbb{R}_+ \times \mathbb{R}}(x,y) r_c(x,y),$$

where r_c *satisfies Assumption 1.1 and* r_u *satisfies Assumption 1.2.*

Thus, in this case, the growth function satisfies the assumption of the environmental gradient case for $x \leq 0$, and the assumption of the confined case for $x \geq 0$. A typical example is given by

$$r(x,y) = 1 - A(y - Bx_- - B'x_+)^2 - \varepsilon {x_+}^2, \tag{5}$$

for some $A > 0$, $B > 0$, $B' > 0$ and $\varepsilon > 0$. Note that we have used the notations $x_- = \min(x,0)$, $x_+ = \max(x,0)$. In Figure 1 (right), we represent the function r given by (5) with $A = 4$, $B = \frac{1}{2}$, $B' = \frac{1}{5}$, and $\varepsilon = \frac{1}{15}$.

Our main results in this case are given in subsection 5.2. We show that one can extend the critical speeds, c^* and c^{**}, obtained in the previous two cases. We prove that the population persists if the climate change speed is below either one of these critical speeds whereas it goes extinct when it is above both. This is stated in details in Theorem 5.4 where we also describe more precisely the large time behavior of the population, depending on the position of c w.r.t. c^* and c^{**}. Furthermore, a new and interesting phenomenon arises in this case: when c^* and c^{**} are close, then, as c varies, the dynamics of the population can rapidly change from fast expansion to extinction, see Remark 5.5.

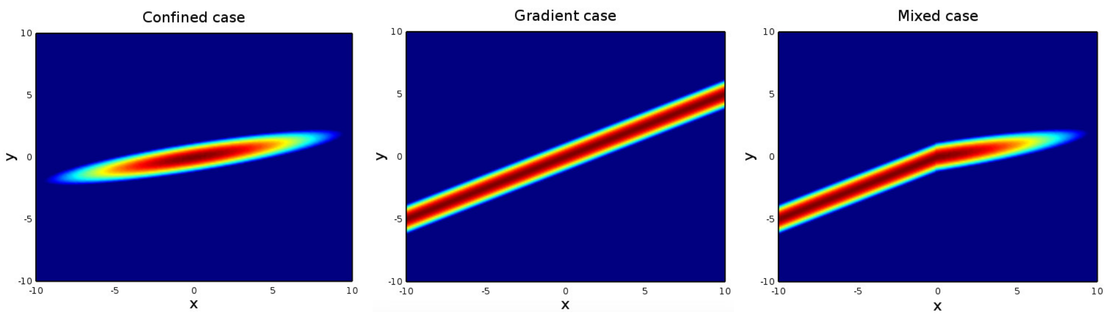

Figure 1: The function $r(x, y)$, describing the growth rate of the population when the competition effects are neglected, as a function of the spacial variable $x \in \mathbb{R}$ and the phenotypic trait $y \in \mathbb{R}$, for the three scenarios considered in this article: confined case (left), unconfinded case (center), mixed case (right). The red color represents high values of r, while $r(x, y) \leq -5$ is represented in blue.

1.4 Estimating the nonlocal competition term

When studying the extinction cases, it follows from the parabolic comparison principle that we can neglect the nonlocal term $\int_{\mathbb{R}} K(t, x, y, y')n(t, x, y')\, dy'$ in (1). On the contrary, careful estimates on this nonlocal term are necessary to study the survival and propagation phenomena. The strategy consists in first proving estimates on the tails of the solutions, which provides a control of the nonlocal term for large x, y. Next, on the remaining compact region, a rough uniform bound on the mass $\int_{\mathbb{R}} n(t, x, y)\, dy$ enables us to apply an argument based on the parabolic Harnack inequality for linear equations with bounded coefficients, and therefore to control the nonlocal term. This idea is similar to the method developed in [2] to study travelling wave solutions of a related problem. In this previous work however, the solution was time independent, and we could use the elliptic Harnack inequality. In the present work, an additional difficulty arises: for parabolic equations, the Harnack inequality involves a necessary time shift, see Remark 2.6. Nevertheless, we show in subsection 2.3 that if the solution u of a parabolic Harnack inequality is uniformly bounded (which, in our situations, will be proved in Lemma 2.4 and Lemma 5.3), then for any $\bar{t} > 0$, $\bar{x} \in \mathbb{R}^N$, $R > 0$ and $\delta > 0$, there exists $C > 0$ such that the solution u satisfies

$$\max_{x \in B(\bar{x}, R)} u(\bar{t}, x) \leq C \min_{x \in B(\bar{x}, R)} u(\bar{t}, x) + \delta,$$

thus getting rid of the time shift. This refinement of the parabolic Harnack inequality is a very efficient tool for our analysis, since used in the proofs of Lemma 2.4 (exponential decay of tails), Theorem 3.4 (survival in the confined case), Theorem 4.2 (survival and invasion in the unconfined case), Theorem 5.4 (iii) (survival and invasion in the mixed case). Since we believe that such rather involved technics are also of independent interest for further utilizations, we present them as a separate result in Theorem 2.7 for a general parabolic equation.

1.5 Mathematical assumptions, and organization of the paper

Throughout the paper we always assume the following on the coefficients of the nonlocal reaction diffusion equation (1): $r \in L^\infty_{loc}(\mathbb{R}^2)$ and there exists $r_{max} > 0$ such that

$$r(x, y) \leq r_{max} \quad \text{a.e. in } \mathbb{R}^2; \tag{6}$$

also $K \in L^\infty((0, \infty) \times \mathbb{R}^3)$ is bounded from above and from below, in the sense that there are $k^- > 0$, $k^+ > 0$ such that

$$k^- \leq K(t, x, y, y') \leq k^+ \quad \text{a.e. in } (0, \infty) \times \mathbb{R}^3. \tag{7}$$

Moreover, we consider initial conditions $n_0(x, y)$ for which there exists $C_0 > 0$ and $\mu_0 > 0$ such that

$$0 \leq n_0(x, y) \begin{cases} \leq C_0 e^{-\mu_0(|x|+|y|)} & \text{under Assumption 1.1} \\ \text{is compactly supported} & \text{under Assumption 1.2} \\ \text{is compactly supported} & \text{under Assumption 1.3.} \end{cases} \tag{8}$$

In other words, under Assumption 1.1, we allow the initial data to have tails which are "consistent" with the confined case under consideration. In the unconfined and mixed cases, i.e. Assumption 1.2 and Assumption 1.3, we assume that the initial data is compactly supported. Estimating the tails of the underlying eigenfunction in the spirit of Lemma 5.2 would allow us to relax this slightly but, for the sake of simplicity and since we treat the more general case under Assumption 1.1, we restrict to the compactly supported case.

The organization of this work is as follows. In Section 2 we provide some linear material (principal eigenvalue, principal eigenfunction), a preliminary estimate of the tails of $n(t,x,y)$ together with an efficient Harnack tool which is also of independent interest. The confined case is studied in Section 3: we identify the critical speed c^* and, depending on c, prove extinction or survival. The unconfined case is studied in Section 4: we identify the critical speed c^{**} and, depending on c, prove extinction or propagation. Finally, Section 5 is devoted to the analysis of the mixed case, for which we take advantage of the analysis of the confined and unconfined cases, performed in the two previous sections.

2 Preliminary results

Let us first introduce a principal eigenvalue problem that will be crucial in the course of the paper. It will in particular provide the critical climate shift speeds c^*, c^{**}, c_u^{**} (see further) that will allow the survival of the population.

2.1 A principal eigenvalue problem

The theory of generalized principal eigenvalue developed in [9] is well adapted to the present problem, provided r is bounded. Following [9], we can then define, for $r \in L^\infty(\Omega)$ and $\Omega \subset \mathbb{R}^2$ not necessarily bounded, the generalized principal eigenvalue

$$\lambda(r,\Omega) := \sup\left\{\lambda :\, \exists \phi \in W^{2,2}_{loc}(\Omega),\, \phi>0,\, \partial_{xx}\phi(x,y)+\partial_{yy}\phi(x,y)+\left(r(x,y)+\lambda\right)\phi(x,y) \le 0\right\}. \tag{9}$$

As shown in [9], if Ω is bounded and smooth, $\lambda(r,\Omega)$ coincides with the Dirichlet principal eigenvalue $H(r,\Omega)$, that is the unique real number such that there exists $\phi>0$ on Ω (unique up to multiplication by a scalar),

$$\begin{cases} -\partial_{xx}\phi(x,y)-\partial_{yy}\phi(x,y)-r(x,y)\phi(x,y) = H(r,\Omega)\phi & \text{a.e. in } \Omega,\\ \phi = 0 & \text{on } \partial\Omega. \end{cases}$$

Notice that since the operator is self-adjoint, the Dirichlet principal eigenvalue can be obtained through the variational formulation

$$H(r,\Omega) = \inf_{\phi\in H_0^1(\Omega),\, \phi\neq 0} \frac{\int_\Omega |\nabla\phi|^2 - r(x,y)\phi^2}{\int_\Omega \phi^2}.$$

The following proposition then provides known properties of $\lambda(r,\Omega)$. We refer the reader to [9], [6, Proposition 4.2], or to [10, Proposition 1] for more details and proofs.

Proposition 2.1 (Generalized eigenvalues and eigenfunctions)**.** *Assume that $r\in L^\infty(\mathbb{R}^2)$. There is $\lambda(r,\Omega)\in\mathbb{R}$ such that for any subsequence $(\Omega_n)_{n\in\mathbb{N}}$ of non empty open sets such that*

$$\Omega_n \subset \Omega_{n+1}, \quad \cup_{n\in\mathbb{N}}\Omega_n = \Omega.$$

Then, $\lambda(r,\Omega_n) \searrow \lambda(r,\Omega)$ as $n\to\infty$. Furthermore, there exists a generalized principal eigenfunction, that is a positive function $\Gamma \in W^{2,2}_{loc}(\mathbb{R}^2)$ such that

$$-\partial_{xx}\Gamma(x,y)-\partial_{yy}\Gamma(x,y)-r(x,y)\Gamma(x,y) = \lambda(r,\Omega)\Gamma(x,y) \quad \textit{a.e. in } \Omega.$$

Let us also mention that the above generalized eigenfunction Γ is indeed obtained as a limit of principal eigenfunctions, with Dirichlet boundary conditions, on increasing bounded domains.

Since our growth functions are only assumed to be bounded from above, we extend definition (9) in a natural way to $r\in L^\infty_{loc}(\Omega)$ such that $r\le r_{max}$ on Ω, for some $r_{max}>0$. The set

$$\Lambda(r,\Omega) := \left\{\lambda :\, \exists \phi \in W^{2,2}_{loc}(\Omega),\, \phi>0,\, \partial_{xx}\phi(x,y)+\partial_{yy}\phi(x,y)+\left(r(x,y)+\lambda\right)\phi(x,y) \le 0\right\}$$

is not empty, since $\Lambda(\max(r,-M),\Omega)\subset\Lambda(r,\Omega)$, and is bounded from above, thanks to the monotony property of $\Omega\mapsto\Lambda(r,\Omega)$. Finally, going back for example to the proof of [6, Proposition 4.2], we notice that Proposition 2.1 remains valid under the weaker assumption that $r\in L^\infty_{loc}(\Omega)$ is bounded from above.

It follows from the above discussion that, in the confined case, we are equipped with the generalized principal eigenvalue $\lambda_\infty\in\mathbb{R}$, and a generalized eigenfunction $\Gamma_\infty(x,y)$ such that

$$\begin{cases}-\partial_{xx}\Gamma_\infty(x,y)-\partial_{yy}\Gamma_\infty(x,y)-r(x,y)\Gamma_\infty(x,y)=\lambda_\infty\Gamma_\infty(x,y) \quad \text{for all } (x,y)\in\mathbb{R}^2\\ \Gamma_\infty(x,y)>0 \quad \text{for all } (x,y)\in\mathbb{R}^2, \quad \|\Gamma_\infty\|_{L^\infty(\mathbb{R}^2)}=1.\end{cases} \tag{10}$$

Notice that since the operator is self-adjoint and the potential "confining", λ_∞ can also be obtained through some adequate variational formulation.

For the unconfined case, for which $r(x,y)=\bar r(y-Bx)$, we are equipped with the "one dimensional" generalized principal eigenvalue $\lambda_\infty\in\mathbb{R}$, and a generalized eigenfunction $\Gamma_\infty^{1D}(z)$ such that

$$\begin{cases}-(1+B^2)\partial_{zz}\Gamma_\infty^{1D}(z)-\bar r(z)\Gamma_\infty^{1D}(z)=\lambda_\infty\Gamma_\infty^{1D}(z) \quad \text{for all } z\in\mathbb{R}\\ \Gamma_\infty^{1D}(z)>0 \quad \text{for all } z\in\mathbb{R}, \quad \|\Gamma_\infty^{1D}\|_{L^\infty(\mathbb{R})}=1.\end{cases} \tag{11}$$

Indeed, this corresponds to the confined case in 1D. In order to be consistent, if we define $\Gamma_\infty(x,y):=\Gamma_\infty^{1D}(y-Bx)$ then (10) remains valid.

Remark 2.2. *When the unconfined growth rate is the prototype example* (4), (11) *corresponds to the harmonic oscillator, for which the the principal eigenvalue and principal eigenvector are known (see e.g. [33]):*

$$\lambda_\infty=\sqrt{A(1+B^2)}-1, \quad \Gamma_\infty(x,y)=\exp\left(-\frac{1}{2}\sqrt{\frac{A}{1+B^2}}(y-Bx)^2\right). \tag{12}$$

If the confined growth rate is the prototype example (3) *with $\varepsilon>0$, the principal eigenvalue $\lambda_\infty^\varepsilon$ can also be explicitly computed, but the formula is more complicated. One can however notice that we then have $\lambda_\infty^\varepsilon\to\lambda_\infty=\sqrt{A(1+B^2)}-1$, as $\varepsilon\to 0$.*

2.2 Preliminary control of the tails

We first prove the useful property.

Lemma 2.3 (Control of the total mass)**.** *Assume that $r\in L^\infty_{loc}(\mathbb{R}^2)$ and $K\in L^\infty((0,\infty)\times\mathbb{R}^3)$ satisfy* (6) *and* (7) *respectively. Let Assumption 1.1 or 1.2 hold. Assume that n_0 satisfies* (8)*. Then, there exists $C>0$ such that, for any global nonnegative solution n of* (1),

$$\int_{\mathbb{R}} n(t,x,y)\,dy\le C, \tag{13}$$

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

Proof. If we define the mass $N(t,x):=\int_{\mathbb{R}} n(t,x,y)\,dy$, an integration of (1) along the variable y provides the inequality

$$\partial_t N-\partial_{xx}N\le\left(r_{max}-k^-N\right)N.$$

Since $N(0,x)=\int_{\mathbb{R}} n_0(x,y)\,dy\le\frac{2C_0}{\mu_0}$, it then follows from the maximum principle that the mass is uniformly bounded:

$$N(t,x)\le N_\infty:=\max\left(\frac{2C_0}{\mu_0},\frac{r_{max}}{k^-}\right),$$

which proves the lemma. □

Our next result states that, in the confined and unconfined cases, any global nonnegative solution of the Cauchy problem (1) has exponentially decaying tails. Notice that, in the mixed case, Lemma 5.3 will provide an analogous estimate.

Lemma 2.4 (Exponential decay of tails)**.** *Assume that* $r \in L^\infty_{loc}(\mathbb{R}^2)$ *and* $K \in L^\infty((0,\infty)\times\mathbb{R}^3)$ *satisfy* (6) *and* (7) *respectively. Let Assumption 1.1 or 1.2 hold. Assume that* n_0 *satisfies* (8)*. Then, there exist* $C>0$ *and* $\mu>0$ *such that, for any global nonnegative solution* n *of* (1)*,*

$$0 \le n(t,x,y) \le \begin{cases} Ce^{-\mu(|x-ct|+|y|)} & \text{under Assumption 1.1,} \\ Ce^{-\mu|y-B(x-ct)|} & \text{under Assumption 1.2,} \end{cases} \tag{14}$$

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

Proof. Let us first work under Assumption 1.2. In view of Lemma 2.3, it follows from Assumption 1.2 and (7) that there is $M>0$ such that

$$\left| r(x-ct,y) - \int_{\mathbb{R}} K(t,x,y,y')n(t,x,y')\,dy' \right| \le M,$$

in $\Omega_{R+1} := \{(t,x,y) : |y-B(x-ct)| < R+1\}$. Hence $n(t,x,y)$ solves a linear reaction diffusion equation with bounded coefficients on Ω_{R+1}. As a result, we can apply the parabolic Harnack inequality (see [16, page 391] for instance). To do so let us first choose $\varepsilon := (Bc)^{-1}$ so that, for any $T>0$, $[T,T+\varepsilon]\times\{(x,y) : |y-B(x-cT)|\le R\} \subset \Omega_{R+1}$. Then, by the Harnack inequality, there is $C>0$ such that, for all $T>0$,

$$\max_{(x,y),|y-B(x-cT)|\le R} n(T,x,y) \le C \min_{(x,y),|y-B(x-cT)|\le R} n(T+\varepsilon,x,y).$$

It then follows that

$$\max_{(x,y),|y-B(x-cT)|\le R} n(T,x,y) \le \frac{C}{2R}\int_{\mathbb{R}} n(T+\varepsilon,x,y)\,dy = \frac{C}{2R}N(T+\varepsilon,x) \le \frac{C}{2R}N_\infty. \tag{15}$$

Hence, the population $n(t,x,y)$ is bounded by $\frac{C}{2R}N_\infty$ in $\Omega_R := \{(t,x,y) : |y-B(x-ct)|\le R\}$.

Next, to handle the remaining region ${\Omega_R}^c = \{(t,x,y) : |y-B(x-ct)| > R\}$, let us define

$$\varphi(t,x,y) := \kappa e^{-\mu(|y-B(x-ct)|-R)},$$

which, in ${\Omega_R}^c$, satisfies

$$\begin{aligned} \partial_t\varphi - \partial_{xx}\varphi - \partial_{yy}\varphi - r(x-ct,y)\varphi &= (\pm\mu Bc - \mu^2B^2 - \mu^2 - r(x-ct,y))\varphi \\ &\ge (\pm\mu Bc - \mu^2B^2 - \mu^2 + \delta)\varphi \end{aligned}$$

by Assumption 1.2. Choosing $\mu>0$ small enough makes φ a supersolution on ${\Omega_R}^c$, whereas n is a subsolution. If we choose $\kappa = \max(C_0, \frac{C}{2R}N_\infty)$ and $\mu\in(0,\mu_0)$, then we enforce $n(t,x,y)\le\varphi(t,x,y)$ on $\{0\}\times\mathbb{R}^2$ (see (8)) and on the parabolic lateral boundary of ${\Omega_R}^c$ (see (15)). It follows from the parabolic maximum principle that $n(t,x,y)\le\varphi(t,x,y)$ in ${\Omega_R}^c$, which concludes the proof of the lemma under Assumption 1.2.

When Assumption 1.1 holds, arguments are very similar. It suffices to select a $\delta>0$ and an associated $R>0$ such that Assumption 1.1 holds, then to take $\Omega_{R+1} := \{(t,x,y) : |x-ct|+|y| < R+1\}$ and, finally, to use $\varphi(t,x,y) := \kappa e^{-\mu(|x-ct|+|y|-2R)}$ on the remaining region. Details are omitted. □

2.3 Preliminary Harnack-type estimate

We present here our refinement of the parabolic Harnack inequality. We already discussed in subsection 1.4 the relevance of Theorem 2.7, which is also of independent interest.

Let $\Omega\subset\mathbb{R}^N$ an open set with $N\ge 1$. We consider a solution $u(t,x)$, $t>0$, $x\in\Omega$, of a linear parabolic equation, namely

$$\partial_t u(t,x) - \sum_{i,j=1}^N a_{i,j}(t,x)\partial_{x_i,x_j}u(t,x) - \sum_{i=1}^N b_i(t,x)\partial_{x_i}u(t,x) = f(t,x)u(t,x), \tag{16}$$

where the coefficients are bounded, and $(a_{i,j})_{i,j=1,\dots,N}$ is uniformly elliptic. Let us first recall the parabolic Harnack inequality, as proved by Moser [27].

Theorem 2.5 (Parabolic Harnack inequality, [27]). *Let us assume that all the coefficients* $(a_{i,j})_{i,j=1,\dots,N}$*,* $(b_i)_{i=1,\dots,N}$*,* f *belong to* $L^\infty_{loc}((0,\infty)\times\Omega)$*, where* Ω *is an open set of* $\mathbb{R}^N$*, and that* $(a_{i,j})_{i,j=1,\dots,N}$ *is uniformly positive definite on* Ω*. Let* $\tau>0$ *and* $0<R<R'$*.*

There exists $C_H>0$ *such that for any* $(\bar t,\bar x)\in(2\tau,\infty)\times\mathbb{R}^N$ *such that* $B_{\mathbb{R}^N}(\bar x,R')\subset\Omega$*, and for any nonnegative (weak) solution* $u\in H^1((0,\infty)\times\Omega)$ *of* (16) *on* $(\bar t-2\tau,\bar t)\times\Omega$*,*

$$\max_{x\in B(\bar x,R)} u(\bar t-\tau,x)\le C_H\min_{x\in B(\bar x,R)} u(\bar t,x). \tag{17}$$

Remark 2.6. *Let us emphasize that the time shift* $\tau>0$ *is necessary for* (17) *to hold. To see this, consider for* $N=1$ *the family* $u(t,x)=\frac{1}{\sqrt{4\pi t}}e^{-\frac{(x+x_0)^2}{4t}}$ $(x_0\in\mathbb{R})$ *of solutions to the Heat equation. Then, for* $\bar t=1$ *and* $\bar x=0$*, we have*

$$\frac{\max_{x\in B(0,R)}u(1,x)}{\min_{x\in B(0,R)}u(1,x)}\ge\frac{u(1,0)}{u(1,R)}=e^{\frac{(R+x_0)^2-x_0^2}{4}}=e^{\frac{2Rx_0+R^2}{4}},$$

which is not bounded from above as $x_0\to\infty$*. Hence, estimate* (17) *cannot hold with* $\tau=0$*.*

Nevertheless, provided the solution u is uniformly bounded, we can derive from Theorem 2.5 the following refinement, where no time shift is required.

Theorem 2.7 (A refinement of Harnack inequality). *Assume that all the coefficients* $(a_{i,j})_{i,j=1,\dots,N}$*,* $(b_i)_{i=1,\dots,N}$*,* f *belong to* $L^\infty_{loc}\left((0,\infty)\times\mathbb{R}^N\right)$*, and that* $(a_{i,j})_{i,j=1,\dots,N}$ *is uniformly positive definite on* $\mathbb{R}^N$*. Let also* $\omega\subset\mathbb{R}^N$*, and assume that for any* $R'>0$*, there exists* $K>0$ *such that, for all* $1\le i,j\le N$*,*

$$a_{i,j}(t,x)\le K,\ b_i(t,x)\le K,\ f(t,x)\le K\ \text{ a.e. on } (0,\infty)\times(\omega+B_{\mathbb{R}^N}(0,R')). \tag{18}$$

Let $R>0$*,* $\delta>0$*,* $U>0$*,* $\bar t>0$ *and* $\rho>0$*.*

There exists $C>0$ *such that for any* $\bar x\in\mathbb{R}^N$ *satisfying* $d_{\mathbb{R}^N}(\bar x,\omega)\le\rho$*, and any nonnegative (weak) solution* $u\in H^1\left((0,\infty)\times\mathbb{R}^N\right)$ *of* (16) *on* $(0,\infty)\times\mathbb{R}^N$*, and such that* $\|u\|_{L^\infty(\mathbb{R}^N)}\le U$*, we have*

$$\max_{x\in B(\bar x,R)}u(\bar t,x)\le C\min_{x\in B(\bar x,R)}u(\bar t,x)+\delta. \tag{19}$$

Proof. Let us assume without loss of generality that $\bar t=2$ and $\bar x=0$. We introduce

$$\phi(t,x):=e^{K(t-1)}\left[\max_{|x|\le\alpha R}u(1,x)+\frac{2\|u\|_\infty}{(\alpha R)^2}NK(1+\alpha R)(t-1)+\frac{\|u\|_\infty}{(\alpha R)^2}|x|^2\right],$$

where $\alpha>1$ is to be determined later. We aim at applying the parabolic comparison principle on the domain $(1,2)\times B(0,\alpha R)$. We have $\phi(1,x)\ge u(1,x)$ for $|x|\le\alpha R$, and $\phi(t,x)\ge\|u\|_{L^\infty(\Omega)}\ge u(t,x)$ for $1\le t\le 2$, $|x|=\alpha R$. A simple computation shows

$$\partial_t\phi-\sum_{i,j=1}^N a_{i,j}\partial_{x_i,x_j}\phi-\sum_{i=1}^N b_i\partial_{x_i}\phi-K\phi=\frac{2\|u\|_\infty}{(\alpha R)^2}e^{K(t-1)}\left[NK(1+\alpha R)-\sum_{i=1}^N a_{i,i}(t,x)-\sum_{i=1}^N b_i(t,x)x_i\right]$$

which, in view of (18), is nonnegative on $(1,2)\times B(0,\alpha R)$. Since $\partial_t u-\sum_{i,j=1}^N a_{i,j}\partial_{x_i,x_j}u-\sum_{i=1}^N b_i\partial_{x_i}u-Ku\le 0$, the comparison principle yields $u(2,\cdot)\le\phi(2,\cdot)$ on $B(0,\alpha R)$. In particular we have

$$\begin{aligned}\max_{|x|\le R}u(2,x)&\le\max_{|x|\le R}\phi(2,x)\\&\le e^K\left(\max_{|x|\le\alpha R}u(1,x)+\frac{2\|u\|_\infty}{(\alpha R)^2}NK(1+\alpha R)+\frac{\|u\|_\infty}{\alpha^2}\right)\\&\le e^K\max_{|x|\le\alpha R}u(1,x)+\frac{e^KU}{\alpha^2}\left(\frac{2NK(1+\alpha R)}{R^2}+1\right)\\&\le e^K\max_{|x|\le\alpha R}u(1,x)+\delta,\end{aligned}\tag{20}$$

provided we select $\alpha>1$ large enough. Thanks to (18), we can then apply Theorem 2.5 with $\tau:=1$ and $\Omega:=\omega+B_{\mathbb{R}^N}(0,2\alpha R)$, to get that there exists a constant $C_H=C_H(R,\alpha)>0$ such that

$$\max_{|x|\le\alpha R}u(1,x)\le C_H\min_{|x|\le\alpha R}u(2,x)\le C_H\min_{|x|\le R}u(2,x). \tag{21}$$

Theorem 2.7 follows from (20) and (21). □

3 The confined case

In this section, we consider the confined case, namely Assumption 1.1, for which the growth rate $r(x,y)$ is positive for a bounded set of points (x,y) only. We discuss the extinction or the survival of the population, defining a critical speed c^* for the climate shift by

$$c^* := \begin{cases} 2\sqrt{-\lambda_\infty} & \text{if } \lambda_\infty < 0 \\ 0 & \text{if } \lambda_\infty \geq 0, \end{cases} \qquad \text{the critical speed in the confined case,} \tag{22}$$

where λ_∞ is the principal eigenvalue defined by (10). In the whole section, we are then equipped with λ_∞ and $\Gamma_\infty(x,y)$ satisfying (10).

We introduce two changes of variable that will be very convenient in the sequel. Precisely, we define $\tilde{n}(t,x,y)$ the solution in the moving frame and $u(t,x,y)$ its Liouville transform by

$$\tilde{n}(t,x,y) := n(t,x+ct,y), \; u(t,x,y) := e^{\frac{cx}{2}}\tilde{n}(t,x,y) \tag{23}$$

so that the equation (1) is recast as

$$\begin{aligned} &\partial_t \tilde{n}(t,x,y) - c\partial_x \tilde{n}(t,x,y) - \partial_{xx}\tilde{n}(t,x,y) - \partial_{yy}\tilde{n}(t,x,y) \\ &\quad = \left(r(x,y) - \int_{\mathbb{R}} K(t,x+ct,y,y')\tilde{n}(t,x,y')\,dy' \right) \tilde{n}(t,x,y), \end{aligned} \tag{24}$$

or as

$$\begin{aligned} &\partial_t u(t,x,y) - \partial_{xx}u(t,x,y) - \partial_{yy}u(t,x,y) \\ &\quad = \left(r(x,y) - \frac{c^2}{4} - \int_{\mathbb{R}} K(t,x+ct,y,y')e^{-\frac{cx}{2}}u(t,x,y')\,dy' \right) u(t,x,y). \end{aligned} \tag{25}$$

3.1 Extinction

In this subsection, we show extinction of the population for rapid climate shifts $c > c^*$. Since extinction comes from the linear part of the equation (1), the nonlocal term will not be a problem here. If follows that if $c > c^*$, the extinction for any reasonable initial population (see Proposition 3.3) can be proven thanks to an argument similar to the one in [10, Proposition 1.4]. Nevertheless, this argument does not provide any information on the speed of extinction. If we further assume sufficient decay of the tails of the initial data (see Proposition 3.1), we can show that the extinction is exponentially fast. We start with this last situation.

Proposition 3.1 (Extinction with initial control of the tails)**.** *Assume that $r \in L^\infty_{loc}(\mathbb{R}^2)$ and $K \in L^\infty((0,\infty)\times\mathbb{R}^3)$ satisfy* (6) *and* (7) *respectively. Let Assumption 1.1 hold. Assume that n_0 satisfies* (8)*. If $c > c^*$ and the initial population satisfies*

$$M := \sup_{(x,y)\in\mathbb{R}^2} \frac{e^{\frac{cx}{2}} n_0(x,y)}{\Gamma_\infty(x,y)} < \infty, \tag{26}$$

then any global nonnegative solution $n(t,x,y)$ of (1) *satisfies*

$$\sup_{(x,y)\in\mathbb{R}^2} \frac{e^{\frac{cx}{2}} n(t,x+ct,y)}{\Gamma_\infty(x,y)} = \mathcal{O}\left(e^{\left(-\lambda_\infty - \frac{c^2}{4}\right)t} \right) \to 0, \quad \text{as } t \to \infty, \tag{27}$$

and, for some $\gamma_0 > 0$,

$$\sup_{x\in\mathbb{R}} \int_{\mathbb{R}} n(t,x,y)\,dy = \mathcal{O}(e^{-\gamma_0 t}) \to 0, \quad \text{as } t \to \infty. \tag{28}$$

Proof. We consider

$$\phi(t,x,y) := Me^{\left(-\lambda_\infty - \frac{c^2}{4}\right)t}\Gamma_\infty(x,y),$$

which satisfies

$$\partial_t\phi(t,x,y) - \partial_{xx}\phi(t,x,y) - \partial_{yy}\phi(t,x,y) = \left(r(x,y) - \frac{c^2}{4}\right)\phi(t,x,y).$$

In view of (25), $u(t,x,y) = e^{\frac{cx}{2}}n(t,x+ct,y)$ is a subsolution of the above equation. Since the definition of M implies $u(0,x,y) \le \phi(0,x,y)$, it follows from the parabolic maximum principle that $u(t,x,y) \le \phi(t,x,y)$ for any time $t \ge 0$, which proves (27).

To prove (28), we will need

$$\rho := \sup_{x\in\mathbb{R}} \int_{\mathbb{R}} \Gamma_\infty(x,y)\,dy < \infty, \tag{29}$$

whose proof is postponed. If $c = 0$, (28) follows from (27) and (29). If $c > 0$, combining (27) and the control of the tails (14) we obtain, for $\alpha > 0$ to be selected,

$$\begin{aligned}
\sup_{x\in\mathbb{R}} \int_{\mathbb{R}} n(t,x,y)\,dy &= \sup_{x\in\mathbb{R}} \int_{\mathbb{R}} n(t,x+ct,y)\,dy \\
&\le \sup_{x\le-\alpha t} \int_{\mathbb{R}} n(t,x+ct,y)\,dy + \sup_{x\ge-\alpha t} \int_{\mathbb{R}} n(t,x+ct,y)\,dy \\
&\le \sup_{x\le-\alpha t} \int_{\mathbb{R}} Ce^{-\mu(|x|+|y|)}\,dy + \sup_{x\ge-\alpha t} \int_{\mathbb{R}} e^{-\frac{cx}{2}} Me^{\left(-\lambda_\infty - \frac{c^2}{4}\right)t}\Gamma_\infty(x,y)\,dy \\
&\le \frac{2C}{\mu}e^{-\mu\alpha t} + M\rho e^{\left(-\lambda_\infty - \frac{c^2}{4} + \frac{c\alpha}{2}\right)t},
\end{aligned}$$

which proves (28) by selecting $\alpha > 0$ small enough so that $-\lambda_\infty - \frac{c^2}{4} + \frac{c\alpha}{2} < 0$.

To conclude, let us now prove (29). Select $\delta > 0$ such that $\delta \ge 2\lambda_\infty$. For this $\delta > 0$, select $R > 0$ as in Assumption 1.1 so that — in view of equation (10)— the principal eigenfunction satisfies $-\partial_{xx}\Gamma_\infty - \partial_{yy}\Gamma_\infty \le -\frac{\delta}{2}\Gamma_\infty$ in $\{(x,y) : |x| \ge R,\ |y| \ge R\}$ and $\|\Gamma_\infty\|_\infty \le 1$. It therefore follows from the elliptic comparison principle that

$$\Gamma_\infty(x,y) \le e^{-\sqrt{\frac{\delta}{2}}(|y|-R)}e^{-\sqrt{\frac{\delta}{2}}(|x|-R)} \quad \text{in } \{(x,y) : |x| \ge R,\ |y| \ge R\}. \tag{30}$$

Therefore we have, for all $(x,y) \in \mathbb{R}^2$,

$$\Gamma_\infty(x,y) \le Ce^{-\sqrt{\frac{\delta}{2}}(|x|+|y|)}, \tag{31}$$

which implies (29). □

Remark 3.2. *Observe that, in the unconfined case, the estimate* (27) *remains valid but the control of the tails* (14) *under Assumption 1.2 does not imply* (28)*. Roughly speaking, in the unconfined case, even if $c > c^*$ there is a possibility that the population survives, but migrates towards large x at a speed $\omega \in (0,c)$ different from the climate change speed c. Therefore we need a different criterion that will be discussed in Section 4.*

Proposition 3.3 (Extinction for general initial data)**.** *Assume that $r \in L^\infty_{loc}(\mathbb{R}^2)$ and $K \in L^\infty((0,\infty)\times\mathbb{R}^3)$ satisfy* (6) *and* (7) *respectively. Let Assumption 1.1 hold. Assume that $n_0 \in L^\infty(\mathbb{R}^2)$ and that $\sup_{x\in\mathbb{R}}\int_{\mathbb{R}} n_0(x,y)\,dy < \infty$. If $c > c^*$ then any global nonnegative solution $n(t,x,y)$ of* (1) *satisfies*

$$\lim_{t\to\infty} n(t,x,y) = 0, \tag{32}$$

uniformly with respect to $(x,y) \in \mathbb{R}^2$.

Proof. It is equivalent and more convenient to prove (32) for $\tilde{n}(t,x,y) = n(t,x+ct,y)$ which solves (24). Since $r(x,y) \to -\infty$ as $|x|+|y| \to \infty$, we first define, for some $R > 0$, the cut-off function

$$r_{cut}(x,y) := \begin{cases} r(x,y) & \text{if } (x,y) \in B_R \\ \sup_{(x,y)\notin B_R} r(x,y) & \text{if } (x,y) \notin B_R, \end{cases}$$

which is larger than $r(x,y)$ and has the advantage of being bounded. Let $(\lambda_{cut}, \Gamma_{cut}) \in \mathbb{R} \times C^\infty(\mathbb{R})$ solve the generalized principal eigenvalue problem

$$\begin{cases} -\partial_{xx}\Gamma_{cut}(x,y) - \partial_{yy}\Gamma_{cut}(x,y) - r_{cut}(x,y)\Gamma_{cut}(x,y) = \lambda_{cut}\Gamma_{cut}(x,y) \quad \text{for all } (x,y) \in \mathbb{R}^2 \\ \Gamma_{cut}(x,y) > 0 \quad \text{for all } (x,y) \in \mathbb{R}^2, \quad \|\Gamma_{cut}\|_\infty = 1. \end{cases} \tag{33}$$

We claim that

$$\lambda_{cut} \nearrow \lambda_\infty, \text{ as } R \to \infty. \tag{34}$$

Since arguments are rather classical (see [6, Proposition 4.2] for instance), we only sketch the proof. Since $r_{cut} \geq r$ we have $\lambda_{cut} \leq \lambda_\infty$. Also, λ_{cut} is increasing with respect to R. Hence $\lambda_{cut} \nearrow \tilde{\lambda} \leq \lambda_\infty$, as $R \to \infty$. Assume, by way of contradiction, that $\tilde{\lambda} < \lambda_\infty$. Since $r_{cut} \to r$ locally uniformly, it follows from the Harnack inequality, elliptic interior estimates and a diagonal extraction that we can construct a function $\gamma > 0$ such that $-\partial_{xx}\gamma - \partial_{yy}\gamma = (r + \tilde{\lambda})\gamma$, and γ is then a subsolution of the equation satisfied by Γ_∞ (see the first line of (10)). Outside of a large ball, the zero order term of the equation, namely $r + \lambda_\infty$, is negative so the elliptic comparison principle applies outside of a large ball. This enables us to define

$$\varepsilon_0 := \sup\{\varepsilon > 0 : \varepsilon\gamma(x,y) \leq \Gamma_\infty(x,y), \forall (x,y) \in \mathbb{R}^2\}.$$

Hence $\psi := \Gamma_\infty - \varepsilon_0\gamma$ has a zero minimum at some point (x_0, y_0) and therefore $0 \leq (\partial_{xx}\psi + \partial_{yy}\psi + r\psi)(x_0, y_0) \leq (\tilde{\lambda} - \lambda_\infty)\Gamma_\infty(x_0, y_0) < 0$. This contradiction proves the claim (34). As a result, we can choose $R > 0$ large enough so that $r \leq -1$ on the complement of $B_{R/2}$, and such that $-\frac{c^2}{4} < \lambda_{cut}$ (we recall that $c > c^*$ implies $-\frac{c^2}{4} < \lambda_\infty$).

By the parabolic comparison principle, we have

$$0 \leq \tilde{n}(t,x,y) \leq w(t,x,y), \tag{35}$$

where $w(t,x,y)$ is the solution of the following linear problem — obtained by dropping the nonlocal term and replacing $r(x,y)$ by $r_{cut}(x,y)$ in (24)—

$$\begin{cases} \partial_t w - c\partial_x w - \partial_{xx} w - \partial_{yy} w = r_{cut}(x,y) w \\ w(0,x,y) = w_0(x,y) := M + Ae^{-\frac{c}{2}x}\Gamma_{cut}(x,y), \end{cases} \tag{36}$$

where $M := \|n_0\|_{L^\infty}$. Recalling that $\frac{c^2}{4} + \lambda_{cut} > 0$ and that $r_{cut} \leq 0$ on the complement of $B_{R/2}$, we can choose $A > 0$ large enough so that

$$(\partial_t - c\partial_x - \partial_{xx} - \partial_{yy} - r_{cut}(x,y))w_0(x,y) = A\left(\frac{c^2}{4} + \lambda_{cut}\right)e^{-\frac{c}{2}x}\Gamma_{cut}(x,y) - r_{cut}(x,y)M > 0,$$

for all $(x,y) \in \mathbb{R}^2$. In other words, the initial data in (36) is a super solution of the parabolic equation in (36), which implies that $t \mapsto w(t,x,y)$ is decreasing for any $(x,y) \in \mathbb{R}^2$. As a result there is a function $\bar{w}(x,y)$ such that

$$w(t,x,y) \to \bar{w}(x,y) \quad \text{as } t \to \infty, \qquad 0 \leq \bar{w}(x,y) \leq M + Ae^{-\frac{c}{2}x}\Gamma_{cut}(x,y).$$

Let us prove that the above pointwise convergence actually holds locally uniformly w.r.t. (x,y), and that $\bar{w}$ solves

$$-c\partial_x\bar{w} - \partial_{xx}\bar{w} - \partial_{yy}\bar{w} - r_{cut}(x,y)\bar{w} = 0. \tag{37}$$

Let $R' > 0$ be given. Let (t_n) be an arbitrary sequence such that $t_n \to \infty$, and define $w_n(t,x,y) := w(t + t_n, x, y)$. w_n then solves

$$\partial_t w_n - c\partial_x w_n - \partial_{xx} w_n - \partial_{yy} w_n - r_{cut}(x,y) w_n = 0,$$

that is a linear equation whose coefficients are bounded on $(0,\infty) \times \mathbb{R}^2$ uniformly w.r.t. n. By the interior parabolic estimates [25, Section VII], for a fixed $p > 2$, there is a constant $C_{R'} > 0$ such that

$$\|w_n\|_{W_p^{1,2}((1,2)\times B_{R'})} \leq C_{R'}\|w_n\|_{L^p((0,3)\times B_{2R'})} \leq C_{R'}(3|B_{2R'}|)^{1/p}\|w\|_{L^\infty((0,\infty)\times\mathbb{R}^2)} < \infty.$$

Since $p>2$, there is $0<\alpha<1$ such that the injection $W_p^{1,2}((1,2)\times B_{R'})\hookrightarrow C^{\frac{1+\alpha}{2},1+\alpha}\left([1,2]\times\overline{B_{R'}}\right)$ is compact. Therefore there is a subsequence $w_{\varphi(n)}$ which converges in $C^{\frac{1+\alpha}{2},1+\alpha}\left([1,2]\times\overline{B_{R'}}\right)$, and converges weakly in $W_p^{1,2}((1,2)\times B_{R'})$. The limit of $w_{\varphi(n)}$ has to be $\bar w$, which is independent on the sequence $t_n\to\infty$ and the extraction φ. Therefore $w(t,\cdot,\cdot)\to\bar w(\cdot,\cdot)$, in both $C^{\frac{1+\alpha}{2},1+\alpha}$ and $W_p^{1,2}$ locally uniformly. Hence, the convergence $w(t,x,y)\to\bar w(x,y)$, as $t\to\infty$, is locally uniform w.r.t. (x,y). On the other hand, the weak convergence in $W_p^{1,2}$ allows to pass to the limit in equation (36), so that $\bar w$ actually solves (37).

We claim that $\bar w\equiv 0$. Indeed define $\psi(t,x):=e^{\frac{c}{2}x}\bar w(x,y)$ which solves

$$-\partial_{xx}\psi-\partial_{yy}\psi-r_{cut}(x,y)\psi=-\frac{c^2}{4}\psi. \tag{38}$$

Multiplying equation (33) by ψ, equation (38) by Γ_{cut} and integrating the difference over the ball $B_{R'}$, we get

$$\int_{B_{R'}}(\Gamma_{cut}\Delta\psi-\psi\Delta\Gamma_{cut})=\left(\frac{c^2}{4}+\lambda_{cut}\right)\int_{B_{R'}}\psi\Gamma_{cut}.$$

Applying the Stokes theorem implies

$$\int_{\partial B_{R'}}\left(\Gamma_{cut}\frac{\partial\psi}{\partial\nu}-\psi\frac{\partial\Gamma_{cut}}{\partial\nu}\right)=\left(\frac{c^2}{4}+\lambda_{cut}\right)\int_{B_{R'}}\psi\Gamma_{cut}. \tag{39}$$

We want to let $R'\to\infty$ in the left hand side member. It is easily seen that Γ_{cut} also satisfy estimate (31) so that $\|\Gamma_{cut}\|_{L^\infty(\partial B_{R'})}\to 0$, as $R'\to\infty$. Since

$$-\Delta\Gamma_{cut}=f(x,y):=(r_{cut}(x,y)+\lambda_{cut})\Gamma_{cut}(x,y),$$

the interior elliptic estimates [20, Theorem 9.11] provide, for a fixed $p>2$, some $C>0$ such that, for all $P_0=(x_0,y_0)\in\mathbb{R}^2$,

$$\begin{aligned}\|\Gamma_{cut}\|_{W_p^2(B(P_0,1))} &\leq C\left(\|\Gamma_{cut}\|_{L^p(B(P_0,2))}+\|f\|_{L^p(B(P_0,2))}\right)\\ &\leq C|B_2|^{1/p}\left(1+(\|r_{cut}\|_{L^\infty(\mathbb{R}^2)}+|\lambda_{cut}|)\right)\|\Gamma_{cut}\|_{L^\infty(\mathbb{R}^2)}<\infty,\end{aligned}$$

where we have used the analogous of (31) for Γ_{cut}. Since $p>2$, there is $0<\alpha<1$ such that the injection $W_p^2(B(P_0,1))\hookrightarrow C^{1+\alpha}(\overline{B(P_0,1)})$ is compact and therefore $\|\nabla\Gamma_{cut}\|_{L^\infty(\overline{B(P_0,1)})}\leq C$, for some C independent of $P_0\in\mathbb{R}^2$. As a result $\nabla\Gamma_{cut}\in L^\infty(\mathbb{R}^2)$. Let us now deal with ψ and $\nabla\psi$ by using rather similar arguments. First, in view of (38), we have $-\Delta\psi\leq-\psi$ outside $B_{R'}$. It therefore follows from the elliptic comparison principle that $\psi(x,y)\leq Me^{-(|x|+|y|)}$ outside $B_{R'}$, where $M:=\|\psi\|_{L^\infty(\partial B_{R'})}\left(\min_{(x,y)\in\partial B_{R'}}e^{-(|x|+|y|)}\right)^{-1}$. As a result ψ also satisfies an estimate analogous to (31), precisely $\psi(t,x)\leq Ce^{-(|x|+|y|)}$. In particular $\|\psi\|_{L^\infty(\partial B_{R'})}\to 0$, and we can reproduce the above argument to deduce that $\nabla\psi\in L^\infty(\mathbb{R}^2)$. Hence, from the estimates on Γ_{cut}, $\nabla\Gamma_{cut}$, ψ, $\nabla\psi$, the left hand side of (39) tends to zero as $R'\to\infty$. Since $\frac{c^2}{4}+\lambda_{cut}>0$, this implies $\psi\equiv\bar w\equiv 0$.

As a result we have $w(t,x,y)\to 0$ as $t\to\infty$, locally uniformly w.r.t. $(x,y)\in\mathbb{R}^2$. We claim that this convergence is actually uniform w.r.t. $(x,y)\in\mathbb{R}^2$. Indeed, assume by contradiction that there is $\varepsilon>0$, $t_n\to\infty$, $|x_n|+|y_n|\to\infty$, such that $w(t_n,x_n,y_n)\geq\varepsilon$. Define $w_n(t,x,y):=w(t,x+x_n,y+y_n)$ which solves

$$\partial_t w_n-c\partial_x w_n-\partial_{xx}w_n-\partial_{yy}w_n=r_{cut}(x+x_n,y+y_n)w_n, \tag{40}$$

that is a linear equation whose coefficients are bounded on $(0,\infty)\times\mathbb{R}^2$ uniformly w.r.t. n, since $r_{cut}\in L^\infty(\mathbb{R}^2)$. Using the interior parabolic estimates and arguing as above, we see that (modulo extraction) $w_n(t,x,y)$ converge to some $\theta(t,x,y)$ strongly in $C_{loc}^{\frac{1+\alpha}{2},1+\alpha}((0,\infty)\times\mathbb{R}^2)$, and weakly in $W_{p,loc}^{1,2}((0,\infty)\times\mathbb{R}^2)$. Hence, letting $n\to\infty$ into (40), we have

$$\partial_t\theta-c\partial_x\theta-\partial_{xx}\theta-\partial_{yy}\theta\leq-\theta,$$

so that $\theta(t,x,y)\leq Ce^{-t}$ by the comparison principle. In particular

$$0=\lim_{t\to\infty}\theta(t,0,0)=\lim_{t\to\infty}\lim_n w(t,x_n,y_n)\geq\liminf_n w(t_n,w_n,y_n)\geq\varepsilon,$$

that is a contradiction. Hence, $w(t,x,y)\to 0$ as $t\to\infty$, uniformly w.r.t. $(x,y)\in\mathbb{R}^2$. In view of (35), the same holds true for $\tilde n(t,x,y)$. □

3.2 Persistence

For slow climate shifts $0 \le c < c^*$, our result of persistence of the population reads as follows.

Theorem 3.4 (Survival)**.** *Assume that $r \in L^\infty_{loc}(\mathbb{R}^2)$ and $K \in L^\infty((0,\infty)\times\mathbb{R}^3)$ satisfy* (6) *and* (7) *respectively. Let Assumption 1.1 hold. Assume that $n_0 \not\equiv 0$ satisfies* (8)*. If $0 \le c < c^*$, then, for any nonnegative solution n of* (1)*, there exists a nonnegative function h such that*

$$\int_{\mathbb{R}^2} h(x,y)\,dx\,dy > 0, \qquad \int_{\mathbb{R}} h(0,y)\,dy > 0, \tag{41}$$

and

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

Remark 3.5. *Before proving the theorem, observe that the above result cannot hold for a speed $\tilde{c}$ different from c. Indeed it follows from the control of the tails* (14) *that*

$$n(t,\tilde{c}t,y) \le Ce^{-\mu|c-\tilde{c}|t}e^{-\mu|y|},$$

and then, $\int_{\mathbb{R}} Ce^{-\mu|c-\tilde{c}|t}e^{-\mu|y|}\,dy \to 0$, as $t \to \infty$. This indicates that, as stated in the introduction, the species needs to follow the climate shift to survive.

Proof. For $R > 0$ define the rectangle

$$\Omega_R := \{(x,y) : |x| < R,\ |y| < R\},$$

and denote by $(\lambda_R, \Gamma_R) \in \mathbb{R} \times C^\infty\left(\overline{\Omega_R}\right)$ the solution of the principal eigenvalue problem

$$\begin{cases} -\partial_{xx}\Gamma_R(x,y) - \partial_{yy}\Gamma_R(x,y) - r(x,y)\Gamma_R(x,y) = \lambda_R\Gamma_R(x,y) & \text{for all } (x,y) \in \Omega_R \\ \Gamma_R(x,y) = 0 \quad \text{for all } (x,y) \in \partial\Omega_R \\ \Gamma_R(x,y) > 0 \quad \text{for all } (x,y) \in \Omega_R, \quad \|\Gamma_R\|_\infty = 1. \end{cases} \tag{42}$$

Since λ_R converges to λ_∞ as $R \to \infty$, we can select $R > 0$ large enough so that (observe that $0 \le c < c^*$ reads as $\lambda_\infty < -\frac{c^2}{4}$)

$$\varepsilon := -\frac{c^2}{4} - \lambda_R > 0. \tag{43}$$

Next, the control of the tails (14) in Lemma 2.4 implies, that for any $t \ge 0$ and any x such that $|x| \le M$,

$$\begin{aligned} \int_{|y'|\ge M} K(t,x+ct,y,y')\tilde{n}(t,x,y')\,dy' &= \int_{|y'|\ge M} K(t,x+ct,y,y')n(t,x+ct,y')\,dy' \\ &\le Ck^+ \int_{|y'|\ge M} e^{-\mu(|x|+|y'|)}\,dy' \\ &\le Ck^+ \int_{|y'|\ge M} e^{-\mu|y'|}\,dy' \\ &= \frac{2Ck^+}{\mu}e^{-\mu M} < \frac{\varepsilon}{2}, \end{aligned} \tag{44}$$

provide we select $M > R$ large enough.

Recall that $\tilde{n}$ solves (24). Since $r \in L^\infty(\Omega_{M+1})$ and since (13) shows that the nonlocal term is uniformly bounded, we can apply the parabolic Harnack inequality: there exists $C_H > 0$ such that, for all $t \ge 1$,

$$\max_{(x,y)\in\overline{\Omega_M}} \tilde{n}\left(t - \frac{1}{2}, x, y\right) \le C_H \min_{(x,y)\in\overline{\Omega_M}} \tilde{n}(t,x,y). \tag{45}$$

Notice that $\Omega_R \subset \Omega_M$ so that, taking $0 < \nu < {C_H}^{-1}e^{-\frac{cR}{2}}\|\tilde{n}(\frac{1}{2},\cdot,\cdot)\|_{L^\infty(\Omega_R)}$, we get $\nu\Gamma_R(x,y) < e^{\frac{cx}{2}}\tilde{n}(1,x,y) = u(1,x,y)$ for all $(x,y) \in \overline{\Omega_R}$. Now assume that there is a time $t_0 > 1$, which we assume to be the smallest one, such that

$$\nu\Gamma_R(x_0,y_0) = e^{\frac{cx_0}{2}}\tilde{n}(t_0,x_0,y_0) = u(t_0,x_0,y_0) \quad \text{for some } (x_0,y_0) \in \Omega_R, \tag{46}$$

and derive a contradiction, which shall conclude the proof. Thanks to the definition of t_0, $\tilde n(t,x,y)-e^{-\frac{cx}{2}}\nu\Gamma_R(x,y)$ restricted to $(1,t_0]\times\Omega_R$ has a zero minimum value at (t_0,x_0,y_0). The maximum principle then yields

$$(\partial_t - c\partial_x - \partial_{xx} - \partial_{yy})\left[\tilde n(t,x,y) - e^{-\frac{cx}{2}}\nu\Gamma_R(x,y)\right](t_0,x_0,y_0) \le 0. \tag{47}$$

Combining equation (24) for $\tilde n$, equation (42) for the principal eigenfunction Γ_R and the contact condition (47), we arrive at

$$\tilde n(t_0,x_0,y_0)\left(-\int_{\mathbb{R}} K(t_0,x_0+ct_0,y_0,y')\tilde n(t_0,x_0,y')\,dy' - \frac{c^2}{4} - \lambda_R\right) \le 0,$$

which, in view of (43) and (44) implies

$$\varepsilon < \int_{|y'|\le M} K(t_0,x_0+ct_0,y_0,y')\tilde n(t_0,x_0,y')\,dy' \le k^+2M\|\tilde n(t_0,\cdot,\cdot)\|_{L^\infty(\mathbb{R}^2)}. \tag{48}$$

Now, observe that

$$\phi(t) := e^{r_{max}t}\|n(t_0-1/2,\cdot,\cdot)\|_{L^\infty(\mathbb{R}^2)}$$

solves $\partial_t\phi - \partial_{xx}\phi - \partial_{yy}\phi - r_{max}\phi = 0$ on $[t_0-1/2,t_0]\times\mathbb{R}^2$, whereas $n(t,x,y)$ satisfies $\partial_t n - \partial_{xx}n - \partial_{yy}n - r_{max}n \le 0$. Since $\phi(0)\ge n(t_0-1/2,x,y)$ the parabolic comparison principle implies

$$n(t_0,x,y) \le \phi(1/2) = e^{\frac12 r_{max}}\|n(t_0-1/2,\cdot,\cdot)\|_{L^\infty(\mathbb{R}^2)}.$$

Noticing that $\|n(t,\cdot,\cdot)\|_{L^\infty(\mathbb{R}^2)} = \|\tilde n(t,\cdot,\cdot)\|_{L^\infty(\mathbb{R}^2)}$, the above inequality combined with (48) implies

$$\varepsilon < k^+2Me^{\frac12 r_{max}}\|\tilde n(t_0-1/2,\cdot,\cdot)\|_{L^\infty(\mathbb{R}^2)},$$

and therefore

$$\begin{aligned}\varepsilon &< k^+2Me^{\frac12 r_{max}}\max\left(\max_{(x,y)\in\overline{\Omega_M}}\tilde n(t_0-1/2,x,y),\ \sup_{(x,y)\notin\Omega_M}\tilde n(t_0-1/2,x,y)\right)\\ &\le k^+2Me^{\frac12 r_{max}}\max\left(C_H\min_{(x,y)\in\overline{\Omega_M}}\tilde n(t_0,x,y),\ \sup_{|x|\ge M\text{or}|y|\ge M}Ce^{-\mu(|x|+|y|)}\right)\end{aligned}$$

where we have used the Harnack estimate (45) and the control of the tails (14). Using (46) we end up with

$$\varepsilon < k^+2Me^{\frac12 r_{max}}\max\left(C_He^{\frac{cR}{2}}\nu, Ce^{-\mu M}\right)$$

which is a contradiction, provided we select $M>0$ large enough, and then $\nu>0$ small enough. □

4 The environmental gradient case

In this section, we consider a growth function $r(x,y)$ satisfying Assumption 1.2, i.e. the unconfined case. Since $r(x,y)=\bar r(y-Bx)$, the equation (1) under consideration is then written as

$$\begin{cases}\partial_t n(t,x,y) - \partial_{xx}n(t,x,y) - \partial_{yy}n(t,x,y)\\ \qquad = \left(\bar r(y-B(x-ct)) - \int_{\mathbb{R}} K(t,x,y,y')n(t,x,y')\,dy'\right)n(t,x,y)\\ n(0,x,y) = n_0(x,y).\end{cases} \tag{49}$$

We define

$$c^{**} := \begin{cases}2\sqrt{-\lambda_\infty\frac{1+B^2}{B^2}} & \text{if } \lambda_\infty<0\\ 0 & \text{if } \lambda_\infty\ge 0\end{cases} \quad \text{the critical speed in the unconfined case,} \tag{50}$$

where λ_∞ is the principal eigenvalue defined by (11). In the whole section, we are then equipped with λ_∞, $\Gamma^{1D}_\infty(z)$ satisfying (11), and λ_∞, $\Gamma_\infty(x,y) := \Gamma^{1D}_\infty(z)(y-Bx)$ satisfying (10).

Remark 4.1. *Recall that in the case where* $r(x,y) = \bar{r}(y - Bx) = 1 - A(y - Bx)^2$*,* $A > 0$*, we have* $\lambda_\infty = \sqrt{A(B^2+1)} - 1$*, and* $\Gamma_\infty(x,y) = \exp\left(-\sqrt{\frac{A}{B^2+1}}\frac{(y-Bx)^2}{2}\right)$*. Then* $A(B^2+1) \geq 1$ *implies* $c^{**} = 0$*, while* $A(B^2+1) < 1$ *implies*

$$c^{**} = 2\sqrt{\left(1 - \sqrt{A(B^2+1)}\right)\frac{1+B^2}{B^2}}. \tag{51}$$

4.1 Invasion

For slow climate shifts $0 \leq c < c^{**}$, we prove that the population survives, and indeed propagate. We define

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

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

which are the propagation speeds in space x towards $-\infty$, $+\infty$ respectively, in a sense to be made precise in the following theorem:

Theorem 4.2 (Survival and invasion)**.** *Assume that* $r \in L^\infty_{loc}(\mathbb{R}^2)$ *and* $K \in L^\infty((0,\infty)\times\mathbb{R}^3)$ *satisfy* (6) *and* (7) *respectively. Let Assumption 1.2 hold. Assume that* $n_0 \not\equiv 0$ *satisfies* (8)*. If* $0 \leq c < c^{**}$*, then there is a function* $\psi : \mathbb{R} \to \mathbb{R}$ *with* $\psi(+\infty) = 0$ *such that any nonnegative solution* n *of* (49) *satisfies*

$$\forall (t,x) \in [1,\infty)\times\mathbb{R}, \quad \max\left(\|n(t,x,\cdot)\|_\infty, \int_{\mathbb{R}} n(t,x,y)\,dy\right) \leq \psi(x - \omega_x^+ t), \tag{52}$$

$$\forall (t,x) \in [1,\infty)\times\mathbb{R}, \quad \max\left(\|n(t,x,\cdot)\|_\infty, \int_{\mathbb{R}} n(t,x,y)\,dy\right) \leq \psi(-(x - \omega_x^- t)). \tag{53}$$

Moreover, for any $0 < \delta < \frac{\omega_x^+ - \omega_x^-}{2}$*, there exists* $\beta > 0$ *such that any nonnegative solution* n *of* (49) *satisfies*

$$\forall t \in [1,\infty), \quad \int_{\mathbb{R}} n(t,\omega_x t,y)\,dy \geq \beta. \tag{54}$$

for any $\omega_x \in [\omega_x^- + \delta, \omega_x^+ - \delta]$.

Remark 4.3. *As it can be seen in the proof, the population will follow the optimal trait. Also the propagation speeds of the population along the phenotypic trait* y *towards* $-\infty$, $+\infty$ *are respectively*

$$\omega_y^- = B\omega_x^- - Bc, \quad \omega_y^+ = B\omega_x^+ - Bc.$$

Remark 4.4. *In our unconfined model* (49)*, the conditions are shifted by the climate at a speed* $c \geq 0$ *towards large* $x \in \mathbb{R}$*. From Theorem 4.2, the population is able to follow the climate shift only if*

$$\omega_x^- \leq c \leq \omega_x^+.$$

One can check that the first inequality is always satisfied, while the second one is only satisfied if $c \leq 2\sqrt{-\lambda_\infty} < c^{**}$*. Hence, if* $c \in (2\sqrt{-\lambda_\infty}, c^{**})$*, the population survives despite its inability to follow the climate change: it only survives because it is also able to evolve to become adapted to the changing climate. Finally, one can notice that the threshold speed* $2\sqrt{-\lambda_\infty}$ *is similar to the definition of the critical speed* c^* *in the confined case (see* (22)*), which makes sense, since in the confined case, the survival is only possible if the population succeeds to strictly follow the climate change.*

Proof. Rather than working in the (x,y) variables, let us write $n(t,x,y) = v(t,X,Y)$ where X (resp. Y) represents the direction of (resp. the direction orthogonal to) the optimal trait $y = Bx$, that is

$$X = \frac{x+By}{\sqrt{1+B^2}}, \quad Y = \frac{-Bx+y}{\sqrt{1+B^2}}. \tag{55}$$

In these new variables, equation (49) is recast as

$$\begin{aligned}&\partial_t v - \partial_{XX} v - \partial_{YY} v\\ &= \left(\bar{r}\left(\sqrt{1+B^2}\,Y + Bct\right) - \int_{\mathbb{R}} v\left(t, \frac{\frac{X-BY}{\sqrt{1+B^2}} + By'}{\sqrt{1+B^2}}, \frac{-B\frac{X-BY}{\sqrt{1+B^2}} + y'}{\sqrt{1+B^2}}\right) dy'\right) v.\end{aligned} \tag{56}$$

Observe that for ease of writing we have taken $K \equiv 1$, which is harmless since $0 < k^- \leq K \leq k^+$. Note also that defining $\Gamma(Y) := \Gamma_\infty^{1D}(\sqrt{1+B^2}\,Y)$, we have

$$-\partial_{YY}\Gamma - \bar{r}\left(\sqrt{1+B^2}\,Y\right)\Gamma = \lambda_\infty \Gamma. \tag{57}$$

The controls from above (52) **and** (53)**.** To prove (52), we are seeking for a solution of

$$\partial_t \psi - \partial_{XX}\psi - \partial_{YY}\psi - \bar{r}\left(\sqrt{1+B^2}\,Y + Bct\right)\psi = 0 \quad \text{in } (0,\infty)\times\mathbb{R}^2, \tag{58}$$

in the form

$$\psi(t,X,Y) := e^{-\lambda(X-\omega_X^+ t)} e^{-\nu(Y-\omega_Y^+ t)} \Gamma\left(Y - \omega_Y^+ t\right), \tag{59}$$

with $\lambda > 0$, $\nu > 0$, $\omega_X^+ > 0$, $\omega_Y^+ > 0$. If we choose $\lambda := \omega_X^+/2$ and $\nu := \omega_Y^+/2$, then (58) turns out to be equivalent to

$$\left(\frac{{\omega_X^+}^2}{4} + \frac{{\omega_Y^+}^2}{4}\right)\Gamma\left(Y-\omega_Y^+ t\right) - \Gamma_{YY}\left(Y-\omega_Y^+ t\right) - \bar{r}\left(\sqrt{1+B^2}\,Y + Bct\right)\Gamma\left(Y-\omega_Y^+ t\right) = 0. \tag{60}$$

The combination of (57) and (60) shows that ψ is a solution of (58) if we select

$$\omega_X^+ := \sqrt{-4\lambda_\infty - \frac{B^2}{1+B^2}c^2} = \sqrt{\frac{B^2}{1+B^2}\left(c^{**2} - c^2\right)}, \quad \omega_Y^+ := \frac{-B}{\sqrt{1+B^2}}\,c. \tag{61}$$

Now, since $v(0,\cdot,\cdot)$ is compactly supported we can choose $M > 0$ large enough so that $M\,\psi(0,X,Y) \geq v(0,X,Y)$ for all $(X,Y) \in \mathbb{R}^2$. In view of (56), $\partial_t v - \partial_{XX} v - \partial_{YY} v - \bar{r}\left(\sqrt{1+B^2}\,Y + Bct\right)v \leq 0$, so that the parabolic comparison principle yields

$$v(t,X,Y) \leq M\psi(t,X,Y) \leq Me^{-\frac{\omega_X^+}{2}(X-\omega_X^+ t)} e^{-\frac{\omega_Y^+}{2}(Y-\omega_Y^+ t)}. \tag{62}$$

Noticing that

$$\omega_x^+ = \frac{\omega_X^+ - B\omega_Y^+}{\sqrt{1+B^2}}, \quad \omega_y^+ = \frac{B\omega_X^+ + \omega_Y^+}{\sqrt{1+B^2}}, \tag{63}$$

and going back to the original variables, we arrive at

$$n(t,x,y) \leq Me^{-\frac{\omega_x^+}{2}(x-\omega_x^+ t)} e^{-\frac{\omega_y^+}{2}(y-\omega_y^+ t)}.$$

Combining the relation $\omega_y^+ = B\omega_x^+ - Bc$, expressions (63), and the equality ${\omega_x^+}^2 + {\omega_y^+}^2 = {\omega_X^+}^2 + {\omega_Y^+}^2$, we see that the above is recast

$$n(t,x,y) \leq Me^{-\frac{1}{2}\sqrt{1+B^2}\,\omega_X^+(x-\omega_x^+ t)} e^{-\frac{1}{2}\omega_y^+(y-B(x-ct))}. \tag{64}$$

Combining the control above with the control of the tails (14), one obtains (52).

Finally, by using

$$\psi(t,X,Y) := e^{\frac{\omega_X^+}{2}(X+\omega_X^+ t)} e^{-\frac{\omega_Y^+}{2}(Y-\omega_Y^+ t)} \Gamma\left(Y-\omega_Y^+ t\right),$$

rather than (59) and using similar arguments, we prove (53), remarking that

$$\omega_x^- = \frac{-\omega_X^+ - B\omega_Y^+}{\sqrt{1+B^2}}, \quad \omega_y^- = \frac{-B\omega_X^+ + \omega_Y^+}{\sqrt{1+B^2}}. \tag{65}$$

The control from below (54)**.** The first step is to estimate the nonlocal term in (56). To do so, the key point is our refinement of Harnack inequality. Then we use a compactly supported subsolution.

Let $(t_0, X_0, Y_0) \in [1, \infty) \times \mathbb{R}^2$ be given, and the corresponding (x_0, y_0) obtained through the change of variable (55). We select $M > 2$ such that $|y_0 - B(x_0 - ct_0)| \leq M$. The control of the tails (14) then implies

$$\int_{\mathbb{R}} v\left(t_0, \frac{\frac{X_0 - BY_0}{\sqrt{1+B^2}} + By'}{\sqrt{1+B^2}}, \frac{-B\frac{X_0 - BY_0}{\sqrt{1+B^2}} + y'}{\sqrt{1+B^2}}\right) dy' = \int_{\mathbb{R}} n(t_0, x_0, y')\, dy'$$
$$\leq 2M \max_{y \in [-M,M]} n\left(t_0, x_0, B(x_0 - ct_0) + y\right) + \int_{[-M,M]^c} Ce^{-\mu|y|}\, dy. \tag{66}$$

In order to estimate the first term of the above expression, let us recall that the uniform boundedness of the solutions is known since Lemma 2.4. This allows to use the refinement of Harnack inequality, namely Theorem 2.7 with $\omega = \mathbb{R} \times \{0\}$ and $\delta = \frac{C}{2M\mu} e^{-\mu M} > 0$ to $\tilde{v}(t, X, Y) = v\left(t, X, Y - \frac{Bc}{\sqrt{1+B^2}} t\right)$. $\tilde{v}$ indeed satisfies

$$\partial_t \tilde{v} + \frac{Bc}{\sqrt{1+B^2}} \partial_Y \tilde{v} - \partial_{XX} \tilde{v} - \partial_{YY} \tilde{v}$$
$$= \left(\bar{r}\left(\sqrt{1+B^2}\, Y\right) - \int_{\mathbb{R}} v\left(t, \frac{\frac{X-BY}{\sqrt{1+B^2}} + By'}{\sqrt{1+B^2}}, \frac{-B\frac{X-BY}{\sqrt{1+B^2}} + y'}{\sqrt{1+B^2}} - \frac{Bc}{\sqrt{1+B^2}} t\right) dy'\right) \tilde{v},$$

and there exists thus a constant $\tilde{C}_M > 0$, depending on M, such that

$$\max_{(x,y) \in [-M,M]^2} n\left(t_0, x_0 + x, B(x_0 - ct_0) + y\right)$$
$$\leq \tilde{C}_M \min_{(x,y) \in [-M,M]^2} n\left(t_0, x_0 + x, B(x_0 - ct_0) + y\right) + \delta$$
$$\leq \tilde{C}_M n(t_0, x_0, y_0) + \delta, \tag{67}$$

which we plug into (66) to get

$$\int_{\mathbb{R}} v\left(t_0, \frac{\frac{X_0 - BY_0}{\sqrt{1+B^2}} + By'}{\sqrt{1+B^2}}, \frac{-B\frac{X_0 - BY_0}{\sqrt{1+B^2}} + y'}{\sqrt{1+B^2}}\right) dy' \leq C_M v(t_0, X_0, Y_0)) + \frac{3C}{\mu} e^{-\mu M}, \tag{68}$$

where $C_M := 2M\tilde{C}_M$.

Next, for $R > 0$, let us consider $\tilde{\lambda}_R, \tilde{\Gamma}_R(Y)$ solving the "one dimensional" principal eigenvalue problem

$$\begin{cases} -\partial_{YY}\tilde{\Gamma}_R - \bar{r}\left(\sqrt{1+B^2}\, Y\right)\tilde{\Gamma}_R = \tilde{\lambda}_R \tilde{\Gamma}_R & \text{in } (-R, R) \\ \tilde{\Gamma}_R = 0 & \text{on } \partial((-R,R)) \\ \tilde{\Gamma}_R > 0 & \text{on } (-R,R), \quad \tilde{\Gamma}_R(0) = 1. \end{cases} \tag{69}$$

We have $\tilde{\lambda}_R \to \lambda_\infty$ as $R \to \infty$. Defining

$$\Gamma_R(X, Y) := \cos\left(\frac{x}{R}\frac{\pi}{2}\right)\tilde{\Gamma}_R(Y),$$

we get

$$\begin{cases} -\partial_{XX}\Gamma_R - \partial_{YY}\Gamma_R - \bar{r}\left(\sqrt{1+B^2}\, Y\right)\Gamma_R = \lambda_R \Gamma_R & \text{in } (-R, R)^2 \\ \Gamma_R = 0 & \text{on } \partial((-R,R)^2) \\ \Gamma_R > 0 & \text{on } (-R,R)^2, \quad \Gamma_R(0,0) = 1, \end{cases} \tag{70}$$

where $\lambda_R = \tilde{\lambda}_R + \frac{\pi^2}{4R^2} \to \lambda_\infty$ as $R \to \infty$.

We then define, for some ω_X to be specified later and $\beta > 0$ to be selected later,

$$\psi_\beta(t, X, Y) := \beta e^{-\frac{\omega_X}{2}(X - \omega_X t)} e^{-\frac{\omega_Y^+}{2}(Y - \omega_Y^+ t)} \Gamma_R(X - \omega_X t, Y - \omega_Y^+ t), \tag{71}$$

which satisfies

$$\partial_t\psi_\beta - \partial_{XX}\psi_\beta - \partial_{YY}\psi_\beta - \bar r\left(\sqrt{1+B^2}Y + Bct\right)\psi_\beta = \left(\frac{\omega_X^2}{4} + \frac{{\omega_Y^+}^2}{4} + \lambda_R\right)\psi_\beta. \tag{72}$$

Since $\psi_\beta(t,\cdot,\cdot)$ is compactly supported and $v(1,\cdot,\cdot) > 0$, we can assume that $\beta > 0$ is small enough so that

$$\psi_\beta(1,\cdot,\cdot) < v(1,\cdot,\cdot). \tag{73}$$

Assume by contradiction that the set $\{t \geq 1 : \exists (X,Y),\, v(t,X,Y) = \psi_\beta(t,X,Y)\}$ is nonempty, and define

$$t_0 := \min\{t \geq 1 : \exists (X,Y),\, v(t,X,Y) = \psi_\beta(t,X,Y)\} \in (1,\infty).$$

Hence, $\psi_\beta - v$ has a zero maximum value at some point (t_0, X_0, Y_0) which satisfies $t_0 > 1$ and $(X_0 - \omega_X t_0, Y_0 - \omega_Y^+ t_0) \in (-R,R)^2$, since $v(t_0,\cdot,\cdot) > 0$. This implies that

$$\left[\partial_t(\psi_\beta - v) - \partial_{XX}(\psi_\beta - v) - \partial_{YY}(\psi_\beta - v) - \bar r\left(\sqrt{1+B^2}\,Y_0 + Bct_0\right)(\psi_\beta - v)\right](t_0,X_0,Y_0) \geq 0.$$

In view of the equation (56) for v and the equation (72) for ψ_β, we infer that

$$\left[\frac{\omega_X^2}{4} + \frac{{\omega_Y^+}^2}{4} + \lambda_R + \int_{\mathbb{R}} v\left(t_0, \frac{\frac{X_0 - BY_0}{\sqrt{1+B^2}} + By'}{\sqrt{1+B^2}}, \frac{-B\frac{X_0 - BY_0}{\sqrt{1+B^2}} + y'}{\sqrt{1+B^2}}\right) dy'\right]\psi_\beta(t_0,X_0,Y_0) \geq 0.$$

Hence, using $\psi_\beta(t_0,X_0,Y_0) > 0$ and estimate (68), we end up with

$$\begin{aligned} 0 &\leq \frac{\omega_X^2}{4} + \frac{{\omega_Y^+}^2}{4} + \lambda_R + C_M\psi_\beta(t_0,X_0,Y_0) + \frac{3C}{\mu}e^{-\mu M} \\ &\leq \lambda_R - \lambda_\infty + \frac{\omega_X^2 - {\omega_X^+}^2}{4} + C_M\psi_\beta(t_0,X_0,Y_0) + \frac{3C}{\mu}e^{-\mu M}, \end{aligned} \tag{74}$$

thanks to (61) and (71).

Now, let $\delta \in \left(0, \omega_X^+\right)$ be given. For all ω_X — appearing in (71)— such that $|\omega_X| \leq \omega_X^+ - \delta$, we have

$$\frac{\omega_X^2 - {\omega_X^+}^2}{4} \leq -\delta\frac{2\omega_X^+ - \delta}{4} < 0. \tag{75}$$

Since $\lambda_R \to \lambda_\infty$, we can successively select $R > 0$, $M > 2$ large enough and $\beta > 0$ small enough so that

$$|\lambda_R - \lambda_\infty| + \frac{3C}{\mu}e^{-\mu M} + C_M\psi_\beta(t_0,X_0,Y_0) \leq \frac{2\omega_X^+ - \delta}{8}\delta.$$

This estimate and (75) show that (74) then leads to a contradiction.

As a result, we have shown that, for any $\delta \in \left(0, \omega_X^+\right) = \left(0, \sqrt{1+B^2}\frac{\omega_x^+ - \omega_x^-}{2}\right)$, there are $R > 0$ and $\beta > 0$ such that, for any $|\omega_X| \leq \omega_X^+ - \delta$,

$$v(t,X,Y) \geq \beta e^{-\frac{\omega_X}{2}(X - \omega_X t)} e^{-\frac{\omega_Y^+}{2}(Y - \omega_Y^+ t)}\Gamma_R(X - \omega_X t, Y - \omega_Y^+ t),$$

for all $t \geq 1$, $X \in \mathbb{R}$, $Y \in \mathbb{R}$. Defining

$$\omega_x := \frac{\omega_X - B\omega_Y^+}{\sqrt{1+B^2}}, \quad \omega_y := \frac{B\omega_X + \omega_Y^+}{\sqrt{1+B^2}} = B\omega_x - Bc,$$

that is the analogous of expressions (63), we can derive the analogous of (64), that is

$$n(t,x,y) \geq \beta e^{-\frac{\omega_x}{2}(x - \omega_x t)} e^{-\frac{\omega_y}{2}(y - \omega_y t)}\Gamma_R\left(\frac{x + By}{\sqrt{1+B^2}} - \omega_X t, \frac{-Bx + y}{\sqrt{1+B^2}} - \omega_Y^+ t\right).$$

This in turn implies

$$n(t, \omega_x t, y + \omega_y t) \geq \beta\, e^{-\frac{\omega_y}{2}y}\Gamma_R\left(\frac{B}{\sqrt{1+B^2}}\,y, \frac{1}{\sqrt{1+B^2}}\,y\right),$$

which holds for any $\omega_x \in \left[\frac{-(\omega_X^+ - \delta) - B\omega_Y^+}{\sqrt{1+B^2}}, \frac{(\omega_X^+ - \delta) - B\omega_Y^+}{\sqrt{1+B^2}}\right] = \left[\omega_x^- + \frac{\delta}{\sqrt{1+B^2}}, \omega_x^+ - \frac{\delta}{\sqrt{1+B^2}}\right]$. This estimate is then enough to prove (54). □

4.2 Extinction

We state our result of extinction of the population for rapid climate shifts $c > c^{**}$.

Proposition 4.5 (Extinction). *Assume that $r \in L^\infty_{loc}(\mathbb{R}^2)$ and $K \in L^\infty((0,\infty)\times\mathbb{R}^3)$ satisfy* (6) *and* (7) *respectively. Let Assumption 1.2 hold. Assume that n_0 satisfies* (8)*. If $c > c^{**}$, then any nonnegative solution n of* (49) *satisfies, for some $\gamma_0 > 0$,*

$$\sup_{x\in\mathbb{R}} \int_{\mathbb{R}} n(t,x,y)\,dy = \mathcal{O}\left(e^{-\gamma_0 t}\right) \to 0, \quad \text{as } t \to \infty. \tag{76}$$

Proof. Just as in the first part of the proof of Theorem 4.2, we introduce the change of variables (55) and v satisfying (56). We are seeking for a solution φ of (58) in the form

$$\varphi(t,X,Y) := e^{-\gamma t} e^{-\nu(Y-\omega_Y^+ t)} \Gamma\left(Y - \omega_Y^+ t\right),$$

with $\nu > 0$, $\omega_Y^+ > 0$. If we choose $\nu := \omega_Y^+/2$, then φ is a solution of (58) if and only if

$$\left(\frac{\omega_Y^{+2}}{4} - \gamma\right)\Gamma\left(Y-\omega_Y^+ t\right) - \Gamma_{YY}\left(Y-\omega_Y^+ t\right) - \bar{r}\left(\sqrt{1+B^2}\,Y + Bct\right)\Gamma\left(Y-\omega_Y^+ t\right) = 0. \tag{77}$$

The combination of (57) and (77) shows that φ is a solution of (58) if we select $\gamma = \omega_Y^{+2} + \lambda_\infty > 0$. Since $v(0,\cdot,\cdot)$ is compactly supported we can choose $M > 0$ large enough so that $M\varphi(0,X,Y) \geq v(0,X,Y)$. In view of (56), $\partial_t v - \partial_{XX} v - \partial_{YY} v - \bar{r}\left(\sqrt{1+B^2}\,Y + Bct\right) v \leq 0$ so that the parabolic comparison principle yields

$$v(t,X,Y) \leq M\varphi(t,X,Y) \leq M e^{-\gamma t} e^{-\nu(Y-\omega_Y^+ t)}\Gamma\left(Y-\omega_Y^+ t\right) \leq M e^{-\gamma t} e^{-\nu(Y-\omega_Y^+ t)}. \tag{78}$$

Then if, without loss of generality, $c \geq 0$, we get, for $\alpha > 0$ to be chosen later,

$$\sup_{x\in\mathbb{R}} \int_{\mathbb{R}} n(t,x,y)\,dy = \sup_{x\in\mathbb{R}} \left(\int_{y \geq B(x-ct)-\alpha t} n(t,x,y)\,dy + \int_{y \leq B(x-ct)-\alpha t} n(t,x,y)\,dy \right). \tag{79}$$

We can estimate the first term of (79) as follows

$$\begin{aligned}
\int_{y\geq B(x-ct)-\alpha t} n(t,x,y)\,dy &\leq \int_{y\geq B(x-ct)-\alpha t} v\left(t, \frac{x+By}{\sqrt{1+B^2}}, \frac{-Bx+y}{\sqrt{1+B^2}}\right) dy \\
&\leq M \int_{y\geq B(x-ct)-\alpha t} e^{-\gamma t} e^{-\nu\left(\frac{-Bx+y}{\sqrt{1+B^2}} - \omega_Y^+ t\right)}\,dy \\
&\leq M \int_{y\geq B(x-ct)-\alpha t} e^{-\gamma t} e^{-\frac{\nu}{\sqrt{1+B^2}}(y - B(x-ct))}\,dy \\
&\leq M \int_{\mathbb{R}_+} e^{-\gamma t} e^{-\frac{\nu}{\sqrt{1+B^2}}(\tilde{y}-\alpha t)}\,d\tilde{y} \leq M \frac{\sqrt{1+B^2}}{\nu} e^{\frac{-\gamma}{2}t},
\end{aligned}$$

if we choose $\alpha = \frac{\gamma\sqrt{1+B^2}}{2\nu}$. Using the control of the tails (14), we can estimate the second term of (79) by

$$\begin{aligned}
\int_{y\leq B(x-ct)-\alpha t} n(t,x,y)\,dy &\leq \int_{y\leq B(x-ct)-\alpha t} C e^{-\mu|y-B(x-ct)|}\,dy \\
&\leq \int_{\mathbb{R}_+} C e^{-\mu(\tilde{y}+\alpha t)}\,d\tilde{y} \leq \frac{C}{\mu} e^{-\mu\alpha t}.
\end{aligned}$$

Then, (79) becomes

$$\sup_{x\in\mathbb{R}} \int_{\mathbb{R}} n(t,x,y)\,dy \leq C e^{-\min\left(\frac{\gamma}{2},\mu\alpha\right)t},$$

which proves the proposition. ☐

5 Mixed scenarios

In this section, we consider a growth function $r(x,y)$ satisfying Assumption 1.3, that is

$$r(x,y) = \mathbf{1}_{\mathbb{R}_-\times\mathbb{R}}(x,y)r_u(x,y) + \mathbf{1}_{\mathbb{R}_+\times\mathbb{R}}(x,y)r_c(x,y), \tag{80}$$

where $r_c(x,y)$ satisfies Assumption 1.1 and $r_u(x,y) = \bar{r}_u(y-Bx)$ satisfies Assumption 1.2. It follows from subsection 2.1 — see (10) and (11)— that we can define the principal eigenvalues λ_∞, $\lambda_{u,\infty}$, and some principal eigenfunctions $\Gamma_\infty(x,y)$, $\Gamma_{u,\infty}(x,y) = \Gamma_{u,\infty}^{1D}(y-Bx)$ associated to r, r_u respectively. In the sequel, for $\theta > 0$, we shall use the following modified growth functions,

$$r^\theta(x,y) := \max(r(x,y), -\theta), \quad r_u^\theta(x,y) := \max(r_u(x,y), -\theta). \tag{81}$$

We also define the principal eigenvalues λ_∞^θ, $\lambda_{u,\infty}^\theta$ and some principal eigenfunctions $\Gamma_\infty^\theta(x,y)$, $\Gamma_{u,\infty}^\theta(x,y) = \Gamma_{u,\infty}^{\theta,1D}(y-Bx)$ associated to r^θ, r_u^θ respectively. Using the analogous of (11) satisfied by $\Gamma_{u,\infty}^{1D}(z)$ and $\Gamma_{u,\infty}^{\theta,1D}(z)$ and using the same arguments as those used to prove (34), we see that

$$\lambda_{u,\infty}^\theta \nearrow \lambda_{u,\infty}, \qquad \text{as } \theta \to \infty. \tag{82}$$

5.1 More preliminary results on the tails

Let us first provide some estimates on the tails of the four principal eigenfunctions defined above.

Lemma 5.1 (Tails of eigenfunctions from above)**.** *Assume that $r \in L^\infty_{loc}(\mathbb{R}^2)$ satisfies* (6) *and Assumption 1.3. Then, for any $\mu > 0$, there is $C_\mu > 0$ such that, for all $(x,y) \in \mathbb{R}^2$,*

$$\Gamma_{u,\infty}(x,y) \le C_\mu e^{-\mu|y-Bx|}, \quad \Gamma_\infty(x,y) \le C_\mu e^{-\mu\max(|y-Bx|,x)}. \tag{83}$$

On the other hand, for any $\theta > 2\max(\lambda_{u,\infty}, \lambda_\infty, 0)$, there is $C_\theta > 0$ such that, for all $(x,y) \in \mathbb{R}^2$,

$$\Gamma_{u,\infty}^\theta(x,y) \le C_\theta e^{-\sqrt{\frac{\theta}{2(1+B^2)}}|y-Bx|}, \quad \Gamma_\infty^\theta(x,y) \le C_\theta e^{-\sqrt{\frac{\theta}{2(1+B^2)}}\max(|y-Bx|,x)}. \tag{84}$$

Proof. Notice that a similar estimate for the confined case was obtained in (31): the proof consisted in combining the fact that $r_c(x,y) \to -\infty$ as $|x|+|y| \to \infty$ with the elliptic comparison principle. Using $r_u(x,y) \to -\infty$ as $|y-Bx| \to \infty$, and $r(x,y) \to -\infty$ as $\max(|y-Bx|,x) \to \infty$, we obtain (83) in a similar manner.

As far as (84) is concerned, let us only notice that $r_u^\theta(x,y) \ge r_u(x,y)$, $r^\theta(x,y) \ge r(x,y)$, so that $\lambda_{u,\infty}^\theta \le \lambda_{u,\infty}$, $\lambda_\infty^\theta \le \lambda_\infty$ and therefore $\lambda_{u,\infty}^\theta - \theta \le -\frac{\theta}{2}$, $\lambda_\infty^\theta - \theta \le -\frac{\theta}{2}$. These inequalities are valid "far away" (in a appropriate sense with respect to the considered case) and enable us to reproduce again the argument in (31). Details are omitted. □

Next, we estimate from below the tails of the principal eigenfunction $\Gamma_{u,\infty}^\theta(x,y)$.

Lemma 5.2 (Tails of the eigenfunction from below)**.** *Assume that $r \in L^\infty_{loc}(\mathbb{R}^2)$ satisfies* (6) *and Assumption 1.3. Then there is $\theta_1 > 0$ such that, for any $\theta > \theta_1$, there is $C_\theta > 0$ and such that, for all $(x,y) \in \mathbb{R}^2$,*

$$\Gamma_{u,\infty}^\theta(x,y) \ge C_\theta e^{-2\sqrt{\frac{2\theta}{1+B^2}}|y-Bx|}. \tag{85}$$

Proof. Since r_u satisfies Assumption 1.2, there exists $R > 0$ such that $r_u(x,y) = \bar{r}_u(y-Bx) \le -\theta = r_u^\theta(x,y)$ as soon as $|y-Bx| \ge R$. Moreover, $\Gamma_{u,\infty}^\theta$ only depending on $y-Bx$, there is $\delta > 0$ such that $\Gamma_{u,\infty}^\theta(x,y) \ge \delta$ for (x,y) such that $|y-Bx| = R$. Moreover since, for (x,y) such that $|y-Bx| > R$,

$$-\partial_{xx}\Gamma_{u,\infty}^\theta(x,y) - \partial_{yy}\Gamma_{u,\infty}^\theta = (\lambda_{u,\infty}^\theta - \theta)\Gamma_{u,\infty}^\theta(x,y) \ge -2\theta\Gamma_{u,\infty}^\theta(x,y),$$

for any $\theta > \theta_1$, with $\theta_1 > 0$ large enough. It therefore follows from the elliptic comparison principle that

$$\Gamma_{u,\infty}^\theta(x,y) \ge \delta e^{-2\sqrt{\frac{2\theta}{1+B^2}}(|y-Bx|-R)},$$

which concludes the proof. □

Finally, we provide a control of the tails of the solution of the Cauchy problem (1), which is a extension (and an improvement) of Lemma 2.4 to the mixed case.

Lemma 5.3 (Exponential decay of tails of $n(t,x,y)$)**.** *Assume that $r \in L^\infty_{loc}(\mathbb{R}^2)$ and $K \in L^\infty((0,\infty)\times \mathbb{R}^3)$ satisfy* (6) *and* (7) *respectively. Let Assumption 1.3 hold. Assume that n_0 satisfies* (8)*. Then, for any $\mu > 0$, there is $C > 0$ such that, for any global nonnegative solution n of* (1)*,*

$$0 \le n(t,x,y) \le Ce^{-\mu \max(|y-B(x-ct)|, x-ct)}, \tag{86}$$

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

Proof. By using arguments similar to those of Lemma 2.4 (for the bounded and unbounded cases), we see that there are $\bar\mu > 0$ and $\bar C > 0$ such that

$$n(t,x,y) \le \bar C e^{-\bar\mu \max(|y-B(x-ct)|, x-ct)}, \tag{87}$$

for all $t \ge 0$, $x \in \mathbb{R}$, $y \in \mathbb{R}$. Details are omitted.

Next, let $\mu > 0$ be given, and $\nu > 0$ to be determined later. Thanks to Assumption 1.3, there exists $R > 0$ such that $\min(|y - B(x-ct)|, x-ct) > R$ implies $r(x,y) < -\nu$. Similarly to the proof of Lemma 2.4, we introduce $\varphi(t,x,y) := \kappa e^{-\mu(|y-B(x-ct)|-R)}$, which satisfies

$$\partial_t\varphi - \partial_{xx}\varphi - \partial_{yy}\varphi - r(x-ct,y)\varphi = \left(\pm\mu Bc - \mu^2B^2 - \mu^2 + \nu\right)\varphi \ge 0,$$

for all $t \ge 0$, and $|y - B(x-ct)| > R$, provided we chose $\nu > 0$ large enough. Thanks to (87), we can chose κ large enough for $n(t,x,y) \le \varphi(t,x,y)$ to hold for all $t \ge 0$, and $|y - B(x-ct)| = R$. Since moreover n satisfies $\partial_t n - \partial_{xx} n - \partial_{yy} n - r(x-ct,y)n \le 0$, the parabolic maximum principle implies that $n(t,x,y) \le \varphi(t,x,y)$ for $t \ge 0$, and $|y - B(x-ct)| > R$. The same argument can be made with $\varphi(t,x,y) := \kappa e^{-\mu(|x|-R)}$ for $t \ge 0$ and $x \ge R$ with $R > 0$ large enough, which is enough to prove the lemma. ☐

5.2 Extinction, survival, propagation

Equipped with the principal eigenvalues λ_∞, $\lambda_{u,\infty}$, we adapt (22) and (50) by defining

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

and

$$c_u^{**} := \begin{cases} 2\sqrt{-\lambda_{u,\infty}\frac{1+B^2}{B^2}} & \text{if } \lambda_{u,\infty} < 0 \\ 0 & \text{if } \lambda_{u,\infty} \ge 0. \end{cases}$$

Since $-\lambda_{u,\infty}$ can be smaller that $-\lambda_\infty$, it may happen that $c_u^{**} < c^*$, in contrast with Section 4 where $c^* \le c^{**}$ was always true. If r is defined by (5), this situation can be obtained if $0 < B' < B$, and if $\varepsilon > 0$ is small enough. The last result of this study provides a qualitative description of the dynamics of the population depending on the relative values of c^*, c_u^{**}, and the speed c of the climate shift.

Theorem 5.4 (Long time behavior in the mixed case)**.** *Assume that $r \in L^\infty_{loc}(\mathbb{R}^2)$ and $K \in L^\infty((0,\infty)\times \mathbb{R}^3)$ satisfy* (6) *and* (7) *respectively. Let Assumption 1.3 hold. Assume that $n_0 \not\equiv 0$ satisfies* (8)*. Let n be a global nonnegative solution of* (1)*.*

(i) Assume $\max(c^*, c_u^{**}) < c$*. Then the population gets extinct exponentially fast. More precisely, there are $C > 0$ and $\gamma_0 > 0$ such that*

$$\sup_{x\in\mathbb{R}} \int_{\mathbb{R}} n(t,x,y)\,dy \le Ce^{-\gamma_0 t}, \quad \forall t \ge 1. \tag{88}$$

(ii) Assume $c_u^{**} < c < c^*$. Then the population survives and follows the climate shift, but does not succeed to propagate. More precisely, there are $\beta > 0$, $C > 0$ and $\omega > 0$ such that

$$\int_{\mathbb{R}} n(t, x + ct, y)\, dy \geq \beta, \quad \forall t \geq 1, \forall x \in [-1, 1], \tag{89}$$

while

$$\int_{\mathbb{R}} n(t, x + ct, y)\, dy \leq Ce^{-\omega|x|}, \quad \forall t \geq 1, \forall x \in \mathbb{R}. \tag{90}$$

(iii) Assume $c^* < c < c_u^{**}$. Then the population survives, but does not succeed to follow the climate shift. More precisely, there are $\beta > 0$, $C > 0$, $\omega > 0$, and $\gamma > 0$ such that

$$\int_{\mathbb{R}} n\left(t, x + \frac{B^2 c}{1 + B^2} t, y\right) dy \geq \beta, \quad \forall t \geq 1, \forall x \in [-1, 1], \tag{91}$$

while

$$\int_{\mathbb{R}} n(t, x + ct, y)\, dy \leq Ce^{-\omega x} e^{-\gamma t}, \quad \forall t \geq 1, \forall x \in \mathbb{R}. \tag{92}$$

(iv) Assume $c < \min(c^*, c_u^{**})$. Then the population survives with an increasing species' range. More precisely, there is $\beta > 0$ such that

$$\min_{x \in \left[\frac{B^2 c}{1+B^2} t, ct\right]} \int_{\mathbb{R}} n(t, x, y)\, dy \geq \beta, \quad \forall t \geq 1. \tag{93}$$

Remark 5.5. *Notice that if $c < \min(c^*, c_u^{**})$, then the population will survive for $x \in \left[\frac{B^2 c}{1+B^2} t, ct\right]$. The size of its range will then increase at a speed of at least $\frac{c}{1+B^2}$. Moreover, this speed will provide little information on $\max(c^*, c_u^{**}) - c$, that is on the tolerance of the population to an increase of the climate change speed. The situation is then qualitatively different from the unconfined case, where the growth of the range of the population was directly linked to the difference $c^{**} - c$ (see subsection 4.1 for details):*

$$\begin{aligned} \omega_x^+ - \omega_x^- &= 2\sqrt{-\frac{4\lambda_\infty}{1 + B^2} - \frac{B^2}{(1 + B^2)^2} c^2} \\ &= \frac{2B}{1 + B^2} \sqrt{(c^{**})^2 - c^2}. \end{aligned}$$

Proof of (i). Using the supersolution $\phi(t, x, y) := Me^{\left(-\lambda_\infty - \frac{c^2}{4}\right)t} \Gamma_\infty(x, y)$, as in the first lines of the proof of Proposition 3.1, shows that (27) remains valid here. Therefore, in view of (83), for any $\mu > 0$, there is $C_\mu > 0$ such that, for all (x, y),

$$e^{\frac{cx}{2}} n(t, x + ct, y) \leq C_\mu e^{\left(-\lambda_\infty - \frac{c^2}{4}\right)t} e^{-\mu \max(|y - Bx|, x)}. \tag{94}$$

Then, in particular,

$$n(t, ct, y) \leq C_\mu e^{\left(-\lambda_\infty - \frac{c^2}{4}\right)t} e^{-\mu|y|}, \quad \text{for } t \geq 0,\ y \in \mathbb{R}. \tag{95}$$

Next, notice that n satisfies

$$\partial_t n - \Delta n \leq r(x - ct, y)n = r_u(x - ct, y)n \leq r_u^\theta(x - ct, y)n, \quad \text{for } t \geq 0,\ x \leq ct,\ y \in \mathbb{R}. \tag{96}$$

We now build a supersolution for (96), using an approach similar to the one developed in the proof of Proposition 4.5. Recall that ω_Y^+ was defined in (61). Let $\theta > \max\left(2\lambda_{u,\infty}, 2\lambda_\infty, \theta_1, \frac{B^2 c^2}{64(1+B^2)}, 2{\omega_Y^+}^2\right)$ to be chosen later. Define $\Gamma_u^\theta(Y) := \Gamma_u^{\theta,1D}(\sqrt{1 + B^2}\, Y)$, which in turn implies $\Gamma_u^\theta(Y) = \Gamma_{u,\infty}^\theta(x, y)$, with (x, y) related to (X, Y) by (55). Define

$$\varphi(t, X, Y) := e^{-\gamma t} e^{\frac{-\omega_Y^+}{2}(Y - \omega_Y^+ t)} \Gamma_u^\theta(Y - \omega_Y^+ t), \tag{97}$$

with $\gamma > 0$ to be chosen later. Recall that $r_u^\theta(x,y) = \bar r_u^\theta(y-Bx)$. We compute

$$\partial_t \varphi - \Delta \varphi - \bar r_u^\theta\left(\sqrt{1+B^2}\,Y + Bct\right)\varphi = \left(-\gamma + \frac{{\omega_Y^+}^2}{4} + \lambda_{u,\infty}^\theta\right)\varphi \geq 0,$$

as soon as

$$\gamma \leq \bar\gamma := \frac{{\omega_Y^+}^2}{4} + \lambda_{u,\infty}^\theta = \frac{B^2(c^2-(c_u^{**})^2)}{4(1+B^2)} + \left(\lambda_{u,\infty}^\theta - \lambda_{u,\infty}\right). \tag{98}$$

Since $c^2 - (c_u^{**})^2 > 0$ and $\lim_{\theta\to\infty}\lambda_{u,\infty}^\theta = \lambda_{u,\infty}$, we have $\bar\gamma > 0$ provided we fix θ large enough. As a result

$$\bar n(t,x,y) := \varphi\left(t, \frac{x+By}{\sqrt{1+B^2}}, \frac{-Bx+y}{\sqrt{1+B^2}}\right) \tag{99}$$

is the requested supersolution for (96), that is

$$\partial_t \bar n - \Delta \bar n \geq r_u^\theta(x-ct,y)\bar n. \tag{100}$$

Now, we take care of the line $x = ct$. Using the definition (61) of ω_Y^+, we get

$$\begin{aligned}
\bar n(t,ct,y) &= e^{-\gamma t} e^{\frac{-\omega_Y^+}{2}\left(\frac{-Bct+y}{\sqrt{1+B^2}} - \omega_Y^+ t\right)} \Gamma_u^\theta\left(\frac{-Bct+y}{\sqrt{1+B^2}} - \omega_Y^+ t\right)\\
&= e^{-\gamma t} e^{\frac{Bc\,y}{2(1+B^2)}} \Gamma_u^\theta\left(\frac{y}{\sqrt{1+B^2}}\right)\\
&= e^{-\gamma t} e^{\frac{Bc\,y}{2(1+B^2)}} \Gamma_{u,\infty}^\theta(0,y)\\
&\geq C_\theta\, e^{-\gamma t} e^{\frac{Bc\,y}{2(1+B^2)}} e^{-2\sqrt{\frac{2\theta}{1+B^2}}|y|},
\end{aligned}$$

in view of Lemma 5.2. It follows from this and (95) that the ordering

$$n(t,ct,y) \leq C\,\bar n(t,ct,y), \qquad \text{for all } t \geq 0, y \in \mathbb{R}, \tag{101}$$

is guaranteed if $\mu := 2\sqrt{\frac{2\theta}{1+B^2}} - \frac{Bc}{2(1+B^2)} > 0$ (positivity is insured by $\theta \geq \frac{B^2c^2}{64(1+B^2)}$), $\gamma := \min(\bar\gamma, \frac{c^2}{4} + \lambda_\infty) > 0$ (notice that $c > c^*$ implies $\lambda_\infty + \frac{c^2}{4} > 0$) and $C \geq \frac{C_\mu}{C_\theta}$.

Moreover, since $n_0(\cdot,\cdot)$ has a compact support and $\bar n(0,\cdot,\cdot) > 0$, we have

$$n_0(x,y) \leq C\bar n(0,x,y), \qquad \text{for all } x \leq 0, y \in \mathbb{R}, \tag{102}$$

if $C > 0$ is large enough.

It follows from (96), (100), (101), (102) and the parabolic comparison principle on $\{(t, x+ct, y);\, t \geq 0,\, x \leq 0,\, y \in \mathbb{R}\}$ that for any $t \geq 0$, $x \leq 0$ and $y \in \mathbb{R}$,

$$\begin{aligned}
n(t,ct+x,y) &\leq C\,\bar n(t,ct+x,y)\\
&= Ce^{-\gamma t} e^{\frac{-\omega_Y^+}{2\sqrt{1+B^2}}(y-Bx)} \Gamma_{u,\infty}^\theta\left(x + ct + \frac{B}{\sqrt{1+B^2}}\omega_Y^+ t, y - \frac{\omega_Y^+}{\sqrt{1+B^2}}t\right)\\
&= Ce^{-\gamma t} e^{\frac{-\omega_Y^+}{2\sqrt{1+B^2}}(y-Bx)} \Gamma_{u,\infty}^\theta(x,y),
\end{aligned}$$

where we have used the expression (61) for ω_Y^+. Combining again (61) with (84), we arrive at

$$\begin{aligned}
n(t,ct+x,y) &\leq CC_\theta e^{-\gamma t} e^{\frac{-\omega_Y^+}{2\sqrt{1+B^2}}(y-Bx)} e^{-\sqrt{\frac{\theta}{2(1+B^2)}}|y-Bx|}\\
&\leq CC_\theta e^{-\gamma t} e^{-\frac12\sqrt{\frac{\theta}{2(1+B^2)}}|y-Bx|},
\end{aligned}$$

using the fact that $\theta > 2{\omega_Y^+}^2$.

The above estimate for $x \leq 0$ and the estimate (94) for $x \geq 0$ are enough to prove (88). □

Proof of (ii). The proof of (89), that is of the survival of the population around $(t, ct, 0)$ for $t \geq 0$ is similar to the proof of Theorem 3.4. It is indeed possible to extend the proof of Theorem 3.4 to the present assumption on r, using Lemma 5.3 to estimate the tails of the density n. We skip the details of this modification.

We now turn to the proof of the estimate (90). Our approach will be similar to the proof of Theorem 4.2, more specifically, the proof of estimates (52). For some $\theta > 0$ to be determined later, we seek a solution of

$$\partial_t \psi - \partial_{XX}\psi - \partial_{YY}\psi - \bar{r}_u^\theta\left(\sqrt{1+B^2}\,Y + Bct\right)\psi = 0, \tag{103}$$

in the form

$$\psi(t, X, Y) := e^{-\gamma t} e^{\omega X} e^{-\frac{\omega_Y^+}{2}(Y - \omega_Y^+ t)} \Gamma_u^\theta\left(Y - \omega_Y^+ t\right),$$

with $\gamma > 0$, $\omega > 0$ to be chosen. We see that ψ is a solution of (103) if and only if

$$-\gamma - \omega^2 + \frac{{\omega_Y^+}^2}{4} + \lambda_{u,\infty}^\theta = 0. \tag{104}$$

Next, we define

$$\bar{n}(t, x, y) := \psi\left(t, \frac{x + By}{\sqrt{1+B^2}}, \frac{-Bx + y}{\sqrt{1+B^2}}\right), \tag{105}$$

which is then a supersolution of (1) as soon as (104) holds. As far as the line $x = ct$ is concerned, we have

$$\begin{aligned}
\bar{n}(t, ct, y) &= e^{-\gamma t} e^{\omega\left(\frac{ct+By}{\sqrt{1+B^2}}\right)} e^{\frac{-\omega_Y^+}{2}\left(\frac{-Bct+y}{\sqrt{1+B^2}} - \omega_Y^+ t\right)} \Gamma_u^\theta\left(\frac{-Bct + y}{\sqrt{1+B^2}} - \omega_Y^+ t\right) \\
&= e^{\left(\frac{c\omega}{\sqrt{1+B^2}} - \gamma\right)t + \left(\frac{\omega B - \omega_Y^+/2}{\sqrt{1+B^2}}\right)y} \Gamma_{u,\infty}^\theta(0, y),
\end{aligned}$$

by using the definition (61) of ω_Y^+. In view of Lemma 5.2, this yields

$$\bar{n}(t, ct, y) \geq C_\theta e^{\left(\frac{c\omega}{\sqrt{1+B^2}} - \gamma\right)t} e^{-\left(2\sqrt{2\theta} + |\omega B - \omega_Y^+/2|\right)\frac{|y|}{\sqrt{1+B^2}}}. \tag{106}$$

We select $\gamma := \frac{c\omega}{\sqrt{1+B^2}}$ and ω the positive solution of (104). There is a solution of the second order polynomial (104) provided $\theta > 0$ is large enough, since its discriminant satisfies $\Delta = \frac{c^2}{1+B^2} + \left({\omega_Y^+}^2 + 4\lambda_{u,\infty}^\theta\right) \to_{\theta\to\infty} \frac{c^2}{1+B^2} + \frac{B^2\left(c^2 - {c_u^{**}}^2\right)}{1+B^2} > 0$. We can also assume that $\theta > 8(\omega B + \omega_Y^+/2)^2$ so that, in particular, $2\sqrt{2\theta} > 2|\omega B - \omega_Y^+/2|$, and then thanks to Lemma 5.3 and (106), there exists a constant $C > 0$ such that, for all $t \geq 0$ and $y \in \mathbb{R}$,

$$n(t, ct, y) \leq C\bar{n}(t, ct, y).$$

The ordering at $t = 0$ being obtained as in (i) above, the comparison principle implies that $n(t, x+ct, y) \leq C\bar{n}(t, x + ct, y) = C\psi\left(t, \frac{x+By}{\sqrt{1+B^2}}, \frac{-Bx+y}{\sqrt{1+B^2}}\right)$, for all $(t, x, y) \in \mathbb{R}_+ \times \mathbb{R}_- \times \mathbb{R}$. Using the definition of ψ, we arrive at

$$n(t, x + ct, y) \leq Ce^{\omega\sqrt{1+B^2}x} e^{\left(\frac{\omega B}{\sqrt{1+B^2}} - \frac{\omega_Y^+}{2\sqrt{1+B^2}}\right)(y - Bx)} \Gamma_u^\theta\left(\frac{-B(x + ct) + y}{\sqrt{1+B^2}} - \omega_Y^+ t\right).$$

Going back to $\Gamma_{u,\infty}^\theta$ and using estimate (84), we end up with

$$\begin{aligned}
n(t, x + ct, y) &\leq CC_\theta e^{\omega\sqrt{1+B^2}x} e^{\left(\frac{\omega B}{\sqrt{1+B^2}} - \frac{\omega_Y^+}{2\sqrt{1+B^2}}\right)(y - Bx)} e^{-\sqrt{\frac{\theta}{2(1+B^2)}}|y - Bx|} \\
&\leq CC_\theta e^{\omega\sqrt{1+B^2}x} e^{-\frac{1}{2}\sqrt{\frac{\theta}{2(1+B^2)}}|y - Bx|},
\end{aligned}$$

using $\theta > 2(2\omega B + \omega_Y^+)^2$. This estimates proves (90) for $x \leq 0$, the case $x \geq 0$ being known since (86). $\square$

Proof of (*iii*). The proof of Proposition 3.1 shows that (27) still holds true, and then, thanks to Lemma 5.1, for any $\mu > 0$, there exists $C_\mu > 0$ such that, for any $(x, y) \in \mathbb{R}^2$,

$$\begin{aligned} e^{\frac{cx}{2}} n(t, x + ct, y) &\leq C_\mu e^{\left(-\lambda_\infty - \frac{c^2}{4}\right)t} \Gamma_\infty(x, y) \\ &\leq C_\mu e^{\left(-\lambda_\infty - \frac{c^2}{4}\right)t} e^{-\mu \max(|y - Bx|, x)}, \end{aligned}$$

which is enough to prove (92).

We now turn to the proof of the survival of the population, with a shift slower than the climate change, that is estimate (91). For ease of writing we take $K \equiv 1$, which is harmless since $0 < k^- \leq K \leq k^+$. The proof shares some arguments with that of (54). First, for a given $(t_0, x_0, y_0) \in [1, \infty) \times \mathbb{R}^2$, we need a control of the nonlocal term $\int_{\mathbb{R}} n(t_0, x_0, y')dy'$. We claim that we can reproduce the arguments used to prove (68). Indeed, the crucial control of the tails (14) in the unconfined case is replaced by (86) in the present mixed scenario. Hence we can reproduce the proof of subsection 4.1: we derive (66), and apply Theorem 2.7 to obtain (68). As a result, for given $\mu > 0$, there is $C > 0$ (as in Lemma 5.3) that , for a given $(t_0, x_0, y_0) \in [1, \infty) \times \mathbb{R}^2$ and $M > 2$ such that $|y_0 - B(x_0 - ct_0)| \leq M$, there is $C_M < \infty$, such that

$$\int_{\mathbb{R}} n(t_0, x_0, y')dy' \leq C_M n(t_0, x_0, y_0) + \frac{3C}{\mu} e^{-\mu M}. \tag{107}$$

Next, for $R > 0$, proceeding as in the proof of Theorem 4.2 — that is multiplying $\tilde{\Gamma}_{u,R}(Y) := \Gamma^{1D}_{u,R}(\sqrt{1 + B^2}\, Y)$, which solves an analogous of (69), by $\cos\left(\frac{x}{R}\frac{\pi}{2}\right)$— one can construct $\Gamma_{u,R}(X, Y)$ which solves an analogous of (70), namely

$$\begin{cases} -\partial_{XX}\Gamma_{u,R} - \partial_{YY}\Gamma_{u,R} - \bar{r}_u\left(\sqrt{1 + B^2}\, Y\right)\Gamma_{u,R} = \lambda_{u,R}\Gamma_{u,R} & \text{in } (-R, R)^2 \\ \Gamma_{u,R} = 0 \quad \text{on } \partial((-R, R)^2) \\ \Gamma_{u,R} > 0 \quad \text{on } (-R, R)^2, \quad \Gamma_{u,R}(0, 0) = 1, \end{cases} \tag{108}$$

where $\lambda_{u,R} \to \lambda_{u,\infty}$ as $R \to \infty$.

For some $R > 0$ and β to be chosen later, the function

$$\varphi(t, x, y) := \beta e^{-\frac{Bc}{2\sqrt{1+B^2}}\left(\frac{Bx - y}{\sqrt{1+B^2}} - \frac{Bc}{\sqrt{1+B^2}}t\right)} \Gamma_{u,R}\left(x - \frac{B^2 ct}{1 + B^2}, y + \frac{Bct}{1 + B^2}\right)$$

satisfies $\varphi(t, \cdot, \cdot) = 0$ on $\partial\left(\left(\frac{B^2 ct}{1+B^2}, -\frac{Bct}{1+B^2}\right) + (-R, R)^2\right)$, and for $(x, y) \in \left(\left(\frac{B^2 ct}{1+B^2}, -\frac{Bct}{1+B^2}\right) + (-R, R)^2\right)$, some straightforward computations yield

$$\begin{aligned} &\partial_t\varphi(t, x, y) - \Delta\varphi(t, x, y) - r_u\left(x - \frac{B^2 ct}{1 + B^2}, y + \frac{Bct}{1 + B^2}\right)\varphi(t, x, y) \\ &= \left(\frac{B^2 c^2}{4(1 + B^2)} + \lambda_{u,R}\right)\varphi(t, x, y) \\ &= \left(\lambda_{u,R} - \lambda_{u,\infty} + \frac{B^2(c^2 - (c_u^{**})^2)}{4(1 + B^2)}\right)\varphi(t, x, y) \\ &\leq \frac{B^2(c^2 - (c_u^{**})^2)}{8(1 + B^2)}\varphi(t, x, y), \end{aligned} \tag{109}$$

if we fix $R > 1$ large enough since $c^2 - (c_u^{**})^2 < 0$ and $\lambda_{u,R} \to \lambda_{u,\infty}$ as $R \to \infty$. Now, observe that $r_u\left(x - \frac{B^2 ct}{1+B^2}, y + \frac{Bct}{1+B^2}\right) = r_u(x - ct, y)$; also there is $T > 0$ sufficiently large so that, for all $t \geq T$ and all $(x, y) \in \left(\left(\frac{B^2 ct}{1+B^2}, -\frac{Bct}{1+B^2}\right) + (-R, R)^2\right)$, $x - ct \leq 0$ so that $r_u(x - ct, y) = r(x - ct, y)$. As a result (109) is recast as

$$\partial_t\varphi(t, x, y) - \Delta\varphi(t, x, y) - r\,(x - ct, y)\,\varphi(t, x, y) \leq \frac{B^2(c^2 - (c_u^{**})^2)}{8(1 + B^2)}\varphi(t, x, y), \tag{110}$$

for all $t \geq T$, all $(x, y) \in \left(\left(\frac{B^2 ct}{1+B^2}, -\frac{Bct}{1+B^2}\right) + (-R, R)^2\right)$.

We can assume that $\beta > 0$ is small enough so that $\varphi(T,\cdot,\cdot) < n(T,\cdot,\cdot)$. Assume by contradiction that the set $\{t \geq T : \exists(x,y),\, n(t,x,y) = \varphi(t,x,y)\}$ is non empty, and define

$$t_0 := \min\{t \geq T : \exists(x,y),\, n(t,x,y) = \varphi(t,x,y)\} \in (T,\infty).$$

Hence, $\varphi - u$ has a zero maximum value at some point (t_0,x_0,y_0). This implies that

$$\left[\partial_t(\varphi - n) - \Delta(\varphi - u) - r(x_0 - ct_0, y_0)(\varphi - u)\right](t_0,x_0,y_0) \geq 0.$$

Combining (110) with (107), we get

$$0 \leq \frac{B^2(c^2 - (c_u^{**})^2)}{8(1+B^2)} + C_M\varphi(t_0,x_0,y_0) + \frac{2C}{\mu}e^{-\mu M}.$$

Selecting successively $M > 2$ large enough and $\beta > 0$ small enough, we get $0 \leq c^2 - (c_u^{**})^2$, that is a contradiction. As a result, we have

$$n(t,x,y) \geq \beta e^{-\frac{Bc}{2\sqrt{1+B^2}}\left(\frac{Bx-y}{\sqrt{1+B^2}} - \frac{Bc}{\sqrt{1+B^2}}t\right)}\Gamma_{u,R}\left(x - \frac{B^2ct}{1+B^2}, y + \frac{Bct}{1+B^2}\right), \tag{111}$$

for all $t \geq T$, all $(x,y) \in \left(\left(\frac{B^2ct}{1+B^2}, -\frac{Bct}{1+B^2}\right) + (-R,R)^2\right)$. Now, for a given $-1 \leq x_0 \leq 1$, the above yields

$$\begin{aligned}\int_{\mathbb{R}} n\left(t, x_0 + \frac{B^2ct}{1+B^2}, y\right)dy \quad &\geq \quad \beta e^{-\frac{B^2cx_0}{2(1+B^2)}}\int_{\mathbb{R}} e^{\frac{Bc}{2(1+B^2)}\left(y+\frac{Bct}{1+B^2}\right)}\Gamma_{u,R}\left(x_0, y + \frac{Bct}{1+B^2}\right)dy \\ &\geq \quad \beta e^{-\frac{B^2c}{2(1+B^2)}}\min_{-1\leq x\leq 1}\int_{\mathbb{R}} e^{\frac{Bc}{2(1+B^2)}z}\Gamma_{u,R}(x,z)\,dz,\end{aligned}$$

which concludes the proof of (91). □

Proof of (*iv*). Let $R > 0$ to be chosen later. Since $c < c_u^{**}$, we can follow the above proof of (91) and get (111), which in turn provides a small enough $\eta > 0$ such that, for all $t \geq T$, all $\max(|x|,|y|) \leq R$,

$$n\left(t, x + \frac{B^2ct}{1+B^2}, y - \frac{Bct}{1+B^2}\right) \geq \eta. \tag{112}$$

Also, since $c < c^*$, we can follow the proof of (89) (see also Theorem 3.4) and get, up to reducing $\eta > 0$, that for all $t \geq T$, all $\max(|x|,|y|) \leq R$,

$$n(t, x + ct, y) \geq \eta. \tag{113}$$

For $R > 0$, $\tilde{\Gamma}_{u,R}(Y) := \Gamma_{u,R}^{1D}(\sqrt{1+B^2}\,Y)$ solves

$$\begin{cases} -\partial_{YY}\tilde{\Gamma}_{u,R} - \bar{r}_u\left(\sqrt{1+B^2}\,Y\right)\tilde{\Gamma}_{u,R} = \tilde{\lambda}_{u,R}\tilde{\Gamma}_{u,R} & \text{in } (-R,R) \\ \tilde{\Gamma}_{u,R} = 0 \quad \text{on } \partial((-R,R)) \\ \tilde{\Gamma}_{u,R} > 0 \quad \text{on } (-R,R), \quad \tilde{\Gamma}_{u,R}(0) = 1, \end{cases} \tag{114}$$

with $\tilde{\lambda}_{u,R} \to \lambda_{u,\infty}$ as $R \to \infty$.

Define

$$\begin{aligned}\bar{n}(t,x,y) : \quad &= \quad \beta e^{-\frac{\omega_Y^+}{2}\left(\frac{-Bx+y}{\sqrt{1+B^2}} - \omega_Y^+ t\right)}\tilde{\Gamma}_{u,R}\left(\frac{-Bx+y}{\sqrt{1+B^2}} - \omega_Y^+ t\right) \\ &= \quad \beta e^{-\frac{\omega_Y^+}{2}\left(\frac{y-B(x-ct)}{\sqrt{1+B^2}}\right)}\tilde{\Gamma}_{u,R}\left(\frac{y-B(x-ct)}{\sqrt{1+B^2}}\right),\end{aligned}$$

with $\beta > 0$ to be chosen later. We aim at applying the comparison principle on the domain $D := \{(t,x,y) : t \geq T, \frac{B^2ct}{1+B^2} \leq x \leq ct, |y - B(x-ct)| \leq R\}$.

We have

$$\begin{aligned}\partial_t \bar n(t,x,y) - \Delta \bar n(t,x,y) - \bar r_u(y-B(x-ct))\bar n(t,x,y) &= \left(\frac{\omega_Y^{+2}}{4} + \tilde\lambda_{u,R}\right)\bar n(t,x,y)\\ &= \left(\frac{B^2(c^2-c_u^{**2})}{1+B^2} + \tilde\lambda_{u,R} - \lambda_{u,\infty}\right)\bar n(t,x,y)\\ &\le \frac{B^2(c^2-c_u^{**2})}{1+B^2}\bar n(t,x,y),\end{aligned}$$

provided $R>0$ is large enough.

Concerning the boundary of D, if $|y-B(x-ct)|=R$ then $\bar n(t,x,y)=0\le n(t,x,y)$. If $x=ct$ then

$$\bar n(t,ct,y) \le \beta e^{\frac{\omega_Y^+}{2}\frac{R}{\sqrt{1+B^2}}}\|\tilde\Gamma_{u,R}\|_\infty \le \eta \le n(t,ct,y),$$

provided $\beta>0$ is small enough. If $x=\frac{B^2ct}{1+B^2}$, then

$$\bar n\left(t,\frac{B^2ct}{1+B^2},y\right) \le \beta e^{\frac{\omega_Y^+}{2}\frac{R}{\sqrt{1+B^2}}}\|\tilde\Gamma_{u,R}\|_\infty \le \eta \le n\left(t,\frac{B^2ct}{1+B^2},y\right),$$

provided $\beta>0$ is small enough. If $t=T$, $n(T,x,y)>0$, an we then have $\bar n(T,x,y)\le n(T,x,y)$ for all $\frac{B^2cT}{1+B^2}\le x\le cT$, $|y-B(x-cT)|\le R$, provided $\beta>0$ is small enough.

By using again (details are omitted) Theorem 2.7, as done in subsection 4.1 and in the proof of (*iii*) above, we deduce that

$$n(t,x,y)\ge \bar n(t,x,y) = \beta e^{-\frac{\omega_Y^+}{2}\left(\frac{y-B(x-ct)}{\sqrt{1+B^2}}\right)}\tilde\Gamma_{u,R}\left(\frac{y-B(x-ct)}{\sqrt{1+B^2}}\right),$$

for all (t,x,y) such that $t\ge T$, $\frac{B^2ct}{1+B^2}\le x\le ct$, $|y-B(x-ct)|\le R$. This is enough to prove (93). □

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