The influence of space dimension on the large-time behavior in a reaction-diffusion system modeling diallelic selection

Philippe Souplet
Université Paris 13, CNRS UMR 7539, Laboratoire Analyse Géométrie et Applications,
93430 Villetaneuse, France. Email: souplet@math.univ-paris13.fr

Michael Winkler
Fakultät für Mathematik, Universität Duisburg-Essen,
45117 Essen, Germany. Email: michael.winkler@math.uni-due.de

Abstract

We study a mathematical model from population genetics, describing a single-locus diallelic (A/a) selection-migration process. The model consists of a coupled system of three reaction-diffusion equations, one for the density of each genotype, posed in the whole space $\mathbb{R}^n$. The genotype AA is advantageous, due to a smaller death rate, and we consider the fully recessive case where the other two genotypes aa and Aa have the same (higher) death rate. In the nondiffusive (spatially homogeneous) case, the disadvantageous gene a is always eliminated in the large time limit. In the presence of diffusion, when the birth rate exceeds a certain threshold value, we prove that this conclusion is still true for dimensions $n \leq 2$, whereas for $n \geq 3$ there exist initial distributions for which the advantageous gene A ultimately disappears. This is the first rigorous result of this type for the full system, and it solves a problem which seems to have been open since the celebrated work of Aronson and Weinberger (1975, 1977), where similar results had been obtained for a simplified scalar model, that they derived as an approximation of the full system. Interestingly, we moreover show that, at the threshold value of the birth rate, the cut-off dimension shifts from $n = 2$ to $n = 6$.

Key words: population genetics, reaction-diffusion system, selection, extinction, Fisher approximation
AMS Classification: 92D15, 92D25 (primary), 35B40, 35K40 (secondary)

Introduction

0.1 The model

We are concerned with the following mathematical model from population genetics, describing a single-locus diallelic selection-migration process. Consider a population of diploid individuals. We assume that a specific gene exists in two allelic forms denoted by a and A. The densities of individuals with genotypes aa, aA and AA are respectively denoted by ρ_1, ρ_2 and ρ_3, which are functions of x and t (here Aa is identified with aA).

Within the population, we suppose that mating occurs at random, with a birth-rate denoted by r, independent of the genotype, and that diffusion takes place with unit diffusion coefficient. We further assume that the death rate depends only on the genotype with respect to the alleles a and A, and denote the corresponding death rates by τ_1, τ_2, τ_3, respectively. These death rates may differ, so that some genotypes are more viable than others. We here assume that the habitat is the whole Euclidean space $\mathbb{R}^n$. The triple (ρ_1, ρ_2, ρ_3) then satisfies the following reaction-diffusion system:

$$\begin{cases} \partial_t \rho_1 = \Delta \rho_1 - \tau_1 \rho_1 + \dfrac{r}{\hat{\rho}} \Big(\rho_1 + \dfrac{1}{2}\rho_2\Big)^2, & x \in \mathbb{R}^n,\ t > 0, \\ \partial_t \rho_2 = \Delta \rho_2 - \tau_2 \rho_2 + \dfrac{2r}{\hat{\rho}} \Big(\rho_1 + \dfrac{1}{2}\rho_2\Big)\Big(\rho_3 + \dfrac{1}{2}\rho_2\Big), & x \in \mathbb{R}^n,\ t > 0, \\ \partial_t \rho_3 = \Delta \rho_3 - \tau_3 \rho_3 + \dfrac{r}{\hat{\rho}} \Big(\rho_3 + \dfrac{1}{2}\rho_2\Big)^2, & x \in \mathbb{R}^n,\ t > 0, \end{cases} \tag{0.1}$$

where $\hat{\rho} = \rho_1 + \rho_2 + \rho_3$ is the total density of individuals at (x, t). Throughout this article, we assume that $r, \tau_1, \tau_2, \tau_3$ are positive constants. The ODE version of this model seems to have been first introduced by Kostitzin in 1937 [9]. The diffusive model (0.1) has been studied in [1]. In [4], [11], [12], [16], [18], some variants of the model have been considered, where r and τ_i are no longer constant but may depend on x, or even on t and ρ_i, the domain is bounded, and no-flux boundary conditions are imposed. Moreover, r may be replaced by separate functions r_1, r_2, r_3, thus reflecting possible variable fitness according to the genotype. See Remark 0.2 for more details and brief comments on the results obtained in those works. There are various approaches and a large literature on diffusive models of migration-selection processes; we refer for instance to [14], [10] for a discussion of this topic.

From the point of view of applications, it is of interest to investigate the asymptotic behavior of solutions. In particular an important question is to determine under which conditions one can assert that some of the genotypes are outperformed by the others in that their relative frequencies ρ_i/ρ approach 0 as $t \to \infty$. However this question seems difficult to study in general and, in previous work, attempts have been made to reduce the question to the study of a simpler scalar equation, namely the equation of Fisher-KPP (cf. [5, 8]) type:

$$u_t = \Delta u + f(u), \qquad x \in \mathbb{R}^n,\ t > 0, \tag{0.2}$$

where

$$f(u) = u(1-u)\Big[(\tau_1 - \tau_2)(1-u) + (\tau_2 - \tau_3)u\Big]. \tag{0.3}$$

In particular it was shown in [1] (see also [4]) that under certain assumptions, the ratio $z := (\rho_3 + \frac{1}{2}\rho_2)/\hat{\rho}$, which measures the frequency of the allele A, can be expected to be close to the solution of equation (0.2) with initial data $z(\cdot, 0)$. More precisely, if $\varepsilon := |\tau_1 - \tau_2| + |\tau_1 - \tau_3|$ is small – in other words if the selection is weak, if r is large and if $\hat{\rho}_x/\hat{\rho}$ is suitably small initially, then $|z - u|$ remains small up to times of order less than ε^{-1} (see Remark 0.2(a) for more details).

To go further, we shall now concentrate on the case

$$\tau_1 = \tau_2 > \tau_3. \tag{0.4}$$

which we assume throughout the rest of the paper. Note that, in biological terms, this means that the advantageous gene A is fully recessive, i.e., heterozygote individuals aA do not have any improved viability. In this case the function f becomes

$$f(u) = (\tau_1 - \tau_3)u^2(1-u)$$

and, interestingly, it was proved in [2] that the large time behavior for the scalar equation (0.2) crucially depends on the space dimension. Namely, for $n \leq 2$ any nontrivial solution converges to 1 locally uniformly (as do the solutions of the corresponding ODE), whereas for $n \geq 3$ the solution converges to 0 for suitably small initial data. In terms of the model, this means that the disadvantageous gene a always ultimately disappears for $n \leq 2$, but that the advantageous gene A can disappear for suitable initial data if $n \geq 3$. Note that such a dimensional effect is absent if τ_2 is different from τ_1 and τ_3, due to the fact that f then behaves linearly near $u = 0$ and $u = 1$ (cf. [2]).
It is then a very natural question whether similar phenomena also occur in the original model. Notice that, even in the case of weak selection, this cannot be easily deduced from the results in [1] (since the closeness of u and z is only shown on –large but– finite time intervals) and, as far as we know, this has remained an open question so far.

0.2 Main results

For convenience, we perform the following changes of dependent variables:

$$u = e^{(\tau_1 - r)t}\rho_1, \quad v = e^{(\tau_1 - r)t}\rho_2, \quad w = e^{(\tau_1 - r)t}\rho_3, \tag{0.5}$$

We also denote

$$\rho := u + v + w$$

and

$$\beta := \tau_1 - \tau_3 > 0. \tag{0.6}$$

Because of (0.4), the system (0.1) becomes

$$\begin{cases} u_t = \Delta u - ru + \dfrac{r}{\rho}\Big(u + \dfrac{1}{2}v\Big)^2, & x \in \mathbb{R}^n,\ t > 0, \\ v_t = \Delta v - rv + \dfrac{2r}{\rho}\Big(u + \dfrac{1}{2}v\Big)\Big(w + \dfrac{1}{2}v\Big), & x \in \mathbb{R}^n,\ t > 0, \\ w_t = \Delta w + (\beta - r)w + \dfrac{r}{\rho}\Big(w + \dfrac{1}{2}v\Big)^2, & x \in \mathbb{R}^n,\ t > 0. \end{cases} \tag{0.7}$$

System (0.7) is supplemented with the initial conditions

$$u(x,0) = u_0(x), \quad v(x,0) = v_0(x), \quad w(x,0) = w_0(x), \qquad x \in \mathbb{R}^n, \tag{0.8}$$

with given functions

$$u_0, v_0, w_0 \in C(\mathbb{R}^n) \cap L^\infty(\mathbb{R}^n), \quad u_0, v_0, w_0 \geq 0. \tag{0.9}$$

It is easy to show that (0.7)-(0.8) possesses a unique global classical, nonnegative solution, which will be denoted by (u, v, w) in the sequel. In particular, the global existence is clear due to the fact that the nonlinearities are bounded by linear functions of (u, v, w). Our focus lies on the large time behavior of the genotype frequencies. We shall thus consider the fractions

$$\tilde{u} := \frac{u}{\rho}, \quad \tilde{v} := \frac{v}{\rho} \quad \text{and} \quad \tilde{w} := \frac{w}{\rho}. \tag{0.10}$$

Note that, in view of (0.5), these fractions coincide with those associated with the original system (0.1). Our main results are the following.

Theorem 0.1 *Let $r > 0$, $\beta = \tau_1 - \tau_3 > 0$ and suppose (0.9), with $v_0 + w_0 \not\equiv 0$.*
(i) If $n \leq 2$, then we have

$$\begin{aligned} &\tilde{u}(x,t) \to 0, \quad \tilde{v}(x,t) \to 0 \quad \textit{and} \quad \tilde{w}(x,t) \to 1 \\ &\qquad\qquad \textit{as } t \to \infty, \textit{ uniformly on compact subsets of } \mathbb{R}^n. \end{aligned} \tag{0.11}$$

(ii) If $3 \leq n \leq 6$, then (0.11) remains true under the additional assumption that $\beta \geq r$.
(iii) If $n \geq 7$, then (0.11) remains true under the additional assumption that $\beta > r$.

The optimality of our assumptions on n is shown by the next theorem.

Theorem 0.2 *Let $r > 0$, $\beta = \tau_1 - \tau_3 > 0$ and assume (0.9). Let $\gamma \geq 0$, $c_0, \kappa > 0$ and suppose that*

$$u_0(x) \geq c_0(1 + |x|)^{-\gamma} \qquad \textit{for all } x \in \mathbb{R}^n, \tag{0.12}$$

and that

$$v_0(x) + w_0(x) \leq \delta\, e^{-\kappa|x|^2} \qquad \textit{for all } x \in \mathbb{R}^n, \tag{0.13}$$

where $\delta = \delta(n, r, \beta, \gamma, c_0, \kappa) > 0$ is sufficiently small.
(i) If

$$n \geq 3, \quad \beta < r, \quad \gamma < n - 2,$$

then there exists $c > 0$ such that

$$\tilde{v}(x,t) \leq c(t+1)^{-1} \qquad \textit{for all } x \in \mathbb{R}^n \textit{ and } t \geq 0 \tag{0.14}$$

and

$$\tilde{w}(x,t) \leq c(t+1)^{-2} \qquad \textit{for all } x \in \mathbb{R}^n \textit{ and } t \geq 0. \tag{0.15}$$

In particular, we have

$$\begin{aligned} &\tilde{u}(x,t) \to 1, \quad \tilde{v}(x,t) \to 0 \quad \textit{and} \quad \tilde{w}(x,t) \to 0 \\ &\qquad\qquad \textit{as } t \to \infty, \textit{ uniformly with respect to } x \in \mathbb{R}^n. \end{aligned} \tag{0.16}$$

(ii) If

$$n \geq 7, \quad \beta = r, \quad \gamma < n - 6,$$

then one can find $c > 0$ *such that*

$$\tilde{v}(x,t) \leq c(t+1)^{-2} \qquad \textit{for all } x \in \mathbb{R}^n \textit{ and } t \geq 0$$

and

$$\tilde{w}(x,t) \leq c(t+1)^{-3} \qquad \textit{for all } x \in \mathbb{R}^n \textit{ and } t \geq 0.$$

In particular, we have (0.16).

Theorems 0.1 and 0.2 confirm the observation made in [2] about the key role played by the space dimension. Recall that the Fisher approximation in [1] required $\tau_1 \approx \tau_2 \approx \tau_3$ and r large. Interestingly, for $\tau_1 = \tau_2 > \tau_3$, we here find that the dimension threshold is the same as for the Fisher equation (0.2) whenever $r > \beta = \tau_1 - \tau_3 > 0$, but that it becomes different for $r = \beta$ and then disappears when $r < \beta$. Such phenomena are clearly diffusion effects, and moreover rely on the fact that the physical domain is the entire space $\mathbb{R}^n$. Indeed we note that in the case when (0.7) is posed in a bounded domain $\Omega \subset \mathbb{R}^n$ with no-flux boundary conditions, for any positive r and β, all solutions with $v(0) + w(0) \not\equiv 0$ satisfy the analogue of (0.11). This fact may be already known, but since we are not aware of a precise reference in the literature, for the reader's convenience we include a proof in the appendix (see Proposition 4.1 below. We thank the anonymous referee for suggesting a simplification of our original proof). Of course, the latter also covers the non-diffusive or spatially homogeneous case, i.e. the ODE system corresponding to (0.7).

Remark 0.1 (a) For r, β, n as in Theorem 0.2, (0.11) also occurs for *some* initial data. This is for instance the case for spatially homogeneous initial distributions.

(b) It is easy to check that the conclusion of Theorem 0.2 remains true if r in the third equation of (0.1) is replaced with any number $\tilde{r} > 0$. (Note that under this modification, in the third equation of (0.7), the factor r in front of the quadratic term becomes $\tilde{r}$.) As for Theorem 0.1, its proof can be adapted to cover any positive $\tilde{r} > r - \beta$. This is equivalent to $r - \tau_3 > r - \tau_1$, which is the natural definition of the statement that the AA homozygote is fitter than the other genotypes. There is strong evidence that this should remain true for any $\tilde{r} > 0$, but presently we do not have a complete proof of this fact (see Remark 2.1 below).

0.3 Strategy of proof and discussion

For proving our results, it will be useful to further transform the system. Namely, we set

$$\varphi = u + \frac{1}{2}v, \quad \psi := w + \frac{1}{2}v, \tag{0.17}$$

which measure the respective densities of the alleles a and A. The triple (φ, ψ, w) then satisfies the new system

$$\varphi_t = \Delta\varphi, \qquad x \in \mathbb{R}^n,\ t > 0, \tag{0.18}$$

$$\psi_t = \Delta\psi + \beta w, \qquad x \in \mathbb{R}^n,\ t > 0, \tag{0.19}$$

$$w_t = \Delta w + (\beta - r)w + r \cdot \frac{\psi^2}{\varphi + \psi}, \qquad x \in \mathbb{R}^n,\ t > 0. \tag{0.20}$$

Incidentally we note that the function $\rho = u + v + w$ satisfies the same equation as ψ and could be used instead of ψ. Observe that whereas the original system (0.1) is neither cooperative nor competitive, the reduced system

$$\mathcal{P}(\psi, w) := \psi_t - \Delta\psi - \beta w = 0, \quad x \in \mathbb{R}^n,\ t > 0, \tag{0.21}$$

$$\mathcal{Q}_\varphi(\psi, w) := w_t - \Delta w - (\beta - r)w - r \cdot \frac{\psi^2}{\varphi(x,t) + \psi} = 0, \quad x \in \mathbb{R}^n,\ t > 0, \tag{0.22}$$

is cooperative when regarded as a system determining ψ and w with $\varphi = \varphi(x,t) \geq 0$ a given parameter function. Indeed,

$$\frac{d}{d\psi}\Big[r\frac{\psi^2}{\varphi(x,t) + \psi}\Big] = r\Big[1 - \frac{\varphi^2}{(\varphi + \psi)^2}\Big] \geq 0.$$

This fact will be useful for our analysis. Our proofs are based on a suitable combination of various PDE techniques: comparison arguments based on the maximum principle, semigroup techniques (variation-of-constant formula and heat kernel estimates), differential inequalities, test-function and monotonicity arguments. Several parts of the proofs are inspired by ideas in e.g. [1], [17], [3], [15]. We prefer to give the, relatively simpler, proof of Theorem 0.2, before turning to that of Theorem 0.1, which is more delicate.

Remark 0.2 (a) A different approach to the model (0.1) is to consider the equations satisfied by the genotype frequencies $f_i = \rho_i/\hat{\rho}$ (which coincide with $(\tilde{u}, \tilde{v}, \tilde{w})$). In the spatially homogeneous case with equal viabilities ($\tau_i = \tau$), simple computations show that the frequencies satisfy the ODE system

$$\begin{cases} f_1' = r\Big[\Big(f_1 + \frac{1}{2}f_2\Big)^2 - f_1\Big], & t > 0, \\ f_2' = r\Big[2\Big(f_1 + \frac{1}{2}f_2\Big)\Big(f_3 + \frac{1}{2}f_2\Big) - f_2\Big], & t > 0, \\ f_3' = r\Big[\Big(f_3 + \frac{1}{2}f_2\Big)^2 - f_3\Big], & t > 0 \end{cases}$$

and it is fairly easy to see that all equilibria are given by the curve $(f_2)^2 = 4f_1f_3$, subject to $f_1 + f_2 + f_3 = 1$. This curve is well known as the Hardy-Weinberg equilibrium [7]. Such a simple solution is no longer available in the diffusive case with nonequal viabilities. Still,

in the work [1] (see also [4], [12]), the system is transformed by considering the frequency of the gene A as one of the new unknowns. Namely, setting

$$z = f_3 + \frac{1}{2} f_2, \quad \sigma = (f_2)^2 - 4 f_1 f_3, \quad \mu = \hat{\rho}_x / \hat{\rho},$$

it is shown that (z, σ, μ) solves the new system

$$\begin{cases} z_t - z_{xx} - f(z) = 2\mu z_x + \dfrac{1}{4}\Big[(\tau_2 - \tau_1)z - (\tau_2 - \tau_3)(1-z)\Big]\sigma, & x \in \mathbb{R}^n,\ t > 0, \\ \sigma_t - \sigma_{xx} = 2\mu\sigma_x - \Big[r - (\tau_1 - \tau_3)(1-2z) + \dfrac{\tau^*}{4}\sigma\Big]\sigma \\ \qquad\qquad + 4\tau^* z^2 (1-z)^2 - 8(z_x)^2, & x \in \mathbb{R}^n,\ t > 0, \\ \mu_t - \mu_{xx} = \dfrac{\partial}{\partial x}\Big[\mu^2 + \dfrac{\tau^*}{4}\sigma + (\tau_2 - \tau_3)z^2 + (\tau_2 - \tau_1)(1-z)^2\Big], & x \in \mathbb{R}^n,\ t > 0 \end{cases} \tag{0.23}$$

where f is defined by (0.3), $\tau^* = \tau_1 - 2\tau_2 + \tau_3$, and $n = 1$ is taken for simplicity. Here the quantities σ, μ respectively measure the deviation from the Hardy-Weinberg equilibrium and the spatial inhomogeneity. The Fisher approximation in the weak selection limit (cf. after (0.2)) is obtained by a suitable asymptotic analysis of system (0.23).

(b) In [16], [18], system (0.1) with spatially inhomogeneous coefficients $\tau_i = \tau_i(x)$ and $r_i = r_i(x)$ (instead of r) are studied in bounded domains, in the context of the mathematical modeling of optimal transgenic maize crop management. There the large time behavior is investigated by numerical simulations. Their results suggest that the Fisher approximation may not be relevant in general situations.

(c) In [12], system (0.1) is studied with r and the τ_i being nonlinear functions of the total density $\hat{\rho}$. Some results on the stability of the steady states (on bounded domains with no-flux boundary conditions) are obtained by means of invariant region techniques.

1 Extinction of the advantageous gene A for suitable initial data in high dimensions

As a first step, we shall use the following, more or less known, property of the linear heat equation (0.18), which guarantees that a sufficiently slow spatial decay of $\varphi_0 := \varphi(\cdot, 0)$ implies a corresponding lower bound on the space-time decay of φ.

Lemma 1.1 *Suppose that there exist $\gamma \geq 0$ and $c_0 > 0$ such that*

$$\varphi_0(x) \geq c_0 (1 + |x|)^{-\gamma} \qquad \text{for all } x \in \mathbb{R}^n. \tag{1.1}$$

Then for all $\lambda > 0$, the inequality

$$\varphi(x,t) \geq c_\lambda (t + \lambda + |x|^2)^{-\frac{\gamma}{2}} \qquad \text{for all } x \in \mathbb{R}^n \text{ and } t \geq 0 \tag{1.2}$$

is valid with $c_\lambda := c_0 \cdot (\frac{\lambda}{2n\lambda + 1})^{\frac{\gamma}{2}} > 0$.

PROOF. We let

$$\underline{\varphi}(x,t) := a \cdot \Big(2n(t+\lambda) + |x|^2\Big)^{-\frac{\gamma}{2}}, \qquad x \in \mathbb{R}^n,\ t \geq 0,$$

where $a := c_0 \cdot (\frac{2n\lambda}{2n\lambda+1})^{\frac{\gamma}{2}}$. Then by direct computation,

$$\underline{\varphi}_t = -n\gamma a \cdot \Big(2n(t+\lambda) + |x|^2\Big)^{-\frac{\gamma}{2}-1}$$

and

$$\Delta\underline{\varphi} = -n\gamma a \cdot \Big(2n(t+\lambda) + |x|^2\Big)^{-\frac{\gamma}{2}-1} + \gamma(\gamma+2)a \cdot \Big(2n(t+\lambda) + |x|^2\Big)^{-\frac{\gamma}{2}-2} \cdot |x|^2,$$

so that

$$\underline{\varphi}_t - \Delta\underline{\varphi} = -\gamma(\gamma+2)a \cdot \Big(2n(t+\lambda) + |x|^2\Big)^{-\frac{\gamma}{2}-2} \cdot |x|^2 \leq 0 \qquad \text{in } \mathbb{R}^n \times (0,\infty).$$

In view of a scalar parabolic comparison argument, we thus obtain

$$\varphi(x,t) \geq \underline{\varphi}(x,t) \geq a \cdot (2n)^{-\frac{\gamma}{2}} \cdot \Big(t + \lambda + |x|^2\Big)^{-\frac{\gamma}{2}} = c_\lambda \cdot \Big(t + \lambda + |x|^2\Big)^{-\frac{\gamma}{2}}$$

for all $x \in \mathbb{R}^n$ and $t \geq 0$, provided that $\varphi_0 \geq \underline{\varphi}(\cdot,0)$ in $\mathbb{R}^n$. For the latter, however, according to (1.1) it is sufficient that

$$h(s) := \frac{c_0(1+s)^{-\gamma}}{a(2n\lambda + s^2)^{-\frac{\gamma}{2}}}, \qquad s \geq 0,$$

satisfies $h(s) \geq 1$ for all $s \geq 0$. Now a straightforward calculation shows that h attains its minimal value at $s = 2n\lambda$ with

$$h(2n\lambda) = \frac{c_0}{a} \cdot \frac{(1+2n\lambda)^{-\gamma}}{(2n\lambda + (2n\lambda)^2)^{-\frac{\gamma}{2}}} = \frac{c_0}{a} \cdot \Big(\frac{2n\lambda}{2n\lambda+1}\Big)^{\frac{\gamma}{2}} = 1$$

due to our choice of a. □

The next lemma plays a key role in the proof of Theorem 0.2. Under the hypothesis that both v_0 and w_0 are dominated by a small Gaussian, it provides a quantitative upper estimate for v and w. The proof combines the above information on ρ with a comparison argument applied to (0.21)-(0.22).
For convenience in notation, let us introduce the heat kernel

$$G_\sigma(x) := (4\pi\sigma)^{-\frac{n}{2}}\, e^{-\frac{|x|^2}{4\sigma}}, \qquad x \in \mathbb{R}^n,\ \sigma > 0, \tag{1.3}$$

which will be frequently used throughout the sequel.

Lemma 1.2 *(i) Assume $r > \beta > 0$, $n \geq 3$ and let u_0 satisfy*

$$u_0(x) \geq c_0(1+|x|)^{-\gamma} \qquad \text{for all } x \in \mathbb{R}^n \tag{1.4}$$

for some $c_0 > 0$ and some

$$0 \leq \gamma < n-2. \tag{1.5}$$

For all $\kappa > 0$ there exist $\delta > 0$ such that if

$$v_0(x) \leq \delta\, e^{-\kappa|x|^2} \qquad \text{and} \qquad w_0(x) \leq \delta\, e^{-\kappa|x|^2} \qquad \text{for all } x \in \mathbb{R}^n, \tag{1.6}$$

then, for suitable $c, \lambda > 0$ the solution (u, v, w) of (0.7)-(0.8) satisfies

$$v(x,t) \leq c(t+\lambda)^{-1-\frac{\gamma}{2}}\, e^{-\frac{|x|^2}{4(t+\lambda)}} \qquad \text{for all } x \in \mathbb{R}^n \text{ and } t \geq 0 \tag{1.7}$$

and

$$w(x,t) \leq c(t+\lambda)^{-2-\frac{\gamma}{2}}\, e^{-\frac{|x|^2}{4(t+\lambda)}} \qquad \text{for all } x \in \mathbb{R}^n \text{ and } t \geq 0. \tag{1.8}$$

(ii) Assume $r = \beta > 0$ and $n \geq 7$. Then assertion (i) remains valid if (1.5) is replaced with

$$0 \leq \gamma < n-6 \tag{1.9}$$

and γ in (1.7)-(1.8) is replaced with $\gamma + 2$.

Proof. Since $\varphi(\cdot, 0) \geq u_0$, from (1.4) and Lemma 1.1 we know that there exists $c_1 > 0$ such that

$$\varphi(x,t) \geq c_1\Big(t+1+|x|^2\Big)^{-\frac{\gamma}{2}} \qquad \text{for all } x \in \mathbb{R}^n \text{ and } t \geq 0. \tag{1.10}$$

We then let

$$f(t) := \eta(t+\lambda)^\alpha \qquad \text{and} \qquad g(t) := \frac{\eta\alpha}{\beta}(t+\lambda)^{\alpha-1}, \qquad t \geq 0,$$

with $\eta, \alpha > 0$, $\lambda \geq 1$ to be chosen, and define

$$\overline{\psi}(x,t) := f(t) \cdot G_{\lambda+t}(x) \qquad \text{and} \qquad \overline{w}(x,t) := g(t) \cdot G_{\lambda+t}(x), \qquad x \in \mathbb{R}^n,\ t \geq 0,$$

where G_σ is taken from (1.3). Recall that the parabolic operators $\mathcal{P}$, $\mathcal{Q}_\varphi$ are defined in (0.21)-(0.22). Using $f' = \beta g$ and $\partial_t G_{\lambda+t} = \Delta G_{\lambda+t}$, we find that

$$\mathcal{P}(\overline{\psi}, \overline{w}) = f'(t)G_{\lambda+t} - \beta g(t) G_{\lambda+t} = 0 \qquad \text{in } \mathbb{R}^n \times (0,\infty). \tag{1.11}$$

By (1.10) and the fact that $\lambda \geq 1$, we have

$$\begin{aligned} \mathcal{Q}_\varphi(\overline{\psi}, \overline{w}) &\geq \overline{w}_t - \Delta\overline{w} + (r-\beta)\overline{w} - \frac{r}{c_1}\Big(t+\lambda+|x|^2\Big)^{\frac{\gamma}{2}}\overline{\psi}^2 \\ &= g'(t)G_{\lambda+t} + (r-\beta)g(t)G_{\lambda+t} - \frac{r}{c_1}\Big(t+\lambda+|x|^2\Big)^{\frac{\gamma}{2}} f^2(t) G_{\lambda+t}^2 \end{aligned}$$

$$
\begin{aligned}
&= g(t)G_{\lambda+t}\cdot\left\{\frac{g'(t)}{g(t)}+r-\beta-\frac{r}{c_1}\Big(t+\lambda+|x|^2\Big)^{\frac{\gamma}{2}}\cdot\frac{f^2(t)}{g(t)}G_{\lambda+t}\right\}\\
&= g(t)G_{\lambda+t}\cdot\left\{\frac{\alpha-1}{t+\lambda}+r-\beta\right.\\
&\qquad\left.-\frac{r}{c_1}\Big(t+\lambda+|x|^2\Big)^{\frac{\gamma}{2}}\cdot\frac{\eta\beta}{\alpha}\cdot(t+\lambda)^{\alpha+1}\cdot(4\pi)^{-\frac{n}{2}}(t+\lambda)^{-\frac{n}{2}}\,e^{-\frac{|x|^2}{4(t+\lambda)}}\right\}\\
&= g(t)G_{\lambda+t}\cdot\left\{\frac{\alpha-1}{t+\lambda}+r-\beta\right.\\
&\qquad\left.-\frac{r\eta\beta}{(4\pi)^{\frac{n}{2}}\alpha c_1}\cdot(t+\lambda)^{\alpha+1+\frac{\gamma-n}{2}}\cdot\Big(1+\frac{|x|^2}{t+\lambda}\Big)^{\frac{\gamma}{2}}\,e^{-\frac{|x|^2}{4(t+\lambda)}}\right\}\\
&\geq g(t)G_{\lambda+t}\cdot\left\{\frac{\alpha-1}{t+\lambda}+r-\beta-\frac{r\eta\beta c_2}{(4\pi)^{\frac{n}{2}}\alpha c_1}\cdot(t+\lambda)^{\alpha+1+\frac{\gamma-n}{2}}\right\},
\end{aligned}
$$

where

$$
c_2:=\sup_{\xi\geq 0}(1+\xi)^{\frac{\gamma}{2}}e^{-\frac{\xi}{4}}<\infty. \tag{1.12}
$$

Now, if $r>\beta$, then (1.5) allows the choice

$$
\alpha=\frac{n-\gamma}{2}-1>0, \tag{1.13}
$$

hence

$$
\mathcal{Q}(\overline{\psi})\overline{w}\geq g(t)G_{\lambda+t}\cdot\left\{r-\beta-\lambda^{-1}-\frac{r\eta\beta c_2}{(4\pi)^{\frac{n}{2}}\alpha c_1}\right\}\geq 0 \tag{1.14}
$$

if we choose λ large enough and η small enough. Next, if $r=\beta$, then (1.9) allows the choice

$$
\alpha=\frac{n-\gamma}{2}-2>1, \tag{1.15}
$$

hence

$$
\mathcal{Q}(\overline{\psi})\overline{w}\geq\frac{g(t)G_{\lambda+t}}{t+\lambda}\cdot\left\{\alpha-1-\frac{r\eta\beta c_2}{(4\pi)^{\frac{n}{2}}\alpha c_1}\right\}\geq 0 \tag{1.16}
$$

if we choose η small enough. Assuming in addition $\lambda\geq\frac{1}{4\kappa}$ and δ small enough, we see that at $t=0$,

$$
\psi(x,0)=w_0(x)+\frac{1}{2}v_0(x)\leq\frac{3}{2}\delta\,e^{-\kappa|x|^2}\leq\eta\lambda^{\alpha}(4\pi\lambda)^{-\frac{n}{2}}e^{-\frac{|x|^2}{4\lambda}}=\overline{\psi}(x,0)\qquad\text{for all } x\in\mathbb{R}^n, \tag{1.17}
$$

and that similarly

$$
w(x,0)\leq\delta\,e^{-\frac{|x|^2}{4\lambda}}\leq\frac{\eta\alpha}{\beta}\lambda^{\alpha-1}(4\pi\lambda)^{-\frac{n}{2}}\,e^{-\frac{|x|^2}{4\lambda}}=\overline{w}(x,0)\qquad\text{for all } x\in\mathbb{R}^n. \tag{1.18}
$$

Since (ψ,w) solves the cooperative parabolic system (0.21)-(0.22), we may collect (1.11), (1.14), (1.16), (1.17) and (1.18), to see upon invoking a comparison principle that $\psi\leq\overline{\psi}$

and $w \le \overline{w}$ in $\mathbb{R}^n \times (0,\infty)$. In view of (1.13) and (1.15), this immediately implies (1.7) and (1.8). □

Now Theorem 0.2 actually reduces to a corollary.

Proof of Theorem 0.2. We only consider case (i), the other case being completely similar. By combining (1.2) in Lemma 1.1, (1.7) in Lemma 1.2 and (1.12), we obtain

$$\begin{aligned}\frac{v(x,t)}{\rho(x,t)} &\le c(t+\lambda)^{-1-\frac{\gamma}{2}}\, e^{-\frac{|x|^2}{4(t+\lambda)}} \cdot c_1^{-1}\Big(t+\lambda+|x|^2\Big)^{\frac{\gamma}{2}} \\ &= cc_1^{-1}(t+\lambda)^{-1}\Big(1+\frac{|x|^2}{t+\lambda}\Big)^{\frac{\gamma}{2}} e^{-\frac{|x|^2}{4(t+\lambda)}} \\ &\le cc_1^{-1}c_2(t+\lambda)^{-1} \qquad \text{for all } x\in\mathbb{R}^n \text{ and } t\ge 0,\end{aligned}$$

This yields (0.14), whereas (0.15) can be deduced from (1.8) in quite a similar manner. □

Remark 1.1 For a slightly easier, but more particular, example of extinction of the advantageous gene, one may consider the choice $u_0 \equiv c_0$ (positive constant), $v_0 \equiv 0$ and $w_0 \le \delta e^{-\kappa|x|^2}$ in Theorem 0.2. Indeed in that case $\varphi \equiv c_0$, so that Lemma 1.1 is not required, and also the computation in the proof of Lemma 1.2 becomes a bit simpler.

2 Unconditional extinction of the disadvantageous gene a in low dimensions

This section is devoted to the proof of Theorem 0.1. Let us first note that

$$0 \le \varphi = u + \frac{1}{2}v \le A_0 := \|u_0 + \frac{1}{2}v_0\|_{L^\infty(\mathbb{R}^n)}, \qquad (x,t)\in\mathbb{R}^n\times(0,\infty) \tag{2.1}$$

by the maximum principle. Therefore, in order to prove our desired statement $\frac{w}{\rho} \to 1$, it is sufficient to show that the function ψ appearing in (0.21)-(0.22) diverges appropriately as $t\to\infty$. This will be done in a series of steps. We first settle the case $r<\beta$, which is fairly easy.

2.1 Proof of Theorem 0.1 in the case $r<\beta$

Since $w_t \ge \Delta w + (\beta - r)w$, the function $e^{(r-\beta)t}w$ is a supersolution of the linear heat equation. It follows from the maximum principle that

$$w(x,t) \ge e^{(\beta-r)t}(4\pi t)^{-\frac{n}{2}} \int_{\mathbb{R}^n} e^{-\frac{|x-y|^2}{4t}} w_0(y)dy.$$

Thanks to the fact that w_0 is continuous and $w_0 \not\equiv 0$, there exist $c_1, \delta > 0$ and $x_0 \in \mathbb{R}^n$ such that $w_0 \ge c_1$ in $B(x_0,\delta)$. Therefore, for any $R>0$, there exists $c(R)>0$ such that

$$w(x,t) \ge c_1 e^{(\beta-r)t}(4\pi t)^{-\frac{n}{2}} \int_{|y-x_0|<\delta} e^{-\frac{|x-y|^2}{4t}}dy \ge c(R)e^{(\beta-r)t}(4\pi t)^{-\frac{n}{2}}, \quad |x|<R,\ t>0.$$

In particular, $w(x,t)\to\infty$ locally uniformly as $t\to\infty$. By (2.1), we know that both u and v are bounded. The result follows immediately.

2.2 Reduction to a cooperative system

By (2.1), we see that (ψ, w) satisfies

$$\begin{cases} \psi_t = \Delta\psi + \beta w, & x \in \mathbb{R}^n,\ t > 0, \\ w_t \geq \Delta w + (\beta - r)w + r \cdot \dfrac{\psi^2}{\psi + A_0}, & x \in \mathbb{R}^n,\ t > 0, \\ \psi(x,0) = w_0(x) + \dfrac{1}{2}v_0(x), \quad w(x,0) = w_0(x), & x \in \mathbb{R}^n, \end{cases} \tag{2.2}$$

(where A_0 is replaced by any positive number if $u_0 = v_0 \equiv 0$). For given $A > 0$, let us thus consider the system

$$\begin{cases} \psi_t = \Delta\psi + \beta w, & x \in \mathbb{R}^n,\ t > 0, \\ w_t = \Delta w + (\beta - r)w + r \cdot \dfrac{\psi^2}{\psi + A}, & x \in \mathbb{R}^n,\ t > 0, \\ \psi(x,0) = \psi_0(x), \quad w(x,0) = w_0(x), & x \in \mathbb{R}^n, \end{cases} \tag{2.3}$$

with given initial data

$$\psi_0, w_0 \in C(\mathbb{R}^n) \cap L^\infty(\mathbb{R}^n), \quad \psi_0, w_0 \geq 0. \tag{2.4}$$

System (2.3) has a unique globally defined nonnegative classical solution in $\mathbb{R}^n \times (0, \infty)$. Global existence is clear due to the fact that the nonlinearity (in the second equation) is bounded by a linear function of ψ. Since (2.3) is cooperative, we have $\psi \geq \underline{\psi}$, $w \geq \underline{w}$, where $(\underline{\psi}, \underline{w})$ is the solution of (2.3) for $A = A_0$. To establish Theorem 0.1, in view of (2.1), it is then sufficient to prove the following.

Theorem 2.1 *Let $A > 0$ and assume (2.4), with $\psi_0 \not\equiv 0$. Denote by (ψ, w) the solution of (2.3). Also assume that either*

$$r > \beta > 0, \quad n \leq 2,$$

or

$$r = \beta > 0, \quad n \leq 6.$$

Then we have

$$\psi(x,t) \text{ and } w(x,t) \to \infty \qquad \text{as } t \to \infty, \tag{2.5}$$

the convergence being uniform on compact subsets of $\mathbb{R}^n$.

In the rest of the paper, we shall keep the notation (ψ, w) to denote the solution of (2.3). One favorable technical advantage of (2.3) as compared to (0.21)-(0.22) is that it preserves radial symmetry and radial monotonicity.

Lemma 2.2 *Let $\beta > 0$ and $r > 0$. Suppose that for some $x_0 \in \mathbb{R}^n$, both ψ_0 and w_0 are radially symmetric about x_0 and nonincreasing with respect to $|x - x_0|$. Then for all $t > 0$, the solution $(\psi(\cdot,t), w(\cdot,t))$ of (2.3) is also radially symmetric with respect to $x = x_0$ and nonincreasing in $|x - x_0|$.*

PROOF. The symmetry property immediately results from uniqueness of nonnegative solutions to (2.3) and the fact that for radial ψ_0 and w_0, one can easily construct a radial solution of (2.3). To verify the monotonicity statement, we differentiate both PDEs in (2.3) with respect to $\eta = |x - x_0|$ to obtain that the radial derivatives ψ_η and w_η satisfy

$$\begin{cases} \partial_t \psi_\eta = \Delta \psi_\eta + \beta w_\eta, & x \in \mathbb{R}^n,\ t > 0, \\ \partial_t w_\eta = \Delta w_\eta - (r-\beta) w_\eta + r \cdot \frac{\psi^2 + 2A\psi}{(\psi + A)^2} \cdot \psi_\eta & x \in \mathbb{R}^n,\ t > 0. \end{cases}$$

Since $\beta > 0$, $r > 0$ and $\psi \geq 0$, this linear parabolic system again is cooperative. Hence, a standard comparison principle states that ψ_η and w_η, both nonpositive initially, remain nonpositive for all times. □

Before proceeding further, we note that the boundedness property of v (cf. (2.1)) for system (0.7) has its counterpart in the reduced system, which will be used later on in proving Theorem 2.1. Namely, the solution of (2.3) satisfies

$$\psi - w \leq M := \max\Big(A, \sup_{\mathbb{R}^n} (\psi - w)\Big). \tag{2.6}$$

Indeed, since $z := \psi - w$ satisfies

$$z_t - \Delta z + r(z - A) = r \cdot \Big(\psi - \frac{\psi^2}{\psi + A} - A\Big) \leq 0, \qquad x \in \mathbb{R}^n,\ t > 0,$$

inequality (2.6) follows from the maximum principle.

2.3 Unboundedness

The following lemma forms an essential step of our procedure in this section. It provides *some*, albeit weak, first unboundedness feature of ψ which will be successively improved afterwards. For the moment, we focus on the case $r > \beta$, $n \leq 2$, which requires more new ideas. For the case $r = \beta$, $n \leq 6$ several of the main steps will follow from results in [3].

Lemma 2.3 *Let $n \leq 2$, $r > \beta > 0$, $A > 0$, and assume that $\psi_0 \not\equiv 0$. Then there exists $c > 0$ such that the solution (ψ, w) of (2.3) satisfies*

$$\|\psi(\cdot, t)\|_{L^1(\mathbb{R}^n)} \geq c \cdot h(t) \qquad \text{for all } t \geq 0, \tag{2.7}$$

where

$$h(t) := \begin{cases} (1+t)^{\frac{1}{2}} & \text{if } n = 1, \\ \ln(1+t) & \text{if } n = 2. \end{cases} \tag{2.8}$$

PROOF. Let $\mu := r - \beta > 0$. Thanks to the fact that ψ_0 is continuous and $\psi_0 \not\equiv 0$, there exist $c_1 > 0$ and a ball $B \subset \mathbb{R}^n$ such that $\psi_0 \geq c_1$ in B. By the first equation in (2.3), ψ is represented according to

$$\psi(\cdot, t) = e^{t\Delta} \psi_0 + \beta \int_0^t e^{(t-s)\Delta} w(\cdot, s) ds, \qquad t \geq 0. \tag{2.9}$$

As both β and w are nonnegative, we thus have

$$\psi(x,t) \geq (e^{t\Delta}\psi_0)(x) = \int_{\mathbb{R}^n} G_t(x-y)\psi_0(y)dy \qquad \text{for all } x \in \mathbb{R}^n \text{ and } t > 0,$$

where G_σ is defined in (1.3). Writing $R := \sup\{|y| \,|\, y \in B\}$ and estimating $|x-y|^2 \leq 2|x|^2 + 2|y|^2$, we find that in particular

$$\begin{aligned} \psi(x,t) &\geq c_1 \cdot (4\pi t)^{-\frac{n}{2}} \int_B e^{-\frac{|x-y|^2}{4t}} dy \geq c_1 \cdot (4\pi t)^{-\frac{n}{2}} e^{-\frac{R^2}{2}} \cdot |B| \cdot e^{-\frac{|x|^2}{2t}} \\ &= c_2 t^{-\frac{n}{2}} e^{-\frac{|x|^2}{2t}} \qquad \text{for all } x \in \mathbb{R}^n \text{ and } t \geq 1, \end{aligned}$$

where $c_2 = c_1 \cdot (4\pi)^{-\frac{n}{2}} e^{-\frac{R^2}{2}} |B| > 0$. Therefore, at each point $(x,t) \in \mathbb{R}^n \times (1,\infty)$ at which $\psi(x,t) \leq A$, we have

$$\frac{\psi^2}{\psi + A} \geq \frac{\psi^2}{2A} \geq \frac{c_2^2}{2A} t^{-n} e^{-\frac{|x|^2}{t}}, \tag{2.10}$$

whereas if (x,t) is such that $\psi(x,t) > A$, then

$$\frac{\psi^2}{\psi + A} \geq \frac{\psi}{2} \geq \frac{c_2}{2} t^{-\frac{n}{2}} e^{-\frac{|x|^2}{2t}}. \tag{2.11}$$

Since for any $t \geq 1$ and $x \in \mathbb{R}^n$, we have $t^{-\frac{n}{2}} e^{-\frac{|x|^2}{2t}} \geq t^{-n} e^{-\frac{|x|^2}{t}}$, we conclude from (2.10) and (2.11) that

$$\frac{\psi^2}{\psi + A} \geq c_3 t^{-n} e^{-\frac{|x|^2}{t}} = c_4 t^{-\frac{n}{2}} G_{\frac{t}{4}}(x) \qquad \text{for all } x \in \mathbb{R}^n \text{ and } t \geq 1,$$

with positive constants c_3 and c_4. Consequently, the variation of constants formula applied to the second equation in (2.3) says that for all $t > 1$,

$$\begin{aligned} w(\cdot,t) &= e^{-\mu(t-1)} e^{(t-1)\Delta} w(\cdot,1) + \int_1^t e^{-\mu(t-s)} e^{(t-s)\Delta} \cdot r \frac{\psi^2}{\psi + A}(\cdot,s) ds \\ &\geq c_4 \int_1^t e^{-\mu(t-s)} s^{-\frac{n}{2}} e^{(t-s)\Delta} G_{\frac{s}{4}} ds \qquad \text{in } \mathbb{R}^n, \end{aligned}$$

because $w(\cdot,1) \geq 0$. By the heat kernel property of G_σ, we have $e^{\xi\Delta} G_\sigma = G_{\sigma+\xi}$, so that

$$w(\cdot,t) \geq c_4 \int_1^t e^{-\mu(t-s)} s^{-\frac{n}{2}} G_{t-\frac{3s}{4}} ds \qquad \text{in } \mathbb{R}^n \text{ for all } t > 1.$$

Going back to (2.9), this new information gives

$$\psi(\cdot,t) \geq \beta \int_1^t e^{(t-s)\Delta} w(\cdot,s) ds \geq c_4 \beta \int_1^t \int_1^s e^{-\mu(s-\sigma)} \sigma^{-\frac{n}{2}} e^{(t-s)\Delta} G_{s-\frac{3\sigma}{4}} d\sigma ds, \tag{2.12}$$

where again we can explicitly compute

$$e^{(t-s)\Delta} G_{s-\frac{3\sigma}{4}} = G_{s-\frac{3\sigma}{4}+t-s} = G_{t-\frac{3\sigma}{4}}.$$

Therefore, the latter integral in (2.12) can be simplified using Fubini's theorem so as to yield

$$\begin{aligned}
\psi(\cdot,t) &\geq c_4\beta\cdot\int_1^t\int_1^s e^{-\mu(s-\sigma)}\sigma^{-\frac{n}{2}}G_{t-\frac{3\sigma}{4}}d\sigma ds\\
&= c_4\beta\cdot\int_1^t\left(\int_\sigma^t e^{-\mu s}ds\right)\cdot e^{\mu\sigma}\sigma^{-\frac{n}{2}}G_{t-\frac{3\sigma}{4}}d\sigma\\
&= \frac{c_4\beta}{\mu}\cdot\int_1^t\left(1-e^{-\mu(t-\sigma)}\right)\cdot\sigma^{-\frac{n}{2}}G_{t-\frac{3\sigma}{4}}d\sigma\\
&\geq \frac{c_4\beta(1-e^{-\mu})}{\mu}\cdot\int_1^{t-1}\sigma^{-\frac{n}{2}}G_{t-\frac{3\sigma}{4}}d\sigma \qquad \text{in } \mathbb{R}^n \text{ for all } t>2, \qquad (2.13)
\end{aligned}$$

because for such t and any $\sigma\in\{1,t-1\}$ we have $e^{-\mu(t-\sigma)}\leq e^{-\mu}$. Since $\int_{\mathbb{R}^n}G_{t-\frac{3\sigma}{4}}=1$, integrating (2.13) in space gives

$$\|\psi(\cdot,t)\|_{L^1(\mathbb{R}^n)}\geq c_5\int_1^{t-1}\sigma^{-\frac{n}{2}}d\sigma \qquad \text{for all } t>2,$$

with some $c_5>0$, and thus immediately leads to (2.7) with h as defined by (2.8). □

In turning this L^1-divergence assertion into a statement on pointwise unboundedness, we shall need the following blow-up result for an ODE system arising in Lemma 2.5 below.

Lemma 2.4 *Let $a,b,c>0$. There exist $M_1,M_2>0$, depending only on a,b,c, such that if, for some $\varepsilon>0$ and $t_0\geq 0$, (y,z) is a solution of*

$$\begin{cases} y'\geq az-\varepsilon y, & t\geq t_0,\\ z'\geq by^2-cz, & t\geq t_0, \end{cases} \qquad (2.14)$$

with

$$y(t_0)\geq M_1\varepsilon \qquad \text{and} \qquad z(t_0)\geq M_2\varepsilon^2, \qquad (2.15)$$

then (y,z) blows up in finite time.

Proof. **Step 1.** We can assume $a=b=1$ without loss of generality (this can be seen easily upon replacing (y,z) with (aby,a^2bz)). Moreover, it suffices to verify the assertion when (2.14) is replaced with the ODE system

$$\begin{cases} y'=z-\varepsilon y, & t\geq t_0,\\ z'=y^2-cz, & t\geq t_0, \end{cases} \qquad (2.16)$$

and assumption (2.15) is replaced with

$$y(t_0)=M_1\varepsilon \qquad \text{and} \qquad z(t_0)=M_2\varepsilon^2. \qquad (2.17)$$

Indeed, since (2.16) is cooperative, this follows immediately by a comparison argument.

Step 2. For given $\eta > 0$, we define the two functions

$$f(Y,Z) := Z - (\varepsilon + 2\eta)Y, \qquad g(Y,Z) := Y^2 - (c+3\eta)Z, \qquad (Y,Z) \in (0,\infty)^2,$$

and the region

$$R_\eta := \Big\{(Y,Z) \in (0,\infty)^2 \;\Big|\; f(Y,Z) > 0 \text{ and } g(Y,Z) > 0\Big\}.$$

We claim that R_η is positively invariant for system (2.16). To see this, let

$$\tilde f(t) = f(y(t),z(t)), \quad \tilde g(t) = g(y(t),z(t))$$

and assume for the sake of contradiction that, for some $t_1 > t_0$, $(y(t),z(t)) \in R_\eta$ on $[t_0,t_1)$ and $(y(t_1),z(t_1)) \in \partial R_\eta$. Note that $\tilde f, \tilde g > 0$ implies $y', z' > 0$ on $[t_0,t_1)$, hence $y(t_1), z(t_1) > 0$.
Two possibilities arise: First if $\tilde f(t_1) = 0$ and $\tilde g(t_1) \geq 0$, then $z = (\varepsilon+2\eta)y$, $y' = 2\eta y$ and $z' \geq 3\eta z$ at $t = t_1$. Therefore

$$\tilde f'(t_1) = z' - (\varepsilon+2\eta)y' \geq 3\eta z - (\varepsilon+2\eta)2\eta y = (\varepsilon+2\eta)(3\eta y - 2\eta y) = (\varepsilon+2\eta)\eta y > 0,$$

hence $(y(t),z(t)) \notin R_\eta$ for $t < t_1$ close to t_1: a contradiction.
Otherwise, we have $\tilde f(t_1) > 0$ and $\tilde g(t_1) = 0$. Then $y^2 = (c+3\eta)z$, $y' \geq 2\eta y$ and $z' = 3\eta z$ at $t = t_1$. Therefore

$$\tilde g'(t_1) = 2yy' - (c+3\eta)z' \geq 4\eta y^2 - (c+3\eta)3\eta z = (c+3\eta)(4\eta z - 3\eta z) = (c+3\eta)\eta z > 0,$$

which gives a similar contradiction and proves the claim.
Step 3. We next claim that if $(y(t_0),z(t_0)) \in R_\eta$ for some $\eta > 0$, then (y,z) blows up in finite time. Indeed, under this assumption, we have $f(y(t),z(t)), g(y(t),z(t)) > 0$ for all $t \geq t_0$, due to Step 2. Therefore,

$$y' = \varepsilon(\varepsilon+2\eta)^{-1} f(y,z) + 2\eta(\varepsilon+2\eta)^{-1} z \geq c_1 z$$

and

$$z' = c(c+3\eta)^{-1} g(y,z) + 3\eta(c+3\eta)^{-1} y^2 \geq c_2 y^2$$

for all $t \geq t_0$, with $c_1, c_2 > 0$. By Young's inequality, we deduce

$$(yz)' = y'z + yz' \geq c_1 z^2 + c_2 y^3 \geq c_3 (z^{5/3} + y^{5/2})^{6/5} \geq c_4 (yz)^{6/5},$$

for all $t \geq t_0$, with some $c_3, c_4 > 0$, hence the finite time blow-up of (y,z).
Step 4. Now assume (2.17) with $M_1 = 2c$ and $M_2 = 3c$. Then, at $t = t_0$, we have $z - \varepsilon y = (3c - 2c)\varepsilon^2 > 0$ and $y^2 - cz = (4c^2 - 3c^2)\varepsilon^2 > 0$. Therefore $(y(t_0),z(t_0)) \in R_\eta$ for some small $\eta > 0$, so that (y,z) blows up in finite time by Step 3. The Lemma is proved. □

We shall now derive the unboundedness of ψ in L^∞. In the case $r > \beta$, arguing by contradiction, we shall rely on Lemmas 2.3 and 2.4 and on a variant of the classical Fujita argument [6], testing with Gaussians. In the case $r = \beta$, this will be a direct consequence of a result of Escobedo and Herrero [3] concerning the system with pure power nonlinearities.

Lemma 2.5 *Under the assumptions of Theorem 2.1, there exists* $(t_j)_{j\in\mathbb{N}} \subset (0,\infty)$ *such that* $t_j \to \infty$ *and*

$$\|\psi(\cdot,t_j)\|_{L^\infty(\mathbb{R}^n)} \to \infty \qquad \text{as } j\to\infty. \tag{2.18}$$

Proof. Suppose on the contrary that there exists $c_1 > 0$ such that $\psi \le c_1$ in $\mathbb{R}^n\times(0,\infty)$. Then

$$w_t \ge \Delta w - \mu w + d\psi^2 \qquad \text{in } \mathbb{R}^n\times(0,\infty) \tag{2.19}$$

holds with $d := \frac{r}{c_1+A}$, where we again have set $\mu := r-\beta$.
In the case $r=\beta$, i.e. $\mu = 0$, then (ψ, w) is a positive supersolution of the system

$$\begin{cases} \psi_t = \Delta\psi + \beta w, & x\in\mathbb{R}^n,\ t>0,\\ w_t = \Delta w + d\psi^2, & x\in\mathbb{R}^n,\ t>0. \end{cases} \tag{2.20}$$

It follows from the Fujita-type result in [3] and the comparison principle that (ψ, w) blows up in finite time when $n\le 6$: a contradiction.
From now on, we thus assume $r>\beta$, hence $\mu>0$, and $n\le 2$. For any $\lambda>0$, we define the quantities

$$y_\lambda(t) := \int_{\mathbb{R}^n} \psi(x,t)G_\lambda(x)dx \quad \text{and} \quad z_\lambda(t) := \int_{\mathbb{R}^n} w(x,t)G_\lambda(x)dx,$$

where G_λ is defined by (1.3). Multiplying both (2.19) and the first equation in (2.3) by $G_\lambda(x)$, we find upon integrating over $\mathbb{R}^n$ that

$$y'_\lambda(t) = \int_{\mathbb{R}^n} (\Delta\psi + \beta w)\cdot G_\lambda = \int_{\mathbb{R}^n} \psi\Delta G_\lambda + \beta\int_{\mathbb{R}^n} wG_\lambda \qquad \text{for all } t>0$$

and

$$\begin{aligned} z'_\lambda(t) &\ge \int_{\mathbb{R}^n} (\Delta w - \mu w + d\psi^2)\cdot G_\lambda \\ &= \int_{\mathbb{R}^n} w\Delta G_\lambda - \mu\int_{\mathbb{R}^n} wG_\lambda + d\int_{\mathbb{R}^n}\psi^2 G_\lambda \qquad \text{for all } t>0. \end{aligned}$$

Using

$$\Delta G_\lambda(x) = -\frac{n}{2\lambda}G_\lambda(x) + \frac{|x|^2}{4\lambda^2}G_\lambda(x) \ge -\frac{n}{2\lambda}G_\lambda(x) \qquad \text{for all } x\in\mathbb{R}^n,$$

and $\int_{\mathbb{R}^n}\psi^2 G_\lambda \le (\int_{\mathbb{R}^n}\psi G_\lambda)^2$ (due to Hölder's inequality and $\int_{\mathbb{R}^n} G_\lambda(x)dx = 1$), this leads to the inequalities

$$\begin{cases} y'_\lambda \ge -\frac{n}{2\lambda}y_\lambda + \beta z_\lambda, & t>0,\\ z'_\lambda \ge -\Big(\frac{n}{2\lambda}+\mu\Big)z_\lambda + dy_\lambda^2, & t>0. \end{cases} \tag{2.21}$$

Let $M > 0$ to be determined later (depending only on n, β, μ, d). Then according to Lemma 2.3 we can pick $t_0 = t_0(M) > 0$ such that

$$(4\pi)^{-\frac{n}{2}} \int_{\mathbb{R}^n} \psi(x, t_0) dx \geq 2M.$$

Since $e^{-\frac{|x|^2}{4\lambda}} \nearrow 1$ as $\lambda \to \infty$ for each $x \in \mathbb{R}^n$, and since $w(\cdot, t_0) \not\equiv 0$ by the strong maximum principle, we can now fix $\lambda = \lambda(M) > 1$ large enough satisfying

$$(4\pi)^{-\frac{n}{2}} \int_{\mathbb{R}^n} \psi(x, t_0) \cdot e^{-\frac{|x|^2}{4\lambda}} dx \geq M \quad \text{and} \quad (4\pi)^{-\frac{n}{2}} \int_{\mathbb{R}^n} w(x, t_0) \cdot e^{-\frac{|x|^2}{4\lambda}} dx \geq M\lambda^{-2+\frac{n}{2}}.$$

The last inequality only required $n < 4$, but now using $n \leq 2$, it follows that

$$y_\lambda(t_0) = (4\pi\lambda)^{-\frac{n}{2}} \int_{\mathbb{R}^n} \psi(x, t_0)\, e^{-\frac{|x|^2}{4\lambda}} dx \geq M\lambda^{-\frac{n}{2}} \geq \frac{M}{\lambda},$$

and

$$z_\lambda(t_0) = (4\pi\lambda)^{-\frac{n}{2}} \int_{\mathbb{R}^n} w(x, t_0)\, e^{-\frac{|x|^2}{4\lambda}} dx \geq \frac{M}{\lambda^2}.$$

Finally, we apply Lemma 2.4 with $a = \beta$, $b = d$, $c = \mu + (n/2)$ and $\varepsilon = n/(2\lambda)$, and we take $M > \max(nM_1/2, n^2M_2/4)$, where M_1, M_2 are given by Lemma 2.4. It then follows that (y_λ, z_λ) must blow up in finite time. This contradicts the global existence of ψ and w and thereby proves that ψ cannot be bounded. □

Next, we proceed to show that ψ becomes large at some time, *uniformly* in any compact subset of $\mathbb{R}^n$. At this point we essentially rely on the use of radially decreasing solutions of (2.3).

Lemma 2.6 *Under the assumptions of Theorem 2.1, for all $R > 0$, there exists $(t_j)_{j\in\mathbb{N}} \subset (0, \infty)$ such that $t_j \to \infty$ and*

$$\inf_{x\in B_R(0)} \psi(x, t_j) \to \infty \qquad \text{as } j \to \infty. \tag{2.22}$$

Proof. Replacing t by $\tilde{t} := t - 1$ if necessary, we may assume that

$$w(x, 0) \geq \delta\, e^{-\kappa|x|^2} =: \underline{w}_0(x) \qquad \text{and} \qquad \psi(x, 0) \geq \underline{\psi}_0(x) := \underline{w}_0(x) \qquad \text{for all } x \in \mathbb{R}^n$$

with some $\delta > 0$ and $\kappa > 0$. By the cooperativity of (2.3), we find that

$$\psi \geq \underline{\psi} \qquad \text{and} \qquad w \geq \underline{w} \qquad \text{in } \mathbb{R}^n \times (0, \infty), \tag{2.23}$$

where $(\underline{\psi}, \underline{w})$ denotes the solution of (2.3) with initial data $(\underline{\psi}_0, \underline{w}_0)$. By Lemma 2.2, both $\underline{\psi}$ and $\underline{w}$ are radially symmetric with respect to $x = 0$ and nonincreasing with respect to $|x|$. As a consequence, for all $R > 0$ we have

$$\inf_{x\in B_R(0)} \underline{\psi}(x, t) = \underline{\psi}(x_R, t) \qquad \text{for all } t > 0 \tag{2.24}$$

with any $x_R \in \partial B_R(0)$.
Next, let $R > 0$ be given and fix an arbitrary $x_R \in \partial B_R(0)$. It is then possible to find a positive function $\underline{\underline{w}}_0 \in C^\infty(\mathbb{R}^n)$ such that $\underline{\underline{w}}_0 \le \underline{w}_0$ in $\mathbb{R}^n$, and such that $\underline{\underline{w}}_0$ is radially symmetric about x_R and nonincreasing with respect to $|x-x_R|$. (In fact, a possible choice to achieve this is $\underline{\underline{w}}_0(x) := \delta\, e^{-2\kappa R^2} \cdot e^{-2\kappa|x-x_R|^2}$.) Then, again by Lemma 2.2, the solution $(\underline{\underline{\psi}}, \underline{\underline{w}})$ of (2.3) with initial data $(\underline{\underline{\psi}}_0, \underline{\underline{w}}_0)$ is radially symmetric with respect to $x = x_R$ and nonincreasing in $|x - x_R|$ for all $t > 0$, and by comparison it satisfies

$$\underline{\psi} \ge \underline{\underline{\psi}} \qquad \text{and} \qquad \underline{w} \ge \underline{\underline{w}} \qquad \text{in } \mathbb{R}^n \times (0,\infty). \tag{2.25}$$

But Lemma 2.5 ensures that $\underline{\underline{\psi}}$ is unbounded, which in view of the asserted monotonicity properties means that $\underline{\underline{\psi}}(x_R, t_j) \to \infty$ must hold along an appropriate sequence of times $t_j \to \infty$. Combining this with (2.23), (2.24) and (2.25) yields

$$\inf_{x\in B_R(0)} \psi(x,t_j) \ge \inf_{x\in B_R(0)} \underline{\psi}(x,t_j) = \underline{\psi}(x_R,t_j) \ge \underline{\underline{\psi}}(x_R,t_j) \to \infty$$

as $j \to \infty$, and the proof is complete. □

2.4 Construction of time monotone solutions and conclusion

Building on the results from Lemma 2.6, it is now possible to show that divergence in fact occurs along the whole net $t \to \infty$ and is not restricted to subsequences. The proof is based on comparison from below by solutions of system (2.3) that increase with t. To construct such solutions we need the following preparation.

Lemma 2.7 *Let $M, \beta, R_0 > 0$. Then there exist $R_1 > R_0$ and a nonnegative $\chi \in C^\infty(\bar{B}_{R_1}(0))$ such that*

$$\begin{cases} \Delta\chi + \beta\chi \ge M & \text{in } B_{R_1}(0), \\ \chi = 0 & \text{on } \partial B_{R_1}(0). \end{cases} \tag{2.26}$$

Proof. We fix two nonnegative functions g_1 and g_2 belonging to $C^\infty(\bar{B}_1(0))$ such that

$$g_1(x) = 1 \quad \text{for } |x| \le \frac{1}{4} \qquad \text{and} \qquad g_1(x) = 0 \quad \text{for } |x| \ge \frac{1}{2}$$

and

$$g_2(x) = 1 \quad \text{for } \frac{3}{4} \le |x| \le 1 \qquad \text{and} \qquad g_2(x) = 0 \quad \text{for } |x| \le \frac{1}{2}.$$

Then for $i \in \{1,2\}$, the problems

$$\begin{cases} -\Delta\chi_i = g_i & \text{in } B_1(0), \\ \chi_i = 0 & \text{on } \partial B_1(0), \end{cases} \tag{2.27}$$

possess nonnegative solutions $\chi_i \in C^\infty(\bar{B}_1(0))$. In view of the Hopf boundary point lemma, there exist positive constants c_i and C_i such that

$$c_i \operatorname{dist}(x, \partial B_1(0)) \le \chi_i(x) \le C_i \operatorname{dist}(x, \partial B_1(0)) \qquad \text{for all } x \in B_1(0).$$

Picking any $\varepsilon \in (0, c_1/C_2)$ and defining the function $\tilde{\chi} := \chi_1 - \varepsilon\chi_2$, it follows that $\tilde{\chi} > 0$ in $B_1(0)$. It is therefore possible to fix $R_1 > R_0$ large such that

$$\delta := \beta \cdot \inf_{x \in B_{3/4}(0)} \tilde{\chi}(x) - \frac{\|g_2\|_{L^\infty(B_1(0))}}{R_1^2} > 0. \tag{2.28}$$

Upon this choice, setting $\hat{\chi}(x) := \tilde{\chi}(x/R_1)$, $x \in \bar{B}_{R_1}(0)$, one defines a nonnegative $\hat{\chi} \in C^\infty(\bar{B}_{R_1}(0))$ that vanishes on $\partial B_{R_1}(0)$ and satisfies

$$\begin{aligned} \Delta\hat{\chi}(x) + \beta\hat{\chi}(x) &= \frac{1}{R_1^2}\Delta\tilde{\chi}\Big(\frac{x}{R_1}\Big) + \beta\hat{\chi}(x) \\ &\geq -\frac{\|g_2\|_{L^\infty(B_1(0))}}{R_1^2} + \beta\hat{\chi}(x) \geq \delta \qquad \text{for all } x \in B_{3R_1/4}(0), \end{aligned}$$

by (2.27) and (2.28). Moreover, at all remaining points we have

$$\Delta\hat{\chi}(x) + \beta\hat{\chi}(x) \geq \Delta\hat{\chi}(x) = \frac{1}{R_1^2} \qquad \text{for all } x \in B_{R_1}(0) \setminus B_{3R_1/4}(0),$$

so that altogether we obtain

$$\Delta\hat{\chi} + \beta\hat{\chi} \geq \hat{\delta} := \min\Big\{\delta, \frac{1}{R_1^2}\Big\} \qquad \text{in } B_{R_1}(0).$$

Now it immediately follows that $\chi := \frac{M}{\hat{\delta}}\hat{\chi}$ has the desired properties. □

We are now in a position to conclude.

Proof of Theorem 0.1. Set $M := \max(rA, \sup_{\mathbb{R}^n}(\psi - w))$. Fix $R_0 > 0$ and let $R_1 > R_0$ and χ be as provided by Lemma 2.7. By Lemma 2.6 applied with $R = R_1$, we infer that for some $t_0 \geq 0$, ψ satisfies

$$\inf_{x \in B_{R_1}(0)} \psi(x, t_0) \geq \sup_{x \in B_{R_1}(0)} \chi(x) + M.$$

By (2.6), this entails that

$$\psi(x, t_0) \geq \chi(x) \qquad \text{and} \qquad w(x, t_0) \geq \chi(x) \qquad \text{for all } x \in B_{R_1}(0).$$

Denote by $(\underline{\psi}, \underline{w})$ the solution of (2.3) with initial time t_0 instead of 0, and initial data $(\underline{\psi}_0, \underline{w}_0)$, where

$$\underline{\psi}_0(x) := \underline{w}_0(x) := \begin{cases} \chi(x), & \text{if } x \in B_{R_1}(0), \\ 0 & \text{else.} \end{cases}$$

By the comparison principle, it follows that $\psi \geq \underline{\psi}$ and $w \geq \underline{w}$ on $\mathbb{R}^n \times (t_0, \infty)$. Consequently, recalling also (2.6), it is sufficient for proving (2.5) to show that

$$\inf_{x \in B_{R_0}(0)} \underline{\psi}(x, t) \to \infty \qquad \text{as } t \to \infty. \tag{2.29}$$

To prove (2.29), we first apply Lemma 2.6 with $R = R_0$ to $\underline{\psi}(\cdot, \cdot - t_0)$ and $\underline{w}(\cdot, \cdot - t_0)$, to gain a sequence of times $t_j \to \infty$ such that

$$\inf_{x \in B_{R_0}(0)} \underline{\psi}(x, t_j) \to \infty \qquad \text{as } j \to \infty. \tag{2.30}$$

But the properties of χ ensure that

$$\Delta \underline{\psi}_0 + \beta \underline{w}_0 = \Delta\chi + \beta\chi \geq M > 0 \qquad \text{for all } x \in B_{R_1}(0) \tag{2.31}$$

and

$$\begin{aligned} \Delta \underline{w}_0 - (r-\beta)\underline{w}_0 + r \cdot \frac{\underline{\psi}_0^2}{\underline{\psi}_0 + A} &= \Delta\chi + \beta\chi + r\Big(\frac{\chi^2}{\chi + A} - \chi\Big) \\ &= \Delta\chi + \beta\chi - \frac{rA\chi}{\chi + A} \\ &\geq M - \frac{rA\chi}{\chi + A} \geq M - rA, \end{aligned}$$

hence

$$\Delta \underline{w}_0 - (r-\beta)\underline{w}_0 + r \cdot \frac{\underline{\psi}_0^2}{\underline{\psi}_0 + A} \geq 0 \qquad \text{for all } x \in B_{R_1}(0). \tag{2.32}$$

We then claim that

$$\underline{\psi}_t,\ \underline{w}_t \geq 0 \qquad \text{in } \mathbb{R}^n \times (t_0, \infty) \tag{2.33}$$

which, combined with (2.30), will show that (2.29) is valid and thereby complete the proof. Claim (2.33) follows from a well-known and simple argument (see e.g. [15, Ch. 52.6]), which we recall for the convenience of the reader. By the comparison principle for cooperative systems, we infer from (2.31), (2.32) that $\underline{\psi} \geq \underline{\psi}_0$, $\underline{w} \geq \underline{w}_0$ in $B_{R_1}(0) \times (t_0, \infty)$, hence

$$\underline{\psi} \geq \underline{\psi}_0, \quad \underline{w} \geq \underline{w}_0 \qquad \text{in } \mathbb{R}^n \times (t_0, \infty). \tag{2.34}$$

For any fixed $h > 0$, letting $(\underline{\psi}_h, \underline{w}_h) := (\underline{\psi}(\cdot, \cdot + h), \underline{w}(\cdot, \cdot + h))$ and applying the comparison principle once again, we deduce from (2.34) that $\underline{\psi}_h \geq \underline{\psi}$, $\underline{w}_h \geq \underline{w}$ in $\mathbb{R}^n \times (t_0, \infty)$. Dividing by h and letting $h \to 0$, we finally obtain (2.33). □

Remark 2.1 The conclusion of Lemma 2.6 remains true if in the second equation of (2.3), the factor r in front of the quadratic term is replaced with any $\tilde{r} > 0$. Accordingly, for any $\tilde{r} > 0$, ψ grows up to infinity locally uniformly along some time sequence. However, the monotonicity argument of Section 2.4 (here given for $\tilde{r} = r$) can only be adapted to cover the case $\tilde{r} > r - \beta$. Thus, extending to arbitrary $\tilde{r} > 0$ the full statement of Theorem 0.1 (grow-up along the whole net $t \to \infty$) seems to require some new idea.

3 Conclusion

In this paper we are concerned with a mathematical model from population genetics, describing a single-locus diallelic selection-migration process. Here a specific gene gives rise to three genotypes aa, aA and AA; the birth and death rates are constant but it is assumed that the death rate depends on the genotype, contrary to the birth rate. Namely, individuals AA are endowed with a lower death rate than aa, thus making the genotype AA a priori advantageous. We here concentrate on the case when this character is fully recessive, the heterozygote individuals aA being assumed to have the same death rate as aa. We investigate the asymptotic behavior of solutions of the corresponding nonlinear reaction-diffusion system (0.1) satisfied by the three genotype densities, posed in the whole Euclidean space $\mathbb{R}^n$. Our main concern is to determine under which conditions are some of the genotypes outperformed by the others in that their relative frequencies decay to 0 in large time.

It can be seen that in the non-diffusive (spatially homogeneous) case, and also in the case of a bounded domain with no-flux boundary conditions, the disadvantageous gene a is always eliminated in the large time limit. The main outcome of this paper is that this need no longer be the case in the presence of diffusion in the whole space, and that a key role is played by the space dimension. Namely, for dimensions $n \leq 2$, when the birth rate exceeds a certain threshold value, we prove that the disadvantageous gene a is still always eliminated in the large time limit. But on the contrary, for $n \geq 3$, there exist initial distributions for which the advantageous gene A ultimately disappears. Moreover, we show that, at the threshold value of the birth rate, the cut-off dimension shifts from $n = 2$ to $n = 6$, and that below the threshold no dimensional influence any longer occurs.

Our results seem to be the first rigorous ones of this type for the full system and they solve a problem which seems to have been open since the celebrated work of Aronson and Weinberger ([1], [2]). Indeed, due to the apparent difficulty to study the full system, attempt has been made in their work (see also [4]) to reduce the question to the study of a simpler scalar equation of the Fisher-KPP type $z_t = \Delta z + f(z)$, that they derived as an approximation of the full system, and where z is now expected to represent the frequency of the allele A. More precisely, if in the full system the selection is weak, the birth rate is large and the spatial inhomogeneity is suitably small initially, then on a (suitable) long time scale the frequency of the allele A remains close to the solution z of the scalar equation with same initial data. Aronson and Weinberger also proved that, for $n \leq 2$ any nontrivial solution of the scalar equation converges to 1, whereas for $n \geq 3$ the solution converges to 0 for suitably small initial data. We thus see that the Fisher approximation partially reflects some of the qualitative features of the full system.

A first step in our proofs was to transform the system by considering as two of the new dependent variables the respective densities of the alleles a and A, multiplied by a suitable exponential time factor. Whereas the original system was neither cooperative nor competitive, it turned out that a certain sub-system became cooperative after this transformation, thus making more PDE techniques available. Our proofs were then based on a suitable combination of comparison arguments based on the maximum principle, semigroup tech-

niques (variation-of-constant formula and heat kernel estimates), differential inequalities, test function and monotonicity arguments.

Although the above dimension-dependent effects occur only when the problem is considered in the entire space, it is to be expected that if the habitat is bounded *but large*, then the space dimension will play a corresponding role for the selection process on large but finite time scales. In particular, we suspect that in the case $n \geq 3$, even when considered in large but bounded domains the system may exhibit quite a rich dynamical structure on intermediate time scales, possibly including phenomena such as metastability. Questions of this type go beyond the scope of this paper.
We also leave it as an open problem whether in cases other than the fully recessive one, given by (0.4), the Fisher approximation (cf. (0.2)) gives a qualitatively correct description of the asymptotic behavior for system (0.1) in respect of large time selection.
Another interesting question is whether the use of (0.2) can be given deeper rigorous justification by providing further qualitative parallels to (0.1) such as, for instance, the occurrence of wave-like solutions, which are known to exist for $u_t = \Delta u + u^2(1-u)$ ([13]).
Our proofs depend very much on the assumption that diffusivities are the same for all three genotypes. We do not know whether our results may be extended in any way to the case of different diffusivities.

4 Appendix: The case of bounded domains

As mentioned in the introduction, the influence of the dimension in Theorems 0.1 and 0.2 is an effect caused by the diffusion and the fact that the physical domain is the entire space $\mathbb{R}^n$. In order to confirm this rigorously, let us consider the analogue of (0.7) in a bounded domain $\Omega \subset \mathbb{R}^n$ with no-flux boundary conditions:

$$\begin{cases} u_t = \Delta u - ru + \dfrac{r}{\rho}\Big(u + \dfrac{1}{2}v\Big)^2, & x \in \Omega,\ t > 0, \\ v_t = \Delta v - rv + \dfrac{r}{\rho}\Big(u + \dfrac{1}{2}v\Big)\Big(w + \dfrac{1}{2}v\Big), & x \in \Omega,\ t > 0, \\ w_t = \Delta w + (\beta - r)w + \dfrac{r}{\rho}\Big(w + \dfrac{1}{2}v\Big)^2, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = \dfrac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x), \quad v(x,0) = v_0(x), \quad w(x,0) = w_0(x), & x \in \Omega, \end{cases} \tag{4.1}$$

where ν denotes the outer normal vector on $\partial\Omega$. The following result asserts that for any positive r and β, all solutions with $v_0 + w_0 \not\equiv 0$ satisfy the analogue of (0.11).

Proposition 4.1 *Let $\Omega \subset \mathbb{R}^n$ be a bounded domain with smooth boundary, and assume that u_0, v_0 and w_0 are nonnegative and continuous in $\bar{\Omega}$ with $v_0 + w_0 \not\equiv 0$. Then the solution of (0.7) in $\Omega \times (0,\infty)$ satisfies $u/\rho \to 0$, $v/\rho \to 0$ and $w/\rho \to 1$ as $t \to \infty$, uniformly with respect to $x \in \Omega$.*

PROOF. Recall that the functions φ, ψ are defined through the transformation (0.17) and that the differential equations in (0.18)-(0.20) are now satisfied in $\Omega \times (0,\infty)$ with Neumann boundary conditions. By the maximum principle we have $\varphi \le A := \|\varphi(\cdot,0)\|_\infty$, hence u and v are bounded in $\Omega \times (0,\infty)$. It thus suffices to show that $\min_{x\in\overline{\Omega}} \psi(x,t) \to \infty$ as $t \to \infty$.
Now, since $\psi(\cdot,0) \not\equiv 0$, it follows easily from the strong and the Hopf maximum principles that, for given $t_0 > 0$, $w(\cdot,t_0) \ge c > 0$ in $\overline{\Omega}$. By the comparison principle for the cooperative system satisfied by (ψ, w), we deduce that $\psi(\cdot,t) \ge \underline{\psi}(t)$, $w(\cdot,t) \ge \underline{w}(t)$ for all $t \ge t_0$, where $(\underline{\psi}, \underline{w})$ is the solution of ODE system

$$\underline{\psi}' = \beta \underline{w}, \qquad t > t_0, \tag{4.2}$$

$$\underline{w}' = (\beta - r)\underline{w} + r \cdot \frac{\underline{\psi}^2}{\underline{\psi} + A}, \qquad t > t_0, \tag{4.3}$$

$$\underline{\psi}(t_0) = 0, \quad \underline{w}(t_0) = c. \tag{4.4}$$

By (4.2), we have $\underline{\psi}(t) \to L$ as $t \to \infty$ with some limit $L \le \infty$. Therefore we shall be done if we show $L = \infty$. Assume for the sake of contradiction that $L < \infty$, set $c_0 := L + A$ and fix $b > 0$ so large that $b\beta > r - \beta$. Then we obtain

$$(\underline{w} + b\underline{\psi})' \ge \frac{r}{c_0}\underline{\psi}^2 \ge \frac{r}{c_0(1+b)^2}(\underline{w} + b\underline{\psi})^2, \qquad t > t_0, \tag{4.5}$$

due to $\underline{w} + b\underline{\psi} \le (1+b)\underline{\psi}$. However, since $\underline{w}(t_0) > 0$, this leads to the absurd conclusion that $\underline{w} + b\underline{\psi}$ should blow up in finite time. Therefore $L = \infty$ and the proof is completed. □

Acknowledgement. We would like to thank Professor H.F. Weinberger for useful remarks concerning this work. We also thank the anonymous referee for the careful reading of our paper and for interesting suggestions. This research was initiated while the second author visited Université Paris 13. M. Winkler would like to express his gratefulness for the kind hospitality at the Laboratoire Analyse, Géométrie et Applications.

References

[1] D.G. Aronson and H.F. Weinberger, Nonlinear diffusion in population genetics, combustion, and nerve propagation, in "Partial Differential Equations and Related Topics, Lecture Notes in Mathematics", Vol. 446, pp. 5-49, Springer, New York, 1975.

[2] D.G. Aronson and H.F. Weinberger, Multidimensional nonlinear diffusions arising in population genetics, *Adv. Math.* 30 (1977), 33-76.

[3] M. Escobedo and M.A. Herrero, Boundedness and blow up for a semilinear reaction-diffusion system, *J. Differential Equations* 89 (1991), 176-202.

[4] P. Fife, Mathematical Aspects of Reacting and Diffusing Systems, Lect. Notes Biomath., vol. 28, Berlin Heidelberg New York, Springer 1979.

[5] R.A. Fisher, The advance of advantageous genes, *Ann. of Eugenics* 7 (1937), 355-369.

[6] H. Fujita, On the blowing up of solutions of the Cauchy problem for $u_t = \Delta u + u^{1+\alpha}$, J. Fac. Sci. Univ. Tokyo Sec. IA Math. 13 (1966), 109-124.

[7] G.H. Hardy, Mendelian proportions in a mixed population, Science 28 (1908), 49-50.

[8] A.N. Kolmogorov, I. Petrovskii, N. Piscounov, Etude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique, *Bull. Moscow State Univ.*, Sec. A 1 (1937), 1-25.

[9] V. A. Kostitzin, Biologie Mathématique, Librairie Armand Colin, Paris, 1937.

[10] Y. Lou and Th. Nagylaki, Evolution of a semilinear parabolic system for migration and selection without dominance, *J. Differ. Equations* 225 (2006), 624-665.

[11] R. Lui, Convergence to constant equilibrium for a density-dependent selection model with diffusion, *J. Math. Biol.* 26 (1988), 583-592.

[12] R. Lui and J.F. Selgrade, Density-dependent selection migration model with non-monotone fitness functions, *J. Math. Biol.* 31 (1993), 717-734.

[13] J.D. Murray, Mathematical Biology. Vol. 1: An introduction. Interdisciplinary Applied Mathematics **17**, Springer, New York, 2002.

[14] Th. Nagylaki, Introduction to theoretical population genetics. Biomathematics **21**, Springer, Berlin, 1992.

[15] P. Quittner and Ph. Souplet, Superlinear parabolic problems. Blow-up, global existence and steady states, Birkhäuser Advanced Texts, 2007.

[16] Yu. V. Tyutyunova, E.A. Zhadanovskayaa, R. Arditi and A.B. Medvinsky, A Spatial Model of the Development of Pest Resistance to a Transgenic Insecticidal Crop: European Corn Borer on Bt Maize, *Biophysics* 52 (2007), 52-67.

[17] F.B. Weissler, Existence and non-existence of global solutions for a semilinear heat equation, *Israel J. Math.* 38 (1981), 29-40.

[18] E. Zhadonovskaya, Modelling the spatio-temporal dynamics of the European corn borer in the presence of trangenic maize, PhD Thesis, Agro-Paris-Tech, 2007.