Dynamics of dirac concentrations in the evolution of quantitative alleles with sexual reproduction

L. Dekens[*]and S. Mirrahimi[†]

December 24, 2021

Abstract

A proper understanding of the links between varying gene expression levels and complex trait adaptation is still lacking, despite recent advances in sequencing techniques leading to new insights on their importance in some evolutionary processes. This calls for extensions of the continuum-of-alleles framework first introduced by Kimura (1965) that bypass the classical Gaussian approximation. Here, we propose a novel mathematical framework to study the evolutionary dynamics of quantitative alleles for sexually reproducing populations under natural selection and competition through an integro-differential equation. It involves a new reproduction operator which is nonlinear and nonlocal. This reproduction operator is different from the infinitesimal operator used in other studies with sexual reproduction because of different underlying genetic structures. In an asymptotic regime where initially the population has a small phenotypic variance, we analyse the long-term dynamics of the phenotypic distributions according to the methodology of small variance (Diekmann et al. 2005). In particular, we prove that the reproduction operator strains the limit distribution to be a product measure. Under some assumptions on the limit equation, we show that the population remains monomorphic, that is the phenotypic distribution remains concentrated as a moving Dirac mass. Moreover, in the case of a monomorphic distribution, we derive a canonical equation describing the dynamics of the dominant alleles.

Contents

[*]Institut Camille Jordan, UMR5208 UCBL/CNRS, Université de Lyon, 69100 Villeurbanne, France. Email: dekens@math.univ-lyon1.fr.

[†]Institut Montpelliérain Alexander Grothendieck, Univ Montpellier, CNRS, Montpellier, France. Email: sepideh.mirrahimi@umontpellier.fr.

1 Introduction

1.1 Model and biological motivations.

The development and popularization of sequencing techniques of the last twenty years has been leading to a greater understanding of regulatory mechanisms of gene expression levels and to new insights on their importance in evolutionary trajectories of complex traits (see the recent theory of degeneration of the Y chromosome Lenormand et al. (2020)). However, a complete picture of the relationship between varying gene expression levels and phenotypic adaptation is yet to be drawn (Romero, Ruvinsky, and Gilad 2012). To model varying gene expression levels on a trait under selection, one has to think of the effects of a gene as quantitative rather than discrete. One class of models that was motivated by a similar perspective stems from the reference study Kimura (1965): the continuum-of-alleles models in quantitative genetics, that assume that mutations produce always slightly new allelic effects, so that the allelic effect space is considered as continuous. The method indicated by Kimura (1965) is adapted for asexual populations, or haploid sexual populations with only one locus contributing to the trait under quadratic stabilizing selection. Under these specific assumptions, Kimura (1965) shows that the allelic effects are normally distributed under mutation-selection balance. Several studies (Latter 1972; Lande 1975) extended the model to account for finite number of loci with additive effects on the trait for sexual reproducing populations, still relying on the essential link between quadratic stabilizing selection and multivariate normal allelic distributions to derive quantitative information from their non-linear model. The aim of this paper is therefore to first study a quantitative genetics model that can account for polygenic traits under general selection functions (not restricted to quadratic and considering situations where the alleles do not necessarily have additive effects), in a sexually reproducing population regulated by competition for resources. More precisely, we are interested in the following integro-differential equation, where $\boldsymbol{t} \geq 0$ denotes the time:

$$
\begin{cases}
\partial_{\boldsymbol{t}} \boldsymbol{n}(\boldsymbol{t}, x, y) = \frac{r}{2} \left[\frac{\boldsymbol{\rho}^{\boldsymbol{Y}}(\boldsymbol{t}, x)\, \boldsymbol{\rho}^{\boldsymbol{X}}(\boldsymbol{t}, y)}{\rho(\boldsymbol{t})} + \boldsymbol{n}(\boldsymbol{t}, x, y) \right] - (m(x, y) + \kappa\, \boldsymbol{\rho}(\boldsymbol{t}))\, \boldsymbol{n}(\boldsymbol{t}, x, y), \\[2mm]
\boldsymbol{\rho}^{\boldsymbol{X}}(\boldsymbol{t}, y) = \displaystyle\int_I \boldsymbol{n}(\boldsymbol{t}, x', y)\, dx', \quad \boldsymbol{\rho}^{\boldsymbol{Y}}(\boldsymbol{t}, x) = \int_J \boldsymbol{n}(\boldsymbol{t}, x, y')\, dy', \quad \boldsymbol{\rho}(t) = \int_{I \times J} \boldsymbol{n}(\boldsymbol{t}, x', y')\, dx'\, dy', \\[2mm]
\boldsymbol{n}(0, x, y) = \boldsymbol{n^0}(x, y).
\end{cases}
$$

$$(P\,(\boldsymbol{n}))$$

Here, $\boldsymbol{n}(t, x, y)$ denotes the allelic density of individuals of a haploid sexually reproducing population carrying the quantitative alleles x and y at two unlinked loci of interest. The

2

alleles x and y are taken in compact allelic spaces I and J. Individuals experience mortality by natural selection at a rate $m(x,y) \in C^1(I \times J)$ depending on their genotype $(x,y) \in I \times J$ and regulated by a uniform competition for resources with intensity κ. The first term in the r.h.s of $P(\boldsymbol{n})$ is the reproduction term, which translates how alleles are transmitted across generations under random mating. According to Mendel's laws, the alleles x and y can be inherited either each from a different parent or both from the same.

Remark 1.1 (One-locus diploid population.). *One can notice that up to setting $\tilde{m} := m - \frac{r}{2}$, $\tilde{r} = \frac{r}{2}$, $P(\boldsymbol{n})$ also describes the dynamics of a population of diploid individuals (each individual has two copies of each gene) whose adaptation are determined by the quantitative alleles (x,y) carried at a single focal locus. The following equation was derived as deterministic limit of an individual-based model in Collet, Méléard, and Metz (2013)*

$$
\begin{cases}
\partial_t \boldsymbol{n}(\boldsymbol{t},x,y) = \tilde{r}\dfrac{\boldsymbol{\rho^Y}(\boldsymbol{t},x)\,\boldsymbol{\rho^X}(\boldsymbol{t},y)}{\rho(\boldsymbol{t})} - \left(\tilde{m}(x,y) + \kappa\,\boldsymbol{\rho}(\boldsymbol{t})\right)\,\boldsymbol{n}(\boldsymbol{t},x,y), \\[2mm]
\boldsymbol{\rho^X}(\boldsymbol{t},y) = \displaystyle\int_I \boldsymbol{n}(\boldsymbol{t},x',y)\,dx', \quad \boldsymbol{\rho^Y}(\boldsymbol{t},x) = \displaystyle\int_J \boldsymbol{n}(\boldsymbol{t},x,y')\,dy', \quad \rho(t) = \displaystyle\int_{I \times J} \boldsymbol{n}(\boldsymbol{t},x',y')\,dx'\,dy', \\[2mm]
\boldsymbol{n}(0,x,y) = \boldsymbol{n^0}(x,y).
\end{cases}
$$
$$(P_{\text{diploid}}(\boldsymbol{n}))$$

According to Mendel's laws, the copies x and y must be inherited each from a different parent. In that case, $\tilde{r}$ is the reproduction rate and both the selection function $\tilde{m}$ and the initial genotypic density $\boldsymbol{n_0}$ are assumed symmetrical (requiring $I = J$) (one can verify that the genotypic density $\boldsymbol{n}$ remains symmetrical at all times). All qualitative results will also be presented for this case in Section 2.

We place our analysis in an asymptotic regime where we consider that the initial distribution is concentrated, with a small variance ε so that it is convenient to introduce the following transformation:

$$
\boldsymbol{n^0} = \frac{e^{\frac{\boldsymbol{u_\varepsilon^0}}{\varepsilon}}}{\varepsilon}. \tag{1}
$$

The motivation behind (2) comes from a future project that will include mutations on the alleles with a small mutational variance of order ε^2. Here, we expect that starting with such an initial condition (2), the population density $\boldsymbol{n}$ solution of $P(\boldsymbol{n})$ would keep the same exponential form and would remain asymptotically concentrated with a small variance. Consequently, the dynamics of its mean, driven by natural selection with an intensity correlated to its variance, cannot be observed at shallow time scales, and $(P(\boldsymbol{n}))$ needs to be adequately rescaled in order to explore long-term dynamics. To that effect, let us define the following rescaling in time:

$$
t = \varepsilon\,\boldsymbol{t}, \quad n_\varepsilon(t,\cdot,\cdot) = \boldsymbol{n}(\boldsymbol{t},\cdot,\cdot), \quad \rho_\varepsilon^X(t,\cdot) = \boldsymbol{\rho^X}(\boldsymbol{t},\cdot), \quad \rho_\varepsilon^Y(t,\cdot) = \boldsymbol{\rho^Y}(\boldsymbol{t},\cdot), \quad \rho_\varepsilon(t) = \boldsymbol{\rho}(\boldsymbol{t}).
$$

Under the latter, the problem $(P(\boldsymbol{n}))$ becomes, for $t \geq 0$, $(x, y) \in I \times J$:

$$
\begin{cases}
\varepsilon\, \partial_t n_\varepsilon(t, x, y) = \frac{r}{2} \left[\frac{\rho_\varepsilon^Y(t, x)\, \rho_\varepsilon^X(t, y)}{\rho_\varepsilon(t)} + n_\varepsilon(t, x, y) \right] - (m(x, y) + \kappa\, \rho_\varepsilon(t))\, n_\varepsilon(t, x, y), \\[2mm]
\rho_\varepsilon^X(t, y) = \displaystyle\int_I n_\varepsilon(t, x', y)\, dx', \quad \rho_\varepsilon^Y(t, x) = \int_I n_\varepsilon(t, x, y')\, dy', \quad \rho_\varepsilon(t) = \int_{I \times J} n_\varepsilon(t, x', y')\, dx'\, dy', \\[2mm]
n_\varepsilon(0, x, y) = n_\varepsilon^0(x, y).
\end{cases}
$$

$$(P(n_\varepsilon))$$

As we expect the density n_ε to remain concentrated in our regime, the objective is to analytically describe the dynamics of the Dirac masses (ie. of the dominant alleles in the population), for various selection functions.

1.2   State of the art

Integro-differential models for quantitative genetics modelling the evolutionary dynamics of large sexually reproducing populations with selection have been on the rise recently, especially those that model the phenotypic trait inheritance according to the non-linear infinitesimal model introduced by Fisher (1919) (Mirrahimi and Raoul 2013; Raoul 2017; Bourgeron et al. 2017; Calvez, Garnier, and Patout 2019; Patout 2020; Dekens and Lavigne 2021; Dekens 2020; Raoul 2021; Dekens, Otto, and Calvez 2021). According to the latter, the offspring's trait deviates from the mean parental trait according to a Gaussian kernel of fixed segregational variance. The classical interpretation is that the trait under consideration results from the combination of a large number of loci with small additive allelic effects (Lange 1978; Bulmer 1980; Turelli and Barton 1994; Tufto 2000; Turelli 2017), a framework rigorously justified in Barton, Etheridge, and Véber (2017). In another study Perthame, Strugarek, and Taing (2021), asymmetrical kernels are considered to model the effect of asymmetrical trait inheritance or fecundity on the asymptotic behaviour of the trait distribution. The present work also studies sexually reproducing populations, but the genetical framework is different from the ones aforementioned: here, we consider that the allelic effects at the two loci are continuous and not necessarily small nor additive.

Small variance methodology and long term-dynamics.   We choose to place our study in the small variance methodology, introduced for quantitative genetics studies in Diekmann et al. (2005) from a high-frequency method used in geometric optics. When the variance introduced by events of reproduction (by mutations, segregation...) is small compared to the reduction of diversity following natural selection, they propose to unfold Dirac singularities that are expected to arise using the so-called Hopf-Cole transform:

$$
\boldsymbol{n}_\varepsilon = \frac{e^{\frac{\boldsymbol{u}_\varepsilon}{\varepsilon}}}{\varepsilon}.
$$

The idea behind considering u_ε instead of n_ε stems from the fact that, when ε vanishes, the limit u (to be characterized) is expected to have more regularity than the (measure) limit n, making it more suitable for analysis. Moreover, u would retain important quantitative information on the support of n.

The small variance methodology has first been applied successfully to several quantitative genetics settings for asexual reproducing populations in the regime of small variance of mutations: adaptation to homogeneous environments Perthame and Barles (2008) and Barles,

Mirrahimi, and Perthame (2009), to spatially heterogeneous environments Mirrahimi (2017) and Mirrahimi and Gandon (2020), in a time-periodic environment Figueroa Iglesias and Mirrahimi (2018). Recently, it has been extended to quantitative genetics models for sexually reproducing populations characterized by complex traits inherited according to the aforementioned infinitesimal model (Calvez, Garnier, and Patout 2019; Patout 2020; Dekens and Lavigne 2021; Dekens 2020; Dekens, Otto, and Calvez 2021). However, the asymptotic analysis of this non-local, non-monotone, non-linear operator of reproduction presents great analytical challenges, and it has only been rigorously derived in a model for homogeneous environments (Calvez, Garnier, and Patout 2019; Patout 2020). The same methodology is used in Perthame, Strugarek, and Taing (2021) to study the asymptotic behaviour of the trait distribution under asymmetrical reproduction kernels. Here, as described above, our genetical framework differs significantly from the infinitesimal model's one. Therefore, it yields a different reproduction operator (see Eq. ($P\,(n_\varepsilon)$)), which is in fact closer to the ones used for asexual populations (Perthame and Barles 2008; Barles, Mirrahimi, and Perthame 2009), since one can use arguments based on the maximum principle to provide regularity estimates on the solution. However, the nonlinear nonlocal term describing the reproduction operator still leads to new difficulties to be overcomed.

Let us then consider $\left(\boldsymbol{u_\varepsilon^0}\right)_{\varepsilon>0}$ a sequence in $C^1\,(I\times J)$, uniformly bounded when ε vanishes. It defines subsequently a sequence of concentrated initial genotypic densities with decreasingly small variance (Hopf-Cole transform):

$$\boldsymbol{n_\varepsilon^0} = \frac{e^{\frac{\boldsymbol{u_\varepsilon^0}}{\varepsilon}}}{\varepsilon}. \tag{2}$$

Let us define $\boldsymbol{n_\varepsilon}$ solution of ($P\,(\boldsymbol{n})$) with initial distribution $\boldsymbol{n_{0,\varepsilon}}$, and $\boldsymbol{u_\varepsilon}$ similarly as above:

$$\boldsymbol{n_\varepsilon} = \frac{e^{\frac{\boldsymbol{u_\varepsilon}}{\varepsilon}}}{\varepsilon}.$$

We expect indeed that starting with such an initial condition (2), the population density $\boldsymbol{n_\varepsilon}$ would keep the same exponential form and would remain asymptotically concentrated with a small variance. Consequently, the dynamics of its mean, driven by natural selection with an intensity correlated to its variance, cannot be observed at shallow time scales, and ($P\,(\boldsymbol{n})$) needs to be adequately rescaled in order to explore long term dynamics.

Moreover, in order to study the asymptotic properties of n_ε, we align with Perthame and Barles (2008), Barles, Mirrahimi, and Perthame (2009), Mirrahimi (2017), and Mirrahimi and Gandon (2020), and introduce the derived problem on $u_\varepsilon := \varepsilon \log{(\varepsilon\,n_\varepsilon)}$:

$$\begin{cases} \partial_t\,u_\varepsilon = -\left(m(x,y) + \kappa\,\rho_\varepsilon - \frac{r}{2}\right) + \frac{r}{2\rho_\varepsilon}\iint_{I\times J}\frac{1}{\varepsilon}\exp\left[\frac{u_\varepsilon(x,y') + u_\varepsilon(x',y) - u_\varepsilon(x,y)}{\varepsilon}\right]dx\,dy, \\ u_\varepsilon(0,\cdot,\cdot) = u_\varepsilon^0, \\ \rho_\varepsilon = \iint_{I\times J}\frac{1}{\varepsilon}\exp\left[\frac{u_\varepsilon(x',y')}{\varepsilon}\right]dx'\,dy'. \end{cases}$$
$$(P_{u_\varepsilon})$$

1.3   Assumptions

We assume that the selection term m satisfies the following:

$$m \in C^1(I\times J, \mathbb{R}_+), \quad 4\,\|m\|_\infty < r. \tag{H1}$$

For $\varepsilon > 0$, let $u_\varepsilon^0 \in C^1(I \times J)$ be such that:

$$\exists M > 0, \quad \forall \varepsilon \leq 1, \quad \left\| u_\varepsilon^0 \right\|_{W^{1,\infty}(I \times J)} \leq M. \tag{H2}$$

Then we define the initial state by

$$n_\varepsilon^0 = \frac{e^{\frac{u_\varepsilon^0}{\varepsilon}}}{\varepsilon}.$$

Let us define the following uniform bounds:

$$\rho_0^- := \frac{r - \|m\|_\infty}{\kappa}, \quad \rho_0^+ := \frac{r}{\kappa}.$$

We assume that the initial size of population is bounded uniformly by ρ_0^- and ρ_0^+:

$$\forall \varepsilon > 0, \quad \rho_\varepsilon^0 := \iint_{I \times J} n_\varepsilon^0(x, y)\, dx\, dy \ \in \left] \rho_0^-, \rho_0^+ \right[. \tag{H3}$$

Next, to prepare Proposition 1.1, we assume that there exists $0 < \nu_m \leq 1 - 4\frac{\|m\|_\infty}{r} < 1 + 4\frac{\|m\|_\infty}{r} \leq \nu_M$ such that:

$$\forall \varepsilon, \ \forall (x, y) \in I \times J, \quad \nu_m \leq \nu_\varepsilon^0(x, y) := \frac{\rho_\varepsilon^{X,0}(y)\, \rho_\varepsilon^{Y,0}(x)}{n_\varepsilon^0(x, y)\, \rho_\varepsilon^0} \leq \nu_M. \tag{H4}$$

1.4 Presentation of the results and outline

First, we show some preliminary results of well-posedness of $P(n_\varepsilon)$:

Theorem 1.1. *Under the assumption H3,($P(n_\varepsilon)$) has a unique solution with positive values n_ε in $C^1(\mathbb{R}_+ \times I \times J) \cap C^1(\mathbb{R}_+, L^\infty(I \times J))$. More precisely, we have for all ε:*

$$\rho_0^- \leq \rho_\varepsilon \leq \rho_0^+.$$

Hence, for all $T > 0$, (n_ε) converges along subsequences in $L^\infty(w^* - [0, T], M^1(I \times J))$ toward a measure n when ε vanishes.

We recall that we expect n_ε to concentrate as ε vanishes. As such, we expect the weak limit n to be a sum of Dirac masses. The aim of this paper is to determine where n is supported, that is to determine which alleles become dominant in the population. To study the asymptotic properties of n, it is more convenient to shift the asymptotic analysis from n_ε on $u_\varepsilon = \varepsilon \log(\varepsilon n_\varepsilon)$. Consequently, the main result of this paper focuses on the asymptotic behaviour of u_ε:

Theorem 1.2. *Under the assumptions H2-H4, for all $T > 0$, $u_\varepsilon \xrightarrow[\varepsilon \to 0]{} u$ in $C^0([0, T] \times I \times J)$ (along subsequences). Additionally, u satisfies the following properties:*

(i) u is Lipschitz continuous,

(ii) u is non-positive and satisfies an additive separation of variables property:

$$\forall (t, x, y) \in [0, T] \times I \times J, \quad u(t, x, y) = u^Y(t, x) + u^X(t, y) := \max u(t, x, \cdot) + \max u(t, \cdot, y). \tag{3}$$

Furthermore, we have at all time t: $\max u^Y(t, \cdot) = \max u^X(t, \cdot) = 0$.

(iii) $n(t, \cdot, \cdot)$ *is supported at the zeros of* $u(t, \cdot, \cdot)$ *for a.e. t:*

$$\mathrm{supp}(n(t, \cdot, \cdot)) \subset \{(x, y) \,|\, u(t, x, y) = 0\}$$
$$= \{x \,|\, u^Y(t, x) = 0\} \times \{y \,|\, u^X(t, y) = 0\}.$$

(iv) u^X *(resp.* u^Y *) satisfies the following limit equation for a.e. y:*

$$\forall t \in [0, T] \quad u^X(t, y) = u^X(0, y) + r\, t - \kappa \int_0^t \rho(s)\, ds - \int_0^t \left\langle \phi^X(t, \cdot, y), m(\cdot, y) \right\rangle ds, \quad (4)$$

where ϕ^X *is the limit of* $\frac{n_\varepsilon}{\rho_\varepsilon^X}$ *in* $L^\infty\left(w^* - [0, T] \times I, M^1(I)\right)$. *Moreover, for a.e. (t,y)*

$$\mathrm{supp}\left(\phi^X(t, \cdot, y)\right) = \{x \,|\, u^Y(t, x) = 0\}.$$

The second and third point of the results in Theorem 1.2 highlight the originality of this problem: the limit u separates the variables additively and therefore, the limit measure n is a product measure. This asymptotic decorrelation of the effects of the two loci relies on the following proposition, that is key to establish the convergence stated in Theorem 1.2:

Proposition 1.1. *Let us assume H4. FOr all $T > 0$, let n_ε be the positive solution of $(P(n_\varepsilon))$ on $[0, T]$. Define $\nu_\varepsilon = \frac{\rho_\varepsilon^X \rho_\varepsilon^Y}{n_\varepsilon \rho_\varepsilon}$. Then:*

$$\forall t \in [0, T], \quad \forall (x, y) \in I \times J, \quad 0 < \nu_m \le \nu_\varepsilon(t, x, y) \le \nu_M.$$

Indeed, the compactness result of Proposition 1.1 together with some a priori estimates relying on a maximum principle yield the convergence of Theorem 1.2 thanks to the Arzela-Ascoli theorem (see 1 for a flowchart that exposes the layout of the different results).

Moreover, although P_{u_ε} involves an equation on u_ε, one can notice that Theorem 1.2 states limit equations on u^X and u^Y (4). Instead of passing to the limit in the equation of u in P_{u_ε} once the convergence is established (as it is done in most asexual studies in the regime of small variance), the separation of variables $u(x, y) = u^X(y) + u^Y(x)$ allows us to take an alternative approach. In the proof Theorem 1.2, we will show indeed that $u^X = \lim\limits_{\varepsilon \to 0} \varepsilon \log\left(\rho_\varepsilon^X\right)$ and $u^Y = \lim\limits_{\varepsilon \to 0} \varepsilon \log\left(\rho_\varepsilon^Y\right)$. The idea is then to focus on the equations satisfied by ρ_ε^X and ρ_ε^Y instead of the equation satisfied by n_e:

$$\begin{cases} \varepsilon\, \partial_t \rho_\varepsilon^X(t, y) = (r - \kappa\, \rho_\varepsilon(t))\, \rho_\varepsilon^X(t, y) - \int_I m(x, y)\, n_\varepsilon(t, x, y)\, dx, \\ \varepsilon\, \partial_t \rho_\varepsilon^Y(t, x) = (r - \kappa\, \rho_\varepsilon(t))\, \rho_\varepsilon^Y(t, x) - \int_J m(x, y)\, n_\varepsilon(t, x, y)\, dy. \end{cases} \quad (5)$$

The advantage of considering (5) over (P_{u_ε}) is that the reproduction terms involved are linear, much simpler than the integral operator involved in the equation on u_ε. However, the difficulties are transferred on the selections terms $\int_I m(x, y)\, n_\varepsilon(t, x, y)\, dx$ and $\int_I m(x, y)\, n_\varepsilon(t, x, y)\, dx$ that asymptotically lead to involve ϕ^X and ϕ^Y in (4). These terms are new compared to the typical asexual studies, which only present two unknown variables in their constrained limit equation: u and ρ. Consequently, here, regularity in time, which would allow us to write the limit equation (4) under a differential form, is harder to get for ρ and ϕ^X (resp. ϕ^Y).

Nevertheless, under an additional hypothesis on the selection term m being additive, we show that the limit size of population ρ is BV. This result aligns with the typical analogous regularity obtained on the asymptotic size of population in aforementioned asexual studies.
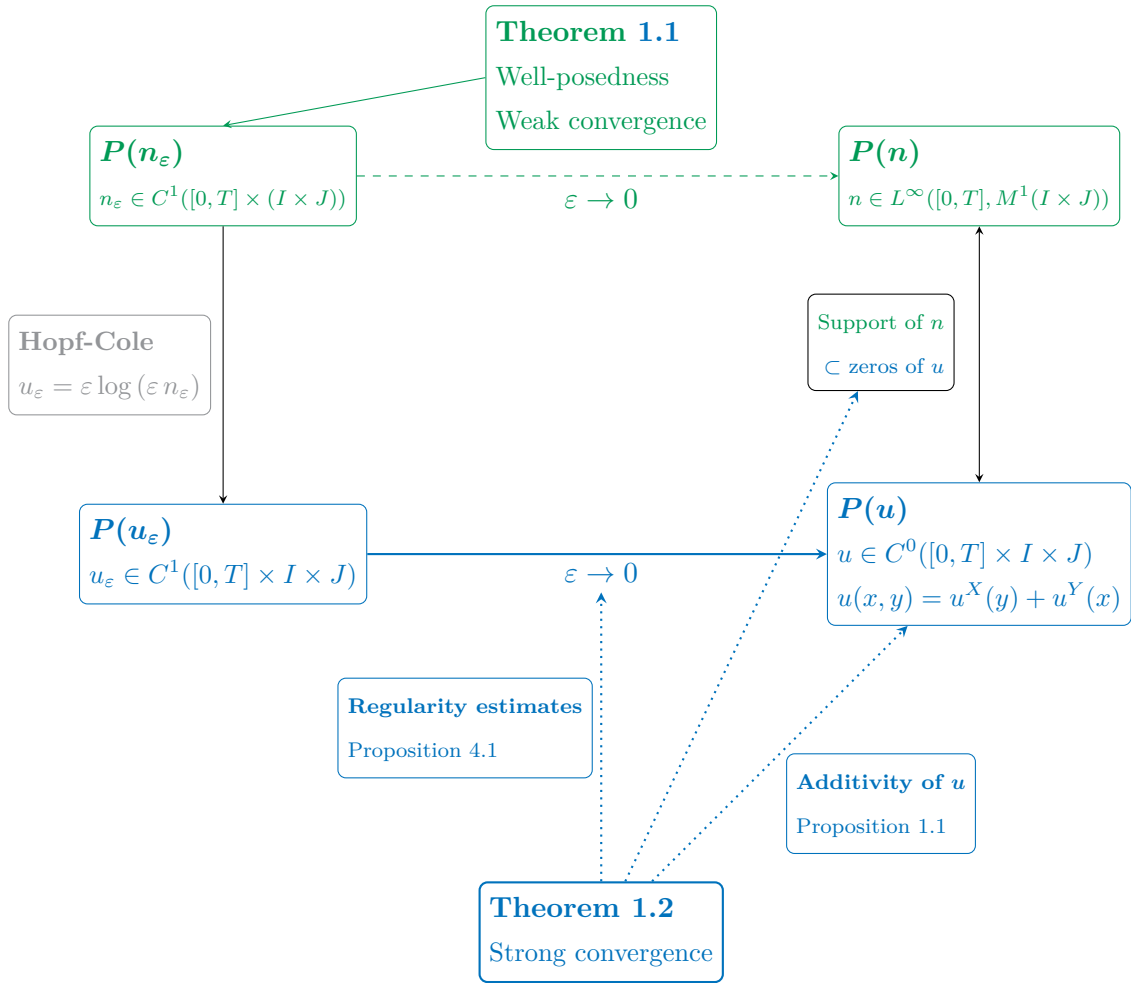
Theorem 1.1

Well-posedness

Weak convergence

$P(n_\varepsilon)$

$n_\varepsilon \in C^1([0,T] \times (I \times J))$

$\varepsilon \to 0$

$P(n)$

$n \in L^\infty([0,T], M^1(I \times J))$

Hopf-Cole

$u_\varepsilon = \varepsilon \log(\varepsilon\, n_\varepsilon)$

Support of n

$\subset$ zeros of u

$P(u_\varepsilon)$

$u_\varepsilon \in C^1([0,T] \times I \times J)$

$\varepsilon \to 0$

$P(u)$

$u \in C^0([0,T] \times I \times J)$

$u(x,y) = u^X(y) + u^Y(x)$

Regularity estimates

Proposition 4.1

Additivity of u

Proposition 1.1

Theorem 1.2

Strong convergence

Figure 1: Flowchart of the analytical results of Section 3, Section 4 and Section 5.

Theorem 1.3. *Suppose that there exists $m^X : I \to \mathbb{R}$ and $m^Y : J \to \mathbb{R}$ such that:*

$$m(x,y) = m^X(x) + m^Y(y). \tag{$\mathrm{H}_{m,\mathrm{add}}$}$$

Let n_ε be the solution to Eq. $(P(n_\varepsilon))$. Then, ρ_ε is locally uniformly bounded in $W^{1,1}(\mathbb{R}_+)$. Consequently, after extraction of a subsequence, ρ_ε converges to a BV-function ρ as ε vanishes. The limit ρ is non-decreasing as soon as there exists a constant $C > 0$ such that:

$$(r - \kappa\,\rho_\varepsilon^0)\,\rho_\varepsilon^0 - \iint_{\mathbb{R}^2} m(x,y)\,n_\varepsilon^0(x,y)\,dx\,dy \geq -C\,e^{\frac{o(1)}{\varepsilon}}. \tag{6}$$

The paper is organized as follows. In Section 2, we present qualitative results and numerical analysis that stem from the analysis of the subsequent sections, and demonstrate the interest of the model by exploring some biologically relevant situations. Next, in Section 3, we prove the well-posedness of $P(n_\varepsilon)$. Section 4 is dedicated to show Proposition 1.1 and derive uniform L^∞ and Lipschitz bounds for u_ε, which prepares the proof of the main result in Section 5. The interplay between the different results until that point is displayed in Fig. 1. Finally, in Section 6, we show that ρ is a BV-function, under the additional hypothesis ($\mathrm{H}_{m,\mathrm{add}}$).

2 Qualitative results and numerical analysis

In this section, we explore the insights on the dynamics of the allelic distribution in a population following the main result of the paper (Theorem 1.2), assuming that $(t,y) \mapsto \phi^X(t,\cdot,y)$, $(t,x) \mapsto \phi^Y(t,x,\cdot)$ and $t \mapsto n(t,\cdot,\cdot)$ (and by extension $t \mapsto \rho^X(t,\cdot)$, $t \mapsto \rho^Y(t,\cdot)$ and ρ) are continuous so that we can formally write:

$$\begin{cases} \forall (t,y) \in [0,T] \times J, & \partial_t u^X(t,y) = r - \kappa\,\rho(t) - \left\langle \phi^X(t,\cdot,y), m(\cdot,y) \right\rangle, \\ \forall (t,x) \in [0,T] \times I, & \partial_t u^Y(t,x) = r - \kappa\,\rho(t) - \left\langle \phi^Y(t,x,\cdot), m(x,\cdot) \right\rangle. \end{cases} \tag{7}$$

We first show that under a hypothesis of strict monotony $\mathrm{H}_{\mathrm{increasing}}$ on the selection, the population is strained to be monomorphic, i.e. all individuals share the same alleles $(\bar{x}(t), \bar{y}(t))$ at all times. Then, we derive canonical equations describing the dynamics of $(\bar{x}(t), \bar{y}(t))$ under monomorphism.

2.1 Monotonic selection yields monomorphism

We first show that a condition of monotony on m (in both variables) yields the limit allelic distribution to be monomorphic at all times:

Proposition 2.1. *For $T > 0$, assume that (7) holds and that m satisfies:*

$$\forall (x,y) \in I \times J, m(x,\cdot) \text{ and } m(\cdot,y) \text{ are increasing (resp. decreasing).} \tag{$\mathrm{H}_{\mathrm{increasing}}$}$$

Then: $\forall t \in [0,T]$, $\exists! \, (\bar{x}(t), \bar{y}(t)) \in I \times J$,

$$Supp\left(\rho^X\right) = \left[u^X\right]^{-1}(\{0\}) = \{\bar{y}(t)\}, \quad Supp\left(\rho^Y\right) = \left[u^Y\right]^{-1}(\{0\}) = \{\bar{x}(t)\}.$$

Diploid case: homozygosity. In the diploid case, the symmetries indicated in Remark 1.1 yield $u^X = u^Y$ and therefore $\bar{x}(t) = \bar{y}(t)$ for all $t \in [0, T]$. All individuals are therefore homozygote in a monomorphic population.

Proof of Proposition 2.1. For $t \in [0, T]$, since $n(t, \cdot, \cdot)$ is supported at the zeros of $u(t, \cdot, \cdot)$ (see Theorem 1.2), $\rho^X(t, \cdot)$ is supported on the set of the zeros of $u^X(t, \cdot)$, that we denote by $F_X(t)$, and $\rho^Y(t, \cdot)$ is supported on the set of the zeros of $u^Y(t, \cdot)$, that we denote by $F_Y(t)$. It is therefore sufficient to prove that $F_X(t)$ and $F_Y(t)$ are both singletons for all $t \in [0, T]$.

Since $u^X(t, \cdot)$ and $u^Y(t, \cdot)$ are continuous, $F_X(t)$ and $F_Y(t)$ are closed subsets of I and J, and are therefore compact sets. In particular, the extreme points of $F_X(t)$ (resp. $F_Y(t)$) denoted by $y_{\inf}(t)$ and $y_{\sup}(t)$ (respectively, $x_{\inf}(t)$ and $x_{\sup}(t)$) lie in $F_X(t)$ (respectively, $F_Y(t)$). As $(t, y_{\inf}(t))$ and $(t, y_{\sup}(t))$ maximise u^X and $(t, x_{\inf}(t))$ and $(t, x_{\sup}(t))$ maximise u^Y (since u^X are u^Y are non-positive, from Theorem 1.2), we obtain that

$$0 = \partial_t u^X(t, y_{\inf}(t)) = \partial_t u^X(t, y_{\sup}(t)) = \partial_t u^Y(t, x_{\inf}(t)) = \partial_t u^Y(t, x_{\sup}(t)).$$

The equations Eq. (7) next implies that

$$\forall t \in [0, t], \left\langle \phi^X(t, \cdot, y_{\inf}(t)), m(\cdot, y_{\inf}(t)) \right\rangle = \left\langle \phi^X(t, \cdot, y_{\sup}(t)), m(\cdot, y_{\sup}(t)) \right\rangle$$
$$= \left\langle \phi^Y(t, x_{\inf}(t), \cdot), m(x_{\inf}(t), \cdot) \right\rangle = \left\langle \phi^Y(t, x_{\sup}(t), \cdot), m(x_{\sup}(t), \cdot) \right\rangle.$$

Recall that, for $(t, x, y) \in [0, T] \times I \times J$, $\phi^X(t, \cdot, y)$ and $\phi^X(t, x, \cdot)$ are probability distributions supported respectively on a subset of $F_X(t)$ and $F_Y(t)$ (from Theorem 1.2). Then, we deduce from $\mathrm{H_{increasing}}$ that:

$$m(x_{\inf}(t), y_{\sup}(t)) \leq \left\langle \phi^X(t, \cdot, y_{\sup}(t)), m(\cdot, y_{\sup}(t)) \right\rangle$$
$$= \left\langle \phi^Y(t, x_{\inf}(t), \cdot), m(x_{\inf}(t), \cdot) \right\rangle$$
$$\leq m(x_{\inf}(t), y_{\sup}(t)).$$

Similarly, we obtain

$$m(x_{\sup}(t), y_{\inf}(t)) \leq \left\langle \phi^Y(t, x_{\sup}(t), \cdot), m(x_{\sup}(t), \cdot) \right\rangle$$
$$= \left\langle \phi^X(t, \cdot, y_{\inf}(t)), m(\cdot, y_{\inf}(t)) \right\rangle$$
$$\leq m(x_{\sup}(t), y_{\inf}(t)).$$

All the inequalities above must be equalities, which implies

$$\phi^X(t, x, y_{\sup}(t)) = \delta_{x=x_{\inf}(t)}, \quad \phi^X(t, x, y_{\inf}(t)) = \delta_{x=x_{\sup}(t)},$$
$$\phi^Y(t, x_{\sup}(t), y) = \delta_{y=y_{\inf}(t)}, \quad \phi^Y(t, x_{\inf}(t), y) = \delta_{y=y_{\sup}(t)}. \tag{8}$$

Since the support of $\phi^X(t, \cdot, y)$ (resp. $\phi^Y(t, x, \cdot)$) does not depend on y (resp. x) (see (*iv*) of Theorem 1.2), we obtain from (8) that $x_{\inf}(t) = x_{\sup}(t)$ and $y_{\inf}(t) = y_{\sup}(t)$. The latter yields the result. $\qquad \square$

Numerical simulations: robustness of monomorphism with regard to $\mathrm{H_{increasing}}$ of Proposition 2.2 with dimorphic initial densities. We show in Fig. 2 the result of numerical simulations solving a discretized version of $(P(n_\varepsilon))$ with initial dimophic states to test the robustness of monomorphic trajectories with regard to $\mathrm{H_{increasing}}$. We consider three

different selection functions $m(x,y) = x^2 + y^2$, $m(x,y) = (x+y)^2$, $m(x,y) = (1 - xy)^2$. Fig. 2 seems to indicate that monomorphic trajectories occur under a wider scope than the what is required by Proposition 2.1. Fig. 2 also gives some insights on the diversity of trajectories that can arise under different selections functions (see the next subsection for a more complete view).

2.2   Canonical equations under monomorphism

In all this section, let us fix $T > 0$ and let us assume that for all time $t \in [0,T]$, there exists unique points $\bar{x}(t)$ and $\bar{y}(t)$ such that:

$$\forall t \in [0,T] \quad u(t,\cdot,\cdot)^{-1}\left(\{0\}\right) = \{(\bar{x}(t), \bar{y}(t))\}. \tag{9}$$

In that case, for all $(t,x,y) \in [0,T] \times I \times J$, we deduced from Theorem 1.2 that:

$$\phi^X(t,\cdot,y) = \delta_{\bar{x}(t)}, \quad \phi^Y(t,x,\cdot) = \delta_{\bar{y}(t)}.$$

Hence, (7) reads:

$$\begin{cases} \forall (t,y) \in [0,T] \times J, \quad \partial_t u^X(t,y) = r - \kappa\,\rho(t) - m(\bar{x}(t)), y), \\ \forall (t,x) \in [0,T] \times I, \quad \partial_t u^Y(t,x) = r - \kappa\,\rho(t) - m(x, \bar{y}(t)). \end{cases} \tag{10}$$

Proposition 2.2. *For $T > 0$, assume that $m, u_0 \in C^2(I \times J)$ and that (10) holds. Then: $u \in C^0([0,T], C^2(I \times J))$ and the dynamics of the dominant alleles $(\bar{x}(t), \bar{y}(t))$ read:*

$$\begin{cases} \partial_{xx} u^Y(\bar{x}(t)) \frac{d\bar{x}}{dt} = \partial_x m(\bar{x}(t), \bar{y}(t)), \\ \partial_{yy} u^X(\bar{y}(t)) \frac{d\bar{y}}{dt} = \partial_y m(\bar{x}(t), \bar{y}(t)). \end{cases} \tag{11}$$

Diploid case: canonical equations. In the diploid case, the symmetries indicated in Remark 1.1 yield $u^X = u^Y$ and $\bar{x} = \bar{y}$, so the canonical equations (11) reduce to

$$\partial_{xx} u^X(\bar{x}(t)) \frac{d\bar{x}}{dt} = \partial_x m(\bar{x}(t), \bar{x}(t)). \tag{12}$$

Proof. Let us show how to obtain the first equation of (11) on $\bar{x}(t)$. The equation on $\bar{y}(t)$ can be obtained similarly.

As $0 = \partial_x u^Y(t, \bar{x}(t)) = u^Y(t, \bar{x}(t)) = \max u^Y(t, \cdot)$ for all $t \in [0,T]$, we get:

$$0 = \frac{d\,\partial_x u^Y(t, \bar{x}(t))}{dt} = \partial_t \partial_x u^Y(t, \bar{x}(t)) + \partial_{xx} u^Y(t, \bar{x}(t)) \frac{d\bar{x}}{dt}.$$

Differentiating (10) with regard to x reads:

$$\forall (t,x) \in [0,T] \times I, \quad \partial_x \partial_t u^Y(t,x) = -\partial_x m(x, \bar{y}(t)).$$

By substitution, we obtain:

$$\frac{d\bar{x}}{dt} \partial_{xx} u^Y(t, \bar{x}(t)) = \partial_x m(\bar{x}(t), \bar{y}(t)).$$
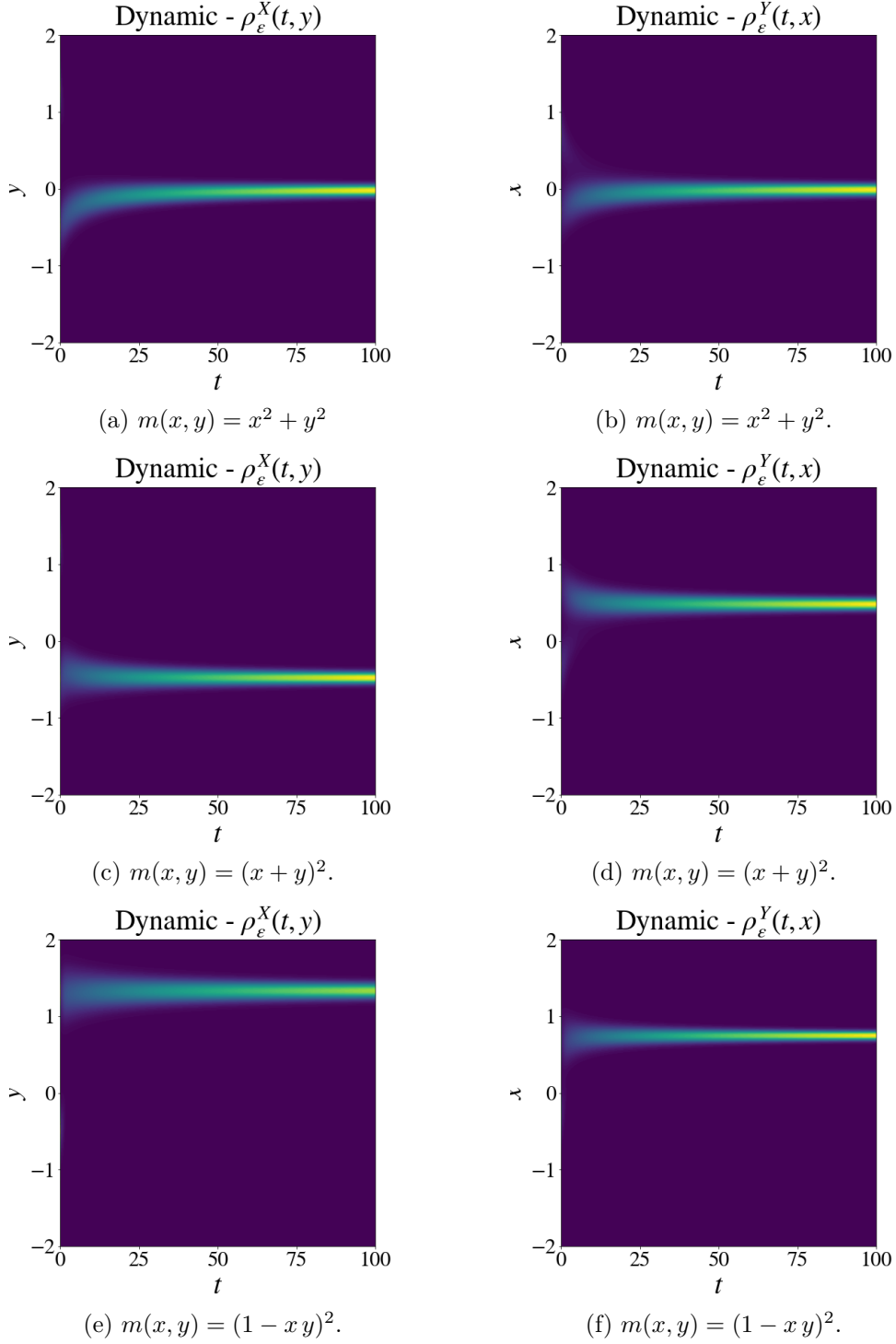
$\square$

(a) $m(x, y) = x^2 + y^2$

(b) $m(x, y) = x^2 + y^2$.

(c) $m(x, y) = (x + y)^2$.

(d) $m(x, y) = (x + y)^2$.

(e) $m(x, y) = (1 - x\,y)^2$.

(f) $m(x, y) = (1 - x\,y)^2$.

Figure 2: **Robustness of monomorphism with regard to assumption $H_{increasing}$ of Proposition 2.2 with dimorphic initial densities.** For each selection function (by row), we display the numerically solved dynamics of $\rho^X(t, y)$ (left panel) and $\rho^Y(t, x)$ (right panel) $((x, y) \in [-2, 2])$. The colors correspond to isolines of ρ^X and ρ^Y. The initial state is sum of two Gaussians centered in $(x_1, y_1) = (-0.3, 1.3)$ and $(x_2, y_2) = (0.7, -0.5)$ and of variance $\varepsilon = 0.05$. Lighter colors indicate stronger densities. The figures seem to indicate that the trajectories become monomorphic almost instantaneously and that this phenomenon actually occur under weaker conditions than $H_{increasing}$ of Proposition 2.2. One can also notice that the stationary dominant alleles that arise vary greatly from one selection function to another.

Remark 2.1. *As $\bar{x}(t)$ maximizes u^Y, we have $\partial_{xx}u^Y(t, \bar{x}(t)) \leq 0$ for all $t \in [0, T]$. If $\partial_{xx}u^Y(t, \bar{x}(t)) < 0$ for all $t \in [0, T]$, then we obtain:*

$$\forall t \in [0, T], \quad \frac{d\bar{x}}{dt} = \frac{\partial_x m(\bar{x}(t), \bar{y}(t))}{\partial_{xx}u^Y(t, \bar{x}(t))}.$$

As $\partial_t \partial_{xx} u^Y(t, x) = -\partial_{xx} m(x, \bar{y}(t))$, we obtain

$$\partial_{xx}u^Y(t, x) = \partial_{xx}u^Y(0, x) - \int_0^t \partial_{xx} m(x, \bar{y}(s))\, ds.$$

Consequently, the strict inequality is ensured if u_0 is strictly concave and m is convex.

Three examples. In this paragraph, we illustrate the insights provided by Proposition 2.2 through the study of the system for three given selection functions m. In all examples, we consider that $I = J = [-2, 2]$ and the initial state u_0 is given by $(\bar{x}_0, \bar{y}_0) \in [-2, 2]^2$ and:

$$u_0(x, y) = -((x - \bar{x}_0)^2 + (y - \bar{y}_0)^2).$$

1) $m(x, y) = x^2 + y^2, \quad \partial_x m(x, y) = 2x, \quad \partial_y m(x, y) = 2y, \quad \partial_{xx} m(x, y) = \partial_{yy} m(x, y) = 2.$

This selection function separates additively the variables. The canonical equation Eq. (11) then reads:

$$\begin{cases} \frac{d\bar{x}(t)}{dt} = -\frac{\bar{x}(t)}{t+1}, \\ \frac{d\bar{y}(t)}{dt} = -\frac{\bar{y}(t)}{t+1}. \end{cases}$$

We obtain that, for $t \geq 0$

$$\bar{x}(t) = \frac{\bar{x}_0}{t+1}, \quad \bar{y}(t) = \frac{\bar{y}_0}{t+1}.$$

Consequently, the system remains monomorphic and the dominant alleles evolve and converge towards $(0, 0)$.

2) $m(x, y) = (x + y)^2, \quad \partial_x m(x, y) = \partial_y m(x, y) = 2(x + y), \quad \partial_{xx} m(x, y) = \partial_{yy} m(x, y) = 2.$
The canonical equation Eq. (11) then reads:

$$\frac{d\bar{x}(t)}{dt} = \frac{d\bar{y}(t)}{dt} = -\frac{\bar{x}(t) + \bar{y}(t)}{t+1}.$$

We deduce that, for $t \geq 0$

$$\bar{x}(t) + \bar{y}(t) = \frac{\bar{x}_0 + \bar{y}_0}{(t+1)^2}, \quad \bar{x}(t) - \bar{y}(t) = \bar{x}_0 - \bar{y}_0,$$

which leads to:

$$\bar{x}(t) = \frac{\bar{x}_0 - \bar{y}_0}{2} + \frac{\bar{x}_0 + \bar{y}_0}{2(t+1)^2}, \quad \bar{y}(t) = \frac{\bar{y}_0 - \bar{x}_0}{2} + \frac{\bar{x}_0 + \bar{y}_0}{2(t+1)^2}.$$

On the contrary to the previous example, the dominant alleles of the monomorphic system evolve to converge towards a state that is dependent on the initial state of the system. Geometrically, it is the orthogonal projection of the initial point $(\bar{x}_0, \bar{y}_0)$ on the diagonal defined by $x + y = 0$.

3) $m(x, y) = (1 - xy)^2, \quad \partial_x m(x, y) = -2\,y\,(1 - xy), \quad \partial_y m(x, y) = -2\,x\,(1 - xy),$
$\partial_{xx} m(x, y) = 2\,y^2, \quad \partial_{yy} m(x, y) = 2\,x^2.$
In this case, the canonical equation (11) reads:

$$\frac{d\bar{x}(t)}{dt} = \frac{\bar{y}(t)\,(1 - \bar{x}(t)\bar{y}(t))}{1 + \int_0^t \bar{y}(s)^2\, ds} \qquad \frac{d\bar{y}(t)}{dt} = \frac{\bar{x}(t)\,(1 - \bar{x}(t)\bar{y}(t))}{1 + \int_0^t \bar{x}(s)^2\, ds}. \tag{13}$$

Without lack of generality, we can assume that $\bar{x}_0 \leq \bar{y}_0$.

Proposition 2.3. *Let $0 < \bar{x}_0 \leq \bar{y}_0 \leq 2$. Then the dominant alleles of the monomorphic system converge towards the stationary state $(x_F, y_F) \in (\mathbb{R}_+^*)^2$ that solves:*

$$\begin{cases} x_F\, y_F = 1, \\ y_F^2 - x_F^2 = \bar{y}_0^2 - \bar{x}_0^2. \end{cases} \tag{14}$$

Proof. First, we treat the case where $x_0\, y_0 = 1$. Then, the function $t \mapsto (x_0, y_0)$ defines a solution of (13). By uniqueness, it is the only solution and (x_0, y_0) satisfies (14).

Let us now suppose that $x_0\, y_0 < 1$ (the case where $x_0\, y_0 > 1$ can be treated following similar arguments). We define, for $A > 0$ yet to be specified:

$$t_A = \min\left\{\inf\{t \geq 0, (\bar{x}(t), \bar{y}(t)) \notin]0, A[^2\}, \inf\{t \geq 0, \bar{x}(t)\bar{y}(t) \notin]0, 1[\}\right\}.$$

For $t \leq t_A$, we have the following inequalities

$$\frac{\bar{y}\,(1 - \bar{x}\bar{y})}{1 + A^2\, t} \leq \frac{d\bar{x}}{dt} \leq \bar{y}\,(1 - \bar{x}\bar{y}), \quad \frac{\bar{x}\,(1 - \bar{x}\bar{y})}{1 + A^2\, t} \leq \frac{d\bar{y}}{dt} \leq \bar{x}\,(1 - \bar{x}\bar{y}). \tag{15}$$

Let us define (x^-, y^-) and (x^+, y^+) solutions of the following equations:

$$\begin{cases} \frac{dx^-(t)}{dt} = \frac{y^-(t)\left(1 - x^-(t)y^-(t)\right)}{1 + A^2\, t}, & \frac{dx^+(t)}{dt} = y^+(t)\,(1 - x^+(t)y^+(t)), \\ \frac{dy^-(t)}{dt} = \frac{x^-(t)\left(1 - x^-(t)y^-(t)\right)}{1 + A^2\, t}, & \frac{dy^+(t)}{dt} = x^+(t)\,(1 - x^+(t)y^+(t)), \\ (x^-(0), y^-(0)) = (\bar{x}_0, \bar{y}_0), & (x^+(0), y^+(0)) = (\bar{x}_0, \bar{y}_0). \end{cases} \tag{16}$$

By comparison, we deduce that (x^-, y^-) and (x^+, y^+) are respectively subsolution and supersolution of $(\bar{x}, \bar{y})$:

$$\forall t \leq t_A, \quad x^-(t) \leq \bar{x}(t) \leq x^+(t), \quad y^-(t) \leq \bar{y}(t) \leq y^+(t). \tag{17}$$

We define t_A^+ by

$$t_A^+ = \min\left\{\inf\{t \geq 0, (x^+(t), y^+(t)) \notin]0, A[^2\}, \inf\{t \geq 0, x^+(t)y^+(t) \notin]0, 1[\}\right\}.$$

We will show that x^+y^+ converges increasingly toward 1. First one can compute that

$$\frac{d\,(x^+y^+)}{dt} = \left(1 - x^+y^+\right)\left(x^{+2} + y^{+2}\right).$$

Next, one can notice from (16) that x^+ and y^+ both increase on $[0, t_A^+]$. We thus obtain that for $t \in [0, t_A^+]$

$$\left(1 - x^+y^+\right)\left(x_0^2 + y_0^2\right) \leq \frac{d(x^+y^+)}{dt} \leq 2A^2\left(1 - x^+y^+\right).$$

Hence, by comparison, x^+y^+ converges increasingly toward 1.

We next notice thanks to (16) that:

$$\frac{1}{2}\frac{dx^{+2}(t)}{dt} = x^+(t)y^+(t)\left(1 - x^+(t)y^+(t)\right) = \frac{1}{2}\frac{dy^{+2}(t)}{dt},$$

and hence:

$$\forall t \leq t_A^+, \quad x^{+2}(t) - y^{+2}(t) = \bar{x}_0^2 - \bar{y}_0^2.$$

Therefore, since $(\bar{x}_0, \bar{y}_0) \in [0,2]^2$, and $0 < x^+(t)\,y^+(t) < 1$ for $t \leq t_A^+$, the latter implies that, if we choose A large enough, x^+ and y^+ remain uniformly bounded above away from A. Therefore, we can consider t_A^+ arbitrarily large. We deduce that x^+ and y^+ converge increasingly to $x_F > 0$ and $y_F > 0$, satisfying (14).

We next show that (x^-, y^-) converges toward the same couple (x_F, y_F). Notice that for $t \leq t_A^+$, we have

$$\left(x^-(t), y^-(t) \right) \in\;]0, A[^2, \quad x^-(t), y^-(t) \leq 1.$$

Similarly as previously, we show by comparison that $x^- y^-$ converges increasingly toward 1, since

$$(1 - x^- y^-)\left(\frac{x_0^2 + y_0^2}{1 + A^2 t_A^+} \right) \leq \frac{d(x^- y^-)}{dt} \leq 2A^2 \left(1 - x^- y^-\right).$$

Next, we notice that we still have:

$$\frac{dx^{-2}(t)}{dt} = \frac{dy^{-2}(t)}{dt} \implies \forall t \leq t_A^+, \quad x^{-2}(t) - y^{-2}(t) = \bar{x}_0^2 - \bar{y}_0^2.$$

We deduce that x^- and y^- converge also increasingly to a solution of (14). As (14) has a unique solution in $\left(\mathbb{R}_+^* \right)^2$, it must be (x_F, y_F).

Finally, we obtain the announced result using (17). $\qquad\square$

Diploid case with the three selection functions. Due to the symmetries indicated in Remark 1.1, the dynamics of the dominant allele (12) are simpler, because they are limited to occur on the diagonal $x = y$.

1) $m(x,y) = x^2 + y^2$. We obtain that, for $t \geq 0$

$$\bar{x}(t) = \bar{y}(t) = \frac{\bar{x}_0}{t + 1}.$$

Consequently, the system remains monomorphic and the dominant alleles evolve and converge towards $(0,0)$.

2) $m(x,y) = (x + y)^2$. We obtain that, for $t \geq 0$

$$\bar{x}(t) = \bar{y}(t) = \frac{\bar{x}_0}{(t + 1)^2}.$$

Consequently, the system remains monomorphic and the dominant alleles evolve and converge towards $(0,0)$.

3) $m(x,y) = (1 - xy)^2$. In that case, we deduce from Proposition 2.3 that the dominant alleles of the monomorphic system converge toward $(1,1)$.

Numerical analysis. Note that Proposition 2.2 relies on the fact that equation (10) holds. Due to lack of regularity estimates, in this paper we have proved this property only in a weaker integral form (4). However, we conjecture that this property would hold in a rather general framework. In Fig. 3 using numerical simulations, we investigate whether the qualitative results obtained above are consistent in the case of the three examples considered in Fig. 2. For each selection function above, we display the trajectories of the dominant allelic effects $\bar{x}$ and $\bar{y}$, for 20 numerical resolution of Eq. $(P(n_\varepsilon))$ with $\varepsilon = 0.01$ (plain lines), with initial conditions uniformly randomized over the square $[-2,2]^2$ (each color corresponds to an initial condition). We confront them to the canonical equations given in Proposition 2.2, for the same set of 20 initial conditions (dashed lines). The corresponding trajectories as well as the final states (full circle for the model and cross for the canonical equations) are quite in agreement.
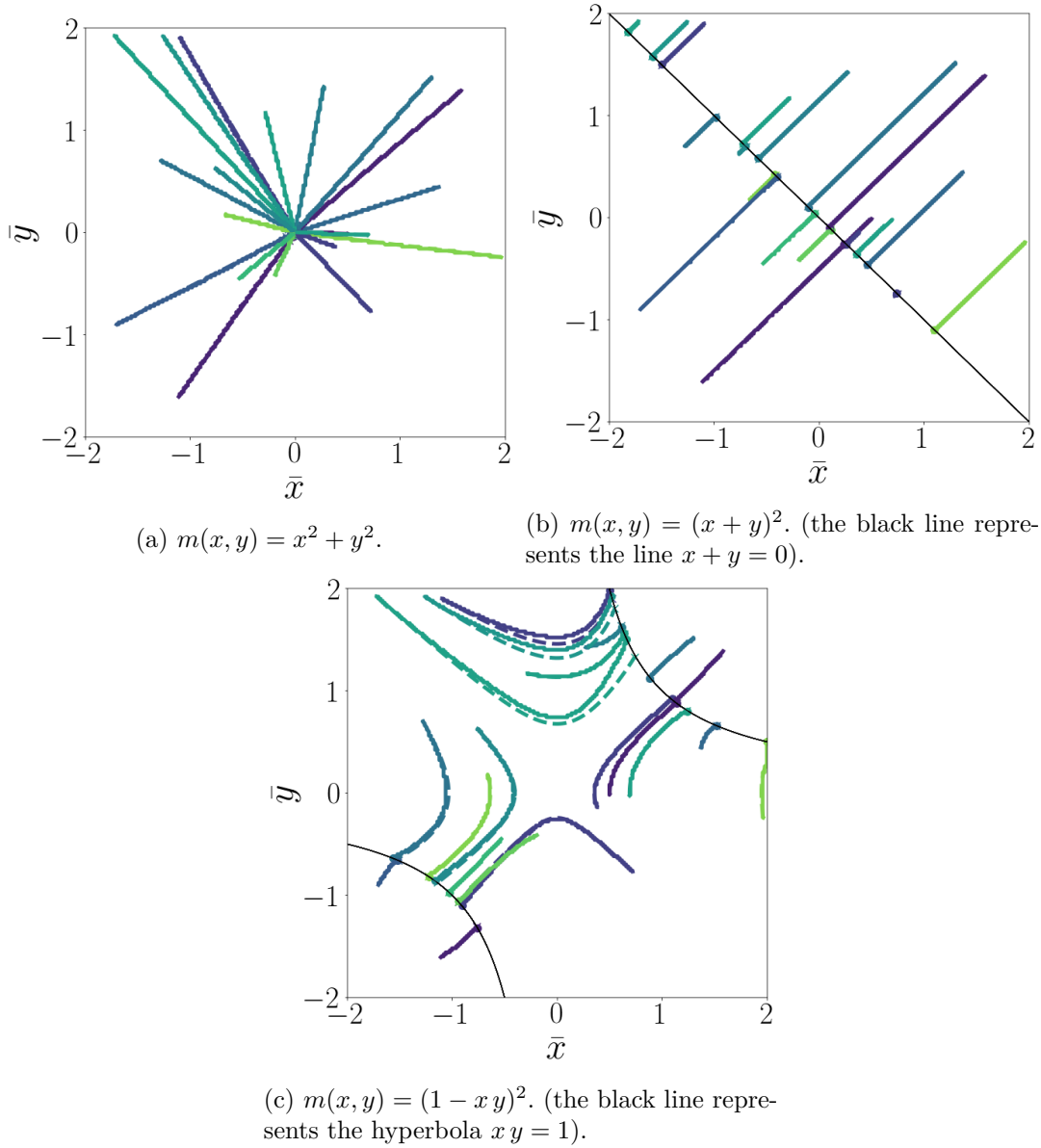
(a) $m(x, y) = x^2 + y^2$.

(b) $m(x, y) = (x + y)^2$. (the black line represents the line $x + y = 0$).

(c) $m(x, y) = (1 - x y)^2$. (the black line represents the hyperbola $x y = 1$).

Figure 3: **Simulated trajectories of the dominant alleles $\bar{x}$ and $\bar{y}$.** The plain lines correspond to the trajectories of $(x^{\max}(t), y^{\max}(t))$ that realizes the maximum of $n_\varepsilon(t, \cdot, \cdot)$ in the numerical resolution of $(P(n_\varepsilon))$, with $\varepsilon = 0.01$. The dashed lines correspond to the numerical resolution of the canonical equations given in Proposition 2.2. Each color corresponds to one trajectory starting at an initial monomorphic state chosen randomly and uniformly in $[-2, 2]^2$. The final states of the trajectories obtained from the discretization of $(P(n_\varepsilon))$ are indicated by full circles. This figure shows that the qualitative derivation of the section are numerically consistent with the model.

16

3 Preliminary results on the well-posedness of $P(n_\varepsilon)$: proof of Theorem 1.1

Well-posedness of $P(n_\varepsilon)$ In this section, we prove Theorem 1.1. The proof relies on two lemmas. We fix $T_M > 0$. The first lemma gives a priori estimates for a solution of $(P(n_\varepsilon))$ on $[0, T_M] \times I \times J$. The second one relies on a contraction mapping argument for $T > 0$ small, chosen uniformly with regard to the initial state, so that the reiteration of the process ensures the existence and uniqueness of a solution on $[0, T_M] \times I \times J$.

Lemma 1. *Let $T_M > 0$ and $n_\varepsilon \in C^1([0, T_M] \times I \times J)$ be a solution of $(P(n_\varepsilon))$. Then, under the assumptions H1 and H3, we have the following a priori bounds for $t \in [0, T_M]$*

$$\rho_0^- \le \rho_\varepsilon(t) \le \rho_0^+, \quad \|\rho_\varepsilon^X(t,\cdot)\|_\infty \le \|\rho_\varepsilon^{X,0}\|_\infty e^{\frac{rt}{\varepsilon}}, \quad \|\rho_\varepsilon^Y(t,\cdot)\|_\infty \le \|\rho_\varepsilon^{Y,0}\|_\infty e^{\frac{rt}{\varepsilon}}, \tag{18}$$

$$
\begin{aligned}
\|n_\varepsilon(t,\cdot,\cdot)\|_\infty &\le e^{\frac{rt}{2\varepsilon}} \|n_\varepsilon(0,\cdot,\cdot)\|_\infty + e^{\frac{2rt}{\varepsilon}} \frac{\|\rho_\varepsilon^{X,0}\|_\infty \|\rho_\varepsilon^{Y,0}\|_\infty}{\rho_0^-} (e^{\frac{rt}{2\varepsilon}} - 1) \\
&\le e^{\frac{rT_M}{2\varepsilon}} \|n_\varepsilon(0,\cdot,\cdot)\|_\infty + e^{\frac{2rT_M}{\varepsilon}} \frac{\|\rho_\varepsilon^{X,0}\|_\infty \|\rho_\varepsilon^{Y,0}\|_\infty}{\rho_0^-} (e^{\frac{rT_M}{2\varepsilon}} - 1) =: N_{T_M},
\end{aligned}
\tag{19}
$$

$$
\begin{aligned}
\|\partial_x n_\varepsilon(t,\cdot,\cdot)\|_\infty &\le \left(\|\partial_x n_\varepsilon^0\|_\infty + N_{T_M} \frac{t}{\varepsilon} \|\partial_x m\|_\infty \right) e^{\frac{\|\rho_\varepsilon^{X,0}\|_\infty |J|}{2\rho_0^-} e^{\frac{rt}{\varepsilon}} + \frac{rt}{2\varepsilon}} \\
&\le \left(\|\partial_x n_\varepsilon^0\|_\infty + N_{T_M} \frac{T_M}{\varepsilon} \|\partial_x m\|_\infty \right) e^{\frac{\|\rho_\varepsilon^{X,0}\|_\infty |J|}{2\rho_0^-} e^{\frac{rT_M}{\varepsilon}} + \frac{rT_M}{2\varepsilon}} =: N_{T_M}^x.
\end{aligned}
\tag{20}
$$

The proof of Lemma 1 relies on classical computations and is left to be consulted in A. Before stating the next lemma, let us define, for $n \in C^1([0, T] \times I \times J, \mathbb{R}_+)$

$$\rho(n) := \iint_{I \times J} n(\cdot, x, y) \, dx \, dy, \quad \rho^X(n)(t,y) := \int_I n(t, x, y) \, dx, \quad \rho^Y(n)(t,x) := \int_J n(t, x, y) \, dy.$$

We also define, for $T \le T_M$

$$
\begin{aligned}
\mathcal{A}_\varepsilon^0 = \Big\{ & n \in C^1([0, T] \times I \times J, \mathbb{R}_+) \,|\, n(0, \cdot, \cdot) = n_\varepsilon^0, \quad \rho(n) \in [\rho_0^-, \rho_0^+], \\
& \rho^X(n)(t,y) \le \|\rho_\varepsilon^{X,0}\|_\infty e^{r\frac{t}{\varepsilon}}, \quad \rho^Y(n)(t,x) \le \|\rho_\varepsilon^{Y,0}\|_\infty e^{r\frac{t}{\varepsilon}}, \\
& \|n(t,\cdot,\cdot)\|_\infty \le e^{\frac{rt}{2\varepsilon}} \|n_\varepsilon^0\|_\infty + \frac{\|\rho_\varepsilon^{X,0}\|_\infty \|\rho_\varepsilon^{Y,0}\|_\infty}{\rho_0^-} e^{\frac{2rt}{\varepsilon}} \left(e^{\frac{rt}{2\varepsilon}} - 1 \right), \\
& \|\partial_x n_\varepsilon(t,\cdot,\cdot)\|_\infty \le \left(\|\partial_x n_\varepsilon^0\|_\infty + N_{T_M} \frac{T_M}{\varepsilon} \|\partial_x m\|_\infty \right) e^{\frac{\|\rho_\varepsilon^{X,0}\|_\infty |J|}{2\rho_0^-} e^{\frac{rt}{\varepsilon}} + \frac{rt}{2\varepsilon}} \\
& \|\partial_y n_\varepsilon(t,\cdot,\cdot)\|_\infty \le \left(\|\partial_y n_\varepsilon^0\|_\infty + N_{T_M} \frac{T_M}{\varepsilon} \|\partial_y m\|_\infty \right) e^{\frac{\|\rho_\varepsilon^{Y,0}\|_\infty |I|}{2\rho_0^-} e^{\frac{rt}{\varepsilon}} + \frac{rt}{2\varepsilon}} \Big\},
\end{aligned}
$$

which is a closed subspace of $X := C^1([0, T] \times I \times J, \mathbb{R}_+)$ and has a Banach space structure with the norm $\|.\|_X := \|.\|_\infty + \|\partial_x \cdot\|_\infty + \|\partial_y \cdot\|_\infty$. Let us also define

$$
\Phi : \begin{cases} \mathcal{A}_\varepsilon^0 \to X \\ n \mapsto \Phi(n) : (t,x,y) \mapsto n_\varepsilon^0(x,y) e^{-\frac{1}{\varepsilon} \int_0^t A[n](s,x,y)ds} + \frac{1}{\varepsilon} \int_0^t B[n](\tau,x,y) e^{-\frac{1}{\varepsilon} \int_\tau^t A[n](s,x,y)ds} \, d\tau, \end{cases}
\tag{21}
$$

where

$$A[n](s,x,y) = m(x,y) + \kappa\,\rho(n)(s), \quad B[n](\tau,x,y) = \frac{r}{2}\left(\frac{\rho^X(n)(\tau,y)\,\rho^Y(n)(\tau,x)}{\rho(n)(\tau)} + n(\tau,x,y)\right).$$

.

Lemma 2. *Let $T \leq T_M$. Then, under the assumptions H1 and H3, we have:*

1. *$\Phi\left(\mathcal{A}_\varepsilon^0\right) \subset \mathcal{A}_\varepsilon^0$.*

2. *For T small enough, Φ is a contraction mapping. Such a T can be chosen uniformly with regard to the intial state.*

The proof of this lemma can be found in Appendix B.

From Lemma 1, any solution of $P\left(n_\varepsilon\right)$ in $C^1\left([0,T]\times I\times J,\mathbb{R}_+\right)$, for all $T\leq T_M$, lies in $\mathcal{A}_\varepsilon^0$. Next, Lemma 2 allows us to use the Banach-Picard fixed point theorem in $\mathcal{A}_\varepsilon^0$ to prove existence and uniqueness of a solution to $P\left(n_\varepsilon\right)$ in $\mathcal{A}_\varepsilon^0$, hence in $C^1\left([0,T]\times I\times J,\mathbb{R}_+\right)$. Since T does not depend on the initial state, we can iterate this process to extend the well-posedness to $C^1\left([0,T_M]\times I\times J,\mathbb{R}_+\right)$. Finally, since T_M can be arbitrarily large, there exists a unique solution to $P\left(n_\varepsilon\right)$ is $C^1\left(\mathbb{R}_+\times I\times J,\mathbb{R}_+\right)$

Weak convergence of (n_ε). From Lemma 1, for $\varepsilon > 0$ and $t \in [0,T]$, we have:

$$\|n_\varepsilon(t,\cdot,\cdot)\|_{L^1(I\times J)} \leq \rho_0^+.$$

Consequently, (n_ε) is bounded in $L^\infty\left([0,T],L^1(I\times J)\right)$. Hence, there exists a subsequence that converges in $L^\infty\left(w^* - [0,T], M^1(I\times J)\right)$ to a measure n.

4 Proof of Proposition 1.1 and regularity estimates on u_ε

In this section, we provide the proofs of the regularity estimates that will be used in the proof of Theorem 1.2.

4.1 Proof of Proposition 1.1

In this subsection, we prove the Proposition 1.1, which is a key step to prove the additive separation of variables for u (see Theorem 1.2).

Let $t \in [0,T]$, $(x,y) \in I \times J$. We differentiate ν_ε with regard to t to find:

$$\begin{aligned}
\varepsilon\,\partial_t\nu_\varepsilon(t,x,y) &= \frac{\rho_\varepsilon^X\,\varepsilon\,\partial_t\rho_\varepsilon^Y + \rho_\varepsilon^Y\,\varepsilon\,\partial_t\rho_\varepsilon^X}{n_\varepsilon\,\rho_\varepsilon} - \left(\frac{\varepsilon\,\partial_t n_\varepsilon}{n_\varepsilon} + \frac{\varepsilon\,\partial_t\rho_\varepsilon}{\rho_\varepsilon}\right)\nu_\varepsilon \\
&= 2\left(r - \kappa\,\rho_\varepsilon\right)\nu_\varepsilon - \int_I m(x',y)\frac{n_\varepsilon(x',y)\,\rho_\varepsilon^Y(x)}{n_\varepsilon(x,y)\rho_\varepsilon}\,dx' - \int_J m(x,y')\frac{n_\varepsilon(x,y'),\rho_\varepsilon^X(y)}{n_\varepsilon(x,y)\rho_\varepsilon}\,dy' \\
&\quad - \nu_\varepsilon\left(\frac{r}{2}\nu_\varepsilon + \frac{r}{2} - m(x,y) - \kappa\,\rho_\varepsilon + r - \kappa\,\rho_\varepsilon - \iint_{I\times J} m(x,y)\frac{n_\varepsilon(x,y)}{\rho_\varepsilon}\,dx\,dy\right) \\
&= \frac{r}{2}\nu_\varepsilon(1-\nu_\varepsilon) + \nu_\varepsilon\left(m(x,y) + \iint_{I\times J} m(x,y)\frac{n_\varepsilon(x,y)}{\rho_\varepsilon}\,dx\,dy\right) \\
&\quad - \iint_{I\times J}\left(m(x',y) + m(x,y')\right)\frac{n_\varepsilon(x',y)\,n_\varepsilon(x,y')}{n_\varepsilon(x,y)\,\rho_\varepsilon}\,dx'\,dy'.
\end{aligned}$$

$$(22)$$

Since $m \geq 0$ and $n_\varepsilon, \rho_\varepsilon^X, \rho_\varepsilon^Y, \rho_\varepsilon > 0$, we get:

$$\varepsilon \, \partial_t \nu_\varepsilon(t, x, y) \leq \left(\frac{r}{2} + 2\|m\|_\infty \right) \nu_\varepsilon - \frac{r}{2} \nu_\varepsilon^2.$$

Hence:

$$\nu_\varepsilon(t, x, y) \leq \frac{1}{\frac{1}{\nu_\varepsilon^0(x,y)} e^{-\left(\frac{r}{2} + 2\|m\|_\infty\right) \frac{t}{\varepsilon}} + \frac{r}{(r+4\|m\|_\infty)} \left(1 - e^{-\left(\frac{r}{2} + 2\|m\|_\infty\right) \frac{t}{\varepsilon}} \right)}$$

$$\leq \frac{1}{\min\left(\frac{1}{\nu_\varepsilon^0(x,y)}, \frac{r}{(r+4\|m\|_\infty)}\right)} \leq \max\left(\|\nu_\varepsilon^0\|_\infty, \left(1 + \frac{4\|m\|_\infty}{r} \right) \right) \leq \nu_M.$$

Similarly, from (22), we have:

$$\varepsilon \, \partial_t \nu_\varepsilon(t, x, y) \geq \left(\frac{r}{2} - 2\|m\|_\infty \right) \nu_\varepsilon - \frac{r}{2} \nu_\varepsilon^2.$$

Recall from H1 that: $r > 2\|m\|_\infty$. Hence:

$$\nu_\varepsilon(t, x, y) \geq \frac{1}{\frac{1}{\nu_\varepsilon^0(x,y)} e^{-\left(\frac{r}{2} - 2\|m\|_\infty\right) \frac{t}{\varepsilon}} + \frac{r}{r-4\|m\|_\infty} \left(1 - e^{-\left(\frac{r}{2} - 2\|m\|_\infty\right) \frac{t}{\varepsilon}} \right)}$$

$$\geq \frac{1}{\max\left(\frac{1}{\nu_\varepsilon^0(x,y)}, \frac{r}{r-4\|m\|_\infty}\right)} \geq \min\left(\|\nu_\varepsilon^0\|_\infty, \left(1 - \frac{4\|m\|_\infty}{r} \right) \right) = \nu_m.$$

4.2 Regularity estimates on u_ε

In this subsection, we prove the regularity estimates that underlie the convergence of u_ε based on the Arzela-Ascoli theorem.

Proposition 4.1. *Assume that H1, H2 and H3 hold. Let $\varepsilon > 0$, $T > 0$, and $u_\varepsilon \in C^1([0,T] \times I \times J)$ be the solution of P_{u_ε}. Then, u_ε is Lipschitz continuous in time and in space, and is bounded in $C([0,T] \times I \times J)$, all the bounds being uniform with regard to ε.*

Proof of Proposition 4.1.

Lipshitz bounds in time. The existence of the upper bound for ν_ε in Proposition 1.1 along with H1 and Theorem 1.1 imply directly the following uniform Lipschitz bound in time on u_ε:

$$\|\partial_t u_\varepsilon\|_\infty \leq \|m\|_\infty + \kappa \, \rho_0^+ + \frac{r}{2} \left(1 + \nu_M \right).$$

Lipschitz bounds in space. In this paragraph, we rely on a maximum principle to show the following inequalities for all $(t, x, y) \in [0, T] \times I \times J$:

$$|\partial_x u_\varepsilon(t, x, y)| < 2\|\partial_x m\|_\infty T + \|\partial_x u_\varepsilon^0\|_\infty + 1, \quad |\partial_y u_\varepsilon(t, x, y)| < 2\|\partial_y m\|_\infty T + \|\partial_y u_\varepsilon^0\|_\infty + 1. \quad (23)$$

The latter together with H2 implies that (u_ε) is uniformly Lipschitz continuous in space.

Let us show (23). For $t \in [0, T], (x, y, x', y') \in \mathring{I}^4$, define $\Delta_\varepsilon(x', y', x, y, t) = u_\varepsilon(t, x', y) + u_\varepsilon(t, x, y') - u_\varepsilon(t, x, y)$. Differentiating the equation on u_ε from P_{u_ε} with regard to x, we obtain:

$$\partial_t \, \partial_x u_\varepsilon = -\partial_x m + \frac{r}{2\rho_\varepsilon} \iint_{I \times J} \frac{1}{\varepsilon} \left[\partial_x u_\varepsilon(x, y') - \partial_x u_\varepsilon(x, y) \right] e^{\Delta_\varepsilon(x', y', x, y, t)} dx' \, dy'.$$

19

Let us define for $(x, y) \in I \times J$:

$$w_\varepsilon(t, x, y) = \partial_x u_\varepsilon(t, x, y) - 2\|\partial_x m\|_\infty \, t - \|\partial_x u_\varepsilon^0\|_\infty - 1.$$

First, we have that for all $(x, y) \in I \times J$: $w_\varepsilon(0, x, y) < 0$. Next, let us assume that there exists $t > 0$ such that $\max_{I \times J} w_\varepsilon(t, \cdot) \geq 0$. Then we can define:

$$t_0 = \inf\{t > 0, \max_{I \times J} w_\varepsilon(t, \cdot) \geq 0\}.$$

By continuity of $\partial_x u_\varepsilon$ at $t = 0$ and compactness of I, we have: $t_0 > 0$. Let $(x_0, y_0) \in I \times J$ be such that: $w_\varepsilon(t_0, x_0, y_0) = \max_{I \times J} w_\varepsilon(t_0, \cdot)$. Then, we have:

$$0 \leq \partial_t w_\varepsilon(t_0, x_0, y_0)$$
$$= -\partial_x m(x_0, y_0) + \frac{r}{2\rho_\varepsilon(t_0)} \iint_{I \times J} \frac{1}{\varepsilon} \left[w_\varepsilon(x_0, y') - w_\varepsilon(x_0, y_0)\right] e^{\Delta_\varepsilon(x', y', x, y, t)} dx' \, dy - 2\|\partial_x m\|_\infty$$
$$\leq -\|\partial_x m\|_\infty < 0.$$

which is a contradiction. Therefore:

$$\forall t \in [0, t], \, (x, y) \in I \times J, w_\varepsilon(t, x, y) < 0,$$

which yields:

$$\partial_x u_\varepsilon(t, x, y) < 2\|\partial_x m\|_\infty t + \|\partial_x u_\varepsilon^0\|_\infty + 1.$$

Next, let us consider, for $(t, x, y) \in [0, T] \times I \times J$:

$$v_\varepsilon(t, x, y) = \partial_x u_\varepsilon(t, x, y) + 2\|\partial_x m\|_\infty \, t + \|\partial_x u_\varepsilon^0\| + 1.$$

We can repeat the argument above switching maximum to minimum. First, we have that $v_\varepsilon(0, \cdot, \cdot) > 0$. If we assume that there exists $t > 0$ such that $\min v_\varepsilon(t, \cdot, \cdot) \leq 0$ and define:

$$t_0 = \inf\{t > 0, \min v_\varepsilon(t, \cdot, \cdot) \leq 0\} > 0,$$

and (x_0, y_0) realising that minimum, we would have:

$$0 \geq \partial_t v_\varepsilon(t_0, x_0, y_0)$$
$$= -\partial_x m(x_0, y_0) + \frac{r}{2\rho_\varepsilon(t_0)} \iint_{I \times J} \frac{1}{\varepsilon} \left[w_\varepsilon(x_0, y') - w_\varepsilon(x_0, y_0)\right] e^{\Delta_\varepsilon(x', y', x, y, t)} dx' \, dy + 2\|\partial_x m\|_\infty$$
$$\geq \|\partial_x m\|_\infty > 0.$$

Which is a contradiction. Thus $v_\varepsilon > 0$ and for all $(t, x, y) \in [0, T] \times I \times J$:

$$\partial_x u_\varepsilon > -2\|\partial_x m\|_\infty \, t - \|\partial_x u_\varepsilon^0\| - 1.$$

The bound on $\partial_y u_\varepsilon$ can be obtained using similar arguments.

Uniform L^∞ bounds on u_ε. Let us show the following lemma:

Lemma 3. *For any $\delta > 0$, there exists $\varepsilon_0 > 0$ such that for all $0 < \varepsilon \leq \varepsilon_0$:*

$$-\delta < \max u_\varepsilon < \delta, \qquad \min u_\varepsilon > -\delta - |I| \left(\|\partial_x u_\varepsilon\|_\infty + \|\partial_y u_\varepsilon\|_\infty\right).$$

Hence, (u_ε) is uniformly bounded for ε small.

Proof.

1. Bounds on $\max u_\varepsilon$. Let $\delta > 0$. On the one hand, we have:

$$\rho_0^- \leq \iint_{I \times J} \frac{\exp\left(\frac{u_\varepsilon(x,y)}{\varepsilon}\right)}{\varepsilon} \, dx \, dy \leq |I|^2 \frac{\exp\left(\frac{\max u_\varepsilon}{\varepsilon}\right)}{\varepsilon},$$

which leads to:

$$\max u_\varepsilon \geq \varepsilon \log\left(\frac{\varepsilon \rho_0^-}{|I|^2}\right) \xrightarrow[\varepsilon \to 0]{} 0.$$

That implies that there exists $\varepsilon_0 > 0$, such that:

$$\forall \, 0 < \varepsilon \leq \varepsilon_0, \quad -\delta < \max u_\varepsilon.$$

On the other hand, if $\max u_\varepsilon = u_\varepsilon(x_m, y_m) > 0$, then, for all $(x,y) \in I \times J$, we have:

$$u_\varepsilon(x,y) \geq u_\varepsilon(x_m, y_m) - \|\partial_x u_\varepsilon\|_\infty \, |x - x_m| - \|\partial_y u_\varepsilon\|_\infty \, |y - y_m|. \tag{24}$$

Therefore, using the fact that u_ε is Lipschitz continuous in space, we obtain, for $(x,y) \in I \times J$ such that $|x - x_m| \leq \frac{u_\varepsilon(x_m, y_m)}{4\|\partial_x u_\varepsilon\|_\infty}$, $|y - y_m| \leq \frac{u_\varepsilon(x_m, y_m)}{4\|\partial_y u_\varepsilon\|_\infty}$:

$$u_\varepsilon(x,y) \geq \frac{u_\varepsilon(x_m, y_m)}{2}.$$

We deduce that:

$$\rho_0^+ \geq \iint_{I \times J} \frac{\exp\left(\frac{u_\varepsilon(x,y)}{\varepsilon}\right)}{\varepsilon} \, dx \, dy \geq \iint_{|x-x_m| \leq \frac{u_\varepsilon(x_m,y_m)}{4\|\partial_x u_\varepsilon\|_\infty}, \, |y-y_m| \leq \frac{u_\varepsilon(x_m,y_m)}{4\|\partial_y u_\varepsilon\|_\infty}} \frac{\exp\left(\frac{u_\varepsilon(x,y)}{\varepsilon}\right)}{\varepsilon} \, dx \, dy$$

$$\geq \frac{u_\varepsilon(x_m, y_m)^2}{4 \, \|\partial_x u_\varepsilon\|_\infty \, \|\partial_y u_\varepsilon\|_\infty} \frac{\exp\left(\frac{u_\varepsilon(x_m, y_m)}{2\varepsilon}\right)}{\varepsilon}.$$

The latter yields that if $u_\varepsilon(x_m, y_m) \geq \delta$, then:

$$\rho_0^+ \geq \frac{\delta^2}{4 \, \|\partial_x u_\varepsilon\|_\infty \, \|\partial_y u_\varepsilon\|_\infty} \frac{\exp\left(\frac{\delta}{2\varepsilon}\right)}{\varepsilon} \xrightarrow[\varepsilon \to 0]{} +\infty.$$

Therefore, there exists $\varepsilon_0 > 0$ such that:

$$\forall \, 0 < \varepsilon \leq \varepsilon_0, \quad -\delta < \max u_\varepsilon < \delta.$$

2. Bound on $\min u_\varepsilon$. From (24), for all $(x,y) \in I \times J$, we have:

$$u_\varepsilon(x,y) > \max u_\varepsilon - |I| \left(\|\partial_x u_\varepsilon\|_\infty + \|\partial_y u_\varepsilon\|_\infty\right) > -\delta - |I| \left(\|\partial_x u_\varepsilon\|_\infty + \|\partial_y u_\varepsilon\|_\infty\right).$$

Thanks to (23), the r.h.s is uniformly bounded. $\qquad\qquad\square$

$\square$

5 Proof of Theorem 1.2

In this section, we provide the proof for the main result of this paper, which is the convergence of u_ε towards a non-positive limit u that separates additively the variables. We also link the support of n to the zeros of u and derive a limit equation.

Limit u. From Proposition 4.1, there exists $\varepsilon_0 > 0$ such that $(u_\varepsilon)_{\varepsilon \leq \varepsilon_0}$ is uniformly bounded in $C^0([0, T] \times I \times J)$, and uniformly Lipschitz continuous in space and time. Hence, from the theorem of Arzela-Ascoli, after extraction of a subsequence, (u_ε) converges uniformly toward a limit $u \in C^0([0, T] \times I \times J)$, that is also Lipschitz continuous.

$u(t, x, y) \leq \max u(t, x, \cdot) + \max u(t, \cdot, y)$. From H4 and Proposition 1.1, there exists $\nu_m > 0$ such that:

$$
\forall (t, x, y) \in [0, T] \times I \times J, \quad \nu_m \leq \nu_\varepsilon(t, x, y)
$$

$$
= \iint_{I \times J} \frac{1}{\varepsilon \, \rho_\varepsilon} \exp\left[\frac{u_\varepsilon(t, x, y') + u_\varepsilon(t, x', y) - u_\varepsilon(t, x, y)}{\varepsilon} \right] dx \, dy
$$

$$
\leq \frac{|I|^2}{\rho_0^-} \frac{1}{\varepsilon} \exp\left[\frac{\max(u_\varepsilon(t, x, \cdot)) + \max u_\varepsilon(t, \cdot, y)) - u_\varepsilon(t, x, y)}{\varepsilon} \right].
$$

Moreover, for all $(t, x, y) \in [0, T] \times I \times J$, and $\delta > 0$, there exists $\varepsilon_0 > 0$ such that for $0 < \varepsilon \leq \varepsilon_0$,

$$
\max(u_\varepsilon(t, x, \cdot)) \leq \max(u(t, x, \cdot)) + \delta, \quad \max(u_\varepsilon(t, \cdot, y)) \leq \max(u(t, \cdot, y)) + \delta.
$$

We deduce that, for $0 < \varepsilon < \varepsilon_0$:

$$
u_\varepsilon(t, x, y) - u(t, x, y) + \varepsilon \log\left(\varepsilon \frac{\rho_0^- \nu_m}{|I|^2} \right) - 2\delta \leq \max(u(t, x, \cdot)) + \max(u(t, \cdot, y)) - u(t, x, y).
$$

Letting δ and ε vanish yields:

$$
u(t, x, y) \leq \max(u(t, x, \cdot)) + \max(u(t, \cdot, y)).
$$

$u(t, x, y) \geq \max u(t, x, \cdot) + \max u(t, \cdot, y)$. For $\delta > 0$, there exists $\varepsilon_0 > 0$ such that for $0 < \varepsilon \leq \varepsilon_0$, for $(t, x, y) \in [0, T] \times I \times J$,

$$
\max(u_\varepsilon(t, x, \cdot)) \geq \max(u(t, x, \cdot)) - \delta, \quad \max(u_\varepsilon(t, \cdot, y)) \geq \max(u(t, \cdot, y)) - \delta.
$$

Let $\varepsilon \leq \varepsilon_0$ and $y_\varepsilon(x)$ be such that: $u_\varepsilon(t, x, y_\varepsilon(x)) = \max(u_\varepsilon(t, x, \cdot))$. Since u_ε is uniformly Lipschitz in space (Proposition 4.1), we can choose $M > 0$ such that:

$$
\forall (y, y') \in I \times J, \; |u_\varepsilon(t, x, y) - u_\varepsilon(t, x, y')| \leq M|y - y'|.
$$

Combining the last two estimations leads to:

$$
|y - y_\varepsilon(x)| \leq \frac{\delta}{M} \implies u_\varepsilon(t, x, y') > \max u(t, x, \cdot) - 2\delta.
$$

The same holds for $\max(u(t, \cdot, y))$. Hence, from Proposition 1.1, there exists ν_M such that:

$$
\rho_0^+ \nu_M \geq \iint_{I \times J} \frac{1}{\varepsilon} \exp\left[\frac{u_\varepsilon(t, x, y') + u_\varepsilon(t, x', y) - u_\varepsilon(t, x, y)}{\varepsilon} \right] dx \, dy
$$

$$
\geq \left(\frac{\delta}{M} \right)^2 \frac{1}{\varepsilon} \exp\left[\frac{\max(u(t, x, \cdot)) + \max(u(t, \cdot, y)) - 4\delta - u_\varepsilon(t, x, y)}{\varepsilon} \right].
$$

We next obtain:

$$
\varepsilon \log\left(\varepsilon \frac{\rho_0^+ \nu_M M^2}{\delta^2} \right) + 4\delta + u_\varepsilon(t, x, y) - u(t, x, y) \geq \max(u(t, x, \cdot)) + \max(u(t, \cdot, y)) - u(t, x, y).
$$

Letting δ and ε vanish yields:

$$
u(t, x, y) \geq \max(u(t, x, \cdot)) + \max(u(t, \cdot, y)).
$$

This concludes the proof of (3).

u is non-positive. This property follows directly from the uniform convergence of u_ε towards u and the uniform estimates on the $\max(u_\varepsilon)$ from Lemma 3.

Support of n and zeros of u. Let $t \in [0, T]$. Let: $(x_0, y_0) \notin \{(x, y) \mid u(t, x, y) = 0\}$. Since $u(t, \cdot, \cdot)$ is uniformly continuous, there exists $\delta > 0$ such that: $\max(|x' - x_0|, |y' - y_0|) \leq \delta \implies u(t, x', y') \leq \frac{u(t, x_0, y_0)}{2}$. Also, from Theorem 1.2, there exists $\varepsilon_0 > 0$ such that, for all $\varepsilon < \varepsilon_0$, we have: $\|u_\varepsilon - u\|_\infty \leq \frac{|u(t, x_0, y_0)|}{4}$. Then, for $\varepsilon < \varepsilon_0$, we have:

$$\int_{[x_0-\delta,x_0+\delta]\times[y_0-\delta,y_0+\delta]} n_\varepsilon(t, x', y') \, dx' \, dy' = \int_{[x-\delta,x+\delta]\times[y_0-\delta,y_0+\delta]} \frac{e^{\frac{u_\varepsilon(t,x',y')}{\varepsilon}}}{\varepsilon} \, dx' \, dy'$$

$$\leq 4\delta^2 \frac{e^{\frac{u(t,x_0,y_0)}{4\varepsilon}}}{\varepsilon}$$

$$\xrightarrow[\varepsilon\to 0]{} 0.$$

From the weak convergence result of Theorem 1.1, $(x_0, y_0) \notin \text{supp}(n(t, \cdot, \cdot))$.

Limit equation on u^X. Let $\varepsilon > 0$. From the equation (5) verified by ρ_ε^X, we get, by integration:

$$\forall (t, y) \in [0, T] \times J, \quad \varepsilon \log\left(\frac{\rho_\varepsilon^X(t, y)}{\rho_\varepsilon^X(0, y)}\right) = rt - \kappa \int_0^t \rho_\varepsilon(s)ds - \int_0^t \int_I m(x, y) \frac{n_\varepsilon(s, x, y)}{\rho_\varepsilon^X(s, y)} dx \, ds. \tag{25}$$

Let us define $\phi_\varepsilon^X \in C([0, T] \times I \times J)$ by:

$$\phi_\varepsilon^X(t, x, y) = \frac{n_\varepsilon(t, x, y)}{\rho_\varepsilon^X(t, y)}.$$

1. Convergence of ϕ_ε^X to ϕ^X. For $(t, y) \in [0, T] \times J$, we have:

$$\int_I \phi_\varepsilon^X(t, x', y) \, dx' = 1.$$

Hence, $\left(\phi_\varepsilon^X\right)_{\varepsilon>0}$ is bounded in $L^\infty([0, T] \times J, L^1(I))$. Thus, from **??**, there exists a subsequence still denoted $\left(\phi_\varepsilon^X\right)_{\varepsilon>0}$ that converges in $L^\infty(w^* - [0, T] \times J, M^1(I))$ toward a measure ϕ^X.

Support of $\phi^X(t, \cdot, y)$. Proposition 1.1 implies that, for $f \in C_c(I, \mathbb{R}_+)$, for a.e. (t, y)

$$\frac{1}{\nu_M \, \rho_0^-} \int_I \rho^Y(t, x) \, f(x) \, dx \leq \left\langle \phi^X(t, \cdot, y), f \right\rangle \leq \frac{1}{\nu_m \, \rho_0^+} \int_I \rho^Y(t, x) \, f(x) \, dx.$$

Hence, for a.e. (t, y), $\phi^X(t, \cdot, y)$ and $\rho^Y(t, \cdot)$ share the same support. As $n(t, \cdot, \cdot)$ is supported at $u(t, \cdot, \cdot)^{-1}(\{(0, 0)\}) = u^X(t, \cdot)^{-1}(\{0\}) \times u^Y(t, \cdot)^{-1}(\{0\})$ for a.e. t, we obtain that $\rho^Y(t, \cdot)$ (and therefore $\phi^X(t, \cdot, y)$) is supported at the zeros of $u^Y(t, \cdot)$.

2. $\varepsilon \log\left(\rho_\varepsilon^X\right) \underset{\varepsilon\to 0}{\longrightarrow} u^X \in C^0([0,T]\times I)$. We fix $\delta > 0$ and let $\varepsilon_0 > 0$ be such that: $\forall \varepsilon < \varepsilon_0$, $\|u_\varepsilon - u\|_\infty \le \delta$. Next, we compute:

$$
\begin{aligned}
\varepsilon \log\left(\rho_\varepsilon^X(t,y)\right) &= \varepsilon \log\left(\int_I \frac{e^{\frac{u_\varepsilon(t,x,y)}{\varepsilon}}}{\varepsilon}\, dx\right) \\
&\le \varepsilon \log\left(\int_I \frac{e^{\frac{u(t,x,y)+\delta}{\varepsilon}}}{\varepsilon}\, dx\right) \\
&= \varepsilon \log\left(\int_I \frac{e^{\frac{u^X(t,y)+\delta}{\varepsilon}}}{\varepsilon}\, e^{\frac{u^Y(t,x)}{\varepsilon}}\, dx\right) \\
&\le u^X(t,y) + \delta - \varepsilon \log(\varepsilon) + \varepsilon \log\left(\int_I e^{\frac{u^Y(t,x)}{\varepsilon}}\, dx\right) \\
&\le u^X(t,y) + \delta - \varepsilon \log(\varepsilon) + \varepsilon \log\left(|I|\right).
\end{aligned}
\tag{26}
$$

Similarly, we have:

$$
\varepsilon \log\left(\rho_\varepsilon^X(t,y)\right) \ge u^X(t,y) - \delta - \varepsilon \log(\varepsilon) + \varepsilon \log\left(\int_I e^{\frac{u^Y(t,x)}{\varepsilon}}\, dx\right).
\tag{27}
$$

For all $t \in [0,T]$, we have shown at the step (ii) that there exists $x_0(t) \in I$ such that $u^Y(x_0(t)) = 0$. We have therefore the following lower bound:

$$
\begin{aligned}
\varepsilon \log\left(\int_I e^{\frac{u^Y(t,x)}{\varepsilon}}\, dx\right) &\ge \varepsilon \log\left(\int_{x_0(t)-\varepsilon}^{x_0(t)+\varepsilon} e^{\frac{u^Y(t,x)}{\varepsilon}}\, dx\right) \\
&\ge \varepsilon \log\left(\int_{x_0(t)-\varepsilon}^{x_0(t)+\varepsilon} e^{\frac{-M|x-x_0(t)|}{\varepsilon}}\, dx\right) \\
&\ge -\varepsilon M + \varepsilon \log\left(2\,\varepsilon\right)
\end{aligned}
$$

where the intermediate inequality is obtained due to the fact that there exists $M > 0$ such that $u(t,\cdot,\cdot)$ is M-lipschitz in space, and thus, so is $u^Y(t,\cdot)$.

The two inequalities (26) and (27) above ensure the convergence of $\varepsilon \log\left(\rho_\varepsilon^X\right)$ toward u^X uniformly in $[0,T]\times J$.

3. Limit equation. For all $(t,y) \in [0,T]\times J$:

$$
\int_0^t \int_I m(x,y)\phi_\varepsilon^X(s,x,y)\, dx\, ds = \varepsilon \log\left(\frac{\rho_\varepsilon^X(t,y)}{\rho_\varepsilon^X(0,y)}\right) - rt + \kappa \int_0^t \rho_\varepsilon(s)ds.
$$

From the strong convergence $\varepsilon \log\left(\rho_\varepsilon^X\right) \underset{\varepsilon\to 0}{\longrightarrow} u^X \in C^0([0,T]\times J)$ shown previously, the r.h.s of the equality above converges toward a function in $C^0([0,T]\times J)$ as ε vanishes. Hence, $G_\varepsilon := (t,y) \mapsto \int_0^t \int_I m(x,y)\phi_\varepsilon^X(t,x,y)\, dx\, ds$ converges uniformly toward a function denoted $G(t,y)$ in $C^0([0,T]\times J)$.

We aim to show that for all $t \in [0,T]$:

$$
G(t,\cdot) = y \mapsto \int_0^t \left\langle \phi^X(t,\cdot,y), m(\cdot,y)\right\rangle ds \in L^\infty(J),
$$

24

which would yield (4). Let $f \in L^1(J)$. We have, for $t \in [0, T]$:

$$\left| \int_J \left(G(t, y) - \int_0^t \left\langle \phi^X(t, \cdot, y), m(\cdot, y) \right\rangle ds \right) f(y) \, dy \right|$$

$$\leq \| G - G_\varepsilon \|_\infty \| f \|_1 + \left| \int_0^T \int_J \left\langle \phi_\varepsilon^X(s, \cdot, y) - \phi^X(s, \cdot, y), m(\cdot, y) \right\rangle \mathbf{1}_{[0,t]}(s) \, f(y) ds \, dy \right|.$$

The first term vanishes because of the uniform convergence of G_ε to G. The second term does the same because of the weak convergence of ϕ_ε^X to ϕ^X in $L^\infty(w^* - [0, T] \times J, M^1(I))$ applied to $(s, x, y) \mapsto \mathbf{1}_{[0,t]}(s) f(y) m(x, y) \in L^1([0, T] \times J, C^0(I))$, since $f \in L^1(J)$ and $m \in C^1(I \times J)$. We obtain that for all $t \in [0, T]$, $f \in L^1(J)$:

$$\int_J \left(G(t, y) - \int_0^t \left\langle \phi^X(t, \cdot, y), m(\cdot, y) \right\rangle ds \right) f(y) \, dy = 0.$$

Therefore, we deduce that for all $t \in [0, T]$, for a.e y, $G(t, y) = \int_0^t \left\langle \phi^X(t, \cdot, y), m(\cdot, y) \right\rangle ds$.

6 Convergence in BV-norm for (ρ_ε): proof of Theorem 1.3

In this section, we provide the proof of Theorem 1.3 under the additional hypothesis that the selection function m is additive ($\mathrm{H}_{m,\mathrm{add}}$).

Let $\varepsilon > 0$. First, we have, for all $t \in [0, T]$:

$$\int_0^t \left| \frac{d\rho_\varepsilon}{dt}(s) \right| ds = \int_0^t \frac{d\rho_\varepsilon}{dt}(s) \, ds + 2 \int_0^t \left(\frac{d\rho_\varepsilon}{dt} \right)_- (s) \, ds$$

$$= \rho_\varepsilon(t) - \rho_\varepsilon(0) + 2 \int_0^t \left(\frac{d\rho_\varepsilon}{dt} \right)_- (s) \, ds$$

$$\leq \rho_0^+ + 2 \int_0^t \left(\frac{d\rho_\varepsilon}{dt} \right)_- (s) \, ds,$$

using the estimates of Lemma 1. Let us define:

$$\mathcal{I}_\varepsilon(t) := \frac{d\rho_\varepsilon}{dt}(t) = \frac{r - \kappa \, \rho_\varepsilon(t)}{\varepsilon} \rho_\varepsilon(t) - \iint_{I \times J} m(x, y) \frac{n_\varepsilon(t, x, y)}{\varepsilon} \, dx \, dy.$$

To prove that ρ_ε is locally uniformly bounded in $W^{1,1}([0, T])$, it is sufficient to give an upper bound on $\int_0^t (\mathcal{I}_\varepsilon)_- \, ds$. To this end, let us notice that for a.e.t:

$$\frac{d (\mathcal{I}_\varepsilon)_-}{dt}(t) = -\mathbf{1}_{\mathcal{I}_\varepsilon \leq 0} \frac{d\mathcal{I}_\varepsilon}{dt}.$$

We deduce that, for a.e.t

$$\frac{d (\mathcal{I}_\varepsilon)_-}{dt}(t) = -\frac{d\mathcal{I}_\varepsilon}{dt}(t) \, \mathbf{1}_{\{\mathcal{I}_\varepsilon(t) \leq 0\}}$$

$$= -\left[\frac{r - 2 \kappa \, \rho_\varepsilon}{\varepsilon} \mathcal{I}_\varepsilon(t) - \iint_{I \times J} m(x, y) \frac{\partial_t n_\varepsilon(t, x, y)}{\varepsilon} \, dx \, dy \right] \mathbf{1}_{\{\mathcal{I}_\varepsilon(t) \leq 0\}}$$

$$= \left[\frac{r - 2 \kappa \, \rho_\varepsilon}{\varepsilon} \, (\mathcal{I}_\varepsilon)_- (t) \right.$$

$$\left. + \iint_{I \times J} m(x, y) \frac{1}{\varepsilon^2} \left(\frac{r}{2} \left[\frac{\rho_\varepsilon^X \, \rho_\varepsilon^Y}{\rho_\varepsilon} + n_\varepsilon \right] - \kappa \, \rho_\varepsilon \, n_\varepsilon - m(x, y) \, n_\varepsilon \right) \, dx \, dy \right] \mathbf{1}_{\{\mathcal{I}_\varepsilon(t) \leq 0\}}.$$

$$\tag{28}$$

Let us show that the following term is non positive:

$$\mathbf{1}_{\{\mathcal{I}_\varepsilon(t)\leq 0\}}\iint_{I\times J} m(x,y)\left(\frac{r}{2}\left[\frac{\rho_\varepsilon^X\,\rho_\varepsilon^Y}{\rho_\varepsilon}+n_\varepsilon\right]-\kappa\,\rho_\varepsilon\,n_\varepsilon-m(x,y)\,n_\varepsilon\right)dx\,dy$$

$$=\mathbf{1}_{\{\mathcal{I}_\varepsilon(t)\leq 0\}}\left[\frac{r}{2}\iint_{I\times J}m(x,y)\frac{\rho_\varepsilon^X\,\rho_\varepsilon^Y}{\rho_\varepsilon}dx\,dy+\left(\frac{r}{2}-\kappa\rho_\varepsilon\right)\iint_{I\times J}m(x,y)\,n_\varepsilon dxdy-\iint_{I\times J}m^2(x,y)\,n_\varepsilon\,dx\,dy\right].$$

On the one hand, from the Cauchy-Schwartz inequality, we get:

$$-\rho_\varepsilon\iint_{I\times J}m^2(x,y)\,n_\varepsilon\,dx\,dy=-\iint_{I\times J}\sqrt{n_\varepsilon}^2\iint_{I\times J}(m(x,y)\sqrt{n_\varepsilon})^2\,dx\,dy\leq-\left(\iint_{I\times J}m(x,y)\,n_\varepsilon\,dx\,dy\right)^2.$$

On the other hand, thanks to the additional hypothesis on m ($\mathrm{H}_{m,\mathrm{add}}$), we have

$$\iint_{I\times J}m(x,y)\frac{\rho_\varepsilon^X\,\rho_\varepsilon^Y}{\rho_\varepsilon}dx\,dy=\iint_{I\times J}\left[m^X(x)+m^Y(y)\right]\frac{\rho_\varepsilon^X(y)\,\rho_\varepsilon^Y(x)}{\rho_\varepsilon}dx\,dy$$

$$=\int_I m^X(x)\rho_\varepsilon^Y(x)\,dx+\int_I m^Y(y)\rho_\varepsilon^X(y)\,dy$$

$$=\iint_{I\times J}m^X(x)\,n_\varepsilon(x,y)\,dx\,dy+\iint_{I\times J}m^Y(y)\,n_\varepsilon(x,y)\,dx\,dy$$

$$=\iint_{I\times J}m(x,y)\,n_\varepsilon(x,y)\,dx\,dy.$$

We deduce that

$$\mathbf{1}_{\{\mathcal{I}_\varepsilon(t)\leq 0\}}\iint_{I\times J}m(x,y)\left(\frac{r}{2}\left[\frac{\rho_\varepsilon^X\,\rho_\varepsilon^Y}{\rho_\varepsilon}+n_\varepsilon\right]-\kappa\,\rho_\varepsilon\,n_\varepsilon-m(x,y)\,n_\varepsilon\right)dx\,dy$$

$$\leq\mathbf{1}_{\{\mathcal{I}_\varepsilon(t)\leq 0\}}\left[r\iint_{I\times J}m\,n_\varepsilon-\kappa\,\rho_\varepsilon\iint_{I\times J}m\,n_\varepsilon-\frac{1}{\rho_\varepsilon}\left(\iint_{I\times J}m(x,y)\,n_\varepsilon\,dx\,dy\right)^2\right]$$

$$\leq\mathbf{1}_{\{\mathcal{I}_\varepsilon(t)\leq 0\}}\frac{\iint_{I\times J}m\,n_\varepsilon\,dx\,dy}{\rho_\varepsilon}\left[(r-\kappa\,\rho_\varepsilon)\,\rho_\varepsilon-\iint_{I\times J}m\,n_\varepsilon\,dx\,dy\right]$$

$$\leq\mathbf{1}_{\{\mathcal{I}_\varepsilon(t)\leq 0\}}\frac{\iint_{I\times J}m\,n_\varepsilon\,dx\,dy}{\rho_\varepsilon}\,\varepsilon\,\mathcal{I}_\varepsilon(t)\leq 0.$$

Consequently, (28) implies the following inequality

$$\frac{d\,(\mathcal{I}_\varepsilon)_-}{dt}(t)\leq\frac{r-2\,\kappa\,\rho_\varepsilon}{\varepsilon}\,(\mathcal{I}_\varepsilon)_-\,(t)$$

$$\leq\frac{r-2\,\kappa\,\overline{\rho_0}}{\varepsilon}\,(\mathcal{I}_\varepsilon)_-\,(t)$$

$$=\frac{2\|m\|_\infty-r}{\varepsilon}\,(\mathcal{I}_\varepsilon)_-\,(t).$$

Let us define $\delta:=r-2\|m\|_\infty>0$ from H1. From the last differential inequality, we deduce that

$$(\mathcal{I}_\varepsilon)_-\,(t)\leq(\mathcal{I}_\varepsilon)_-\,(0)\,e^{-\frac{\delta}{\varepsilon}t},\tag{29}$$

which concludes the first part of the proof.

For the last part of the theorem, recall that $I_\varepsilon(t)=\frac{d\rho_\varepsilon}{dt}(t)$. Then, the inequality (6) implies that there exists $C>0$ such that

$$(\mathcal{I}_\varepsilon(0))_-\leq C\,\frac{e^{\frac{o(1)}{\varepsilon}}}{\varepsilon}.$$

As a corollary of (29), we obtain that for all $t \in [0, T]$

$$(\mathcal{I}_\varepsilon)_- (t) \leq C \frac{e^{\frac{o(1) - \delta t}{\varepsilon}}}{\varepsilon}.$$

We deduce that the limit ρ is non decreasing.

A   Proof of Lemma 1.

Proof of Lemma 1.

1. Bounds on ρ_ε.   Integrating $(P(n_\varepsilon))$ leads to ρ_ε being solution of:

$$\begin{cases} \varepsilon \, \partial_t \rho_\varepsilon = (r - \kappa \, \rho_\varepsilon) \, \rho_\varepsilon - \iint_{I \times J} m(x, y) \, n_\varepsilon(t, x, y) \, dx \, dy. \\ \rho(0) = \rho_\varepsilon^0. \end{cases} \tag{30}$$

Since $m, n_\varepsilon \geq 0$, we get that ρ_ε is a subsolution of the Cauchy problem:

$$\begin{cases} \varepsilon \, d_t f_\varepsilon = (r - \kappa \, f_\varepsilon) \, f_\varepsilon, \\ f_\varepsilon(0) = \rho_\varepsilon^0. \end{cases}$$

whose solution is:

$$\forall t \geq 0, \quad f_\varepsilon(t) = \frac{1}{\frac{e^{-\frac{rt}{\varepsilon}}}{\rho_\varepsilon^0} + \frac{\kappa}{r} \left(1 - e^{-\frac{rt}{\varepsilon}} \right)} \leq \max \left(\rho_\varepsilon^0, \frac{r}{\kappa} \right),$$

since $\rho_\varepsilon^0 \geq 0$ from assumptions. Using the comparison principle, we obtain

$$\forall t \geq 0, \quad \rho_\varepsilon(t) \leq f_\varepsilon(t) \leq \rho_0^+.$$

Similarly, we get:

$$\forall t \geq 0, \quad \rho_0^- = \leq \min \left(\rho_\varepsilon^0, \frac{r - \|m\|_\infty}{\kappa} \right) \leq \rho_\varepsilon(t).$$

2. Bounds on $\rho_\varepsilon^X, \rho_\varepsilon^Y$.   Integrating $(P(n_\varepsilon))$ with regard to x leads to:

$$\begin{cases} \varepsilon \, \partial_t \rho_\varepsilon^X = (r - \kappa \, \rho_\varepsilon) \, \rho_\varepsilon^X - \int_I m(x, y) \, n_\varepsilon(t, x, y) \, dx \leq r \rho_\varepsilon^X, \\ \rho^X(0) = \rho_\varepsilon^{X,0}. \end{cases}$$

The upper bound on ρ_ε^X is then obtained by comparison with $\rho_\varepsilon^{X,0} \, e^{\frac{rt}{\varepsilon}}$. The upper bound on ρ_ε^Y can be proved using similar arguments.

3. Bound on n_ε.   From Duhamel's formula, we obtain, for all $t \geq 0, (x, y) \in I \times J$:

$$n_\varepsilon(t, x, y) = n_\varepsilon^0(x, y) e^{- \int_0^t \frac{m + \kappa \, \rho_\varepsilon(s) - \frac{r}{2}}{\varepsilon} ds} + \frac{r}{2\varepsilon} \int_0^t \frac{\rho_\varepsilon^X(y, \tau) \rho_\varepsilon^Y(x, \tau)}{\rho_\varepsilon(\tau)} e^{- \int_\tau^t \frac{m + \kappa \, \rho_\varepsilon(s) - \frac{r}{2}}{\varepsilon} ds} d\tau.$$

Hence, using the bounds on ρ_ε^X and ρ_ε^Y from (18), we deduce that:

$$\|n_\varepsilon(t, \cdot, \cdot)\|_\infty \leq e^{\frac{rt}{2\varepsilon}} \left\| n_\varepsilon^0 \right\|_\infty + \frac{\|\rho_\varepsilon^{X,0}\|_\infty \|\rho_\varepsilon^{Y,0}\|_\infty}{\rho_0^-} \int_0^t \frac{r}{2\varepsilon} e^{\frac{2r\tau}{\varepsilon}} e^{\frac{r(t-\tau)}{2\varepsilon}} d\tau$$

$$\leq e^{\frac{rt}{2\varepsilon}} \left\| n_\varepsilon^0 \right\|_\infty + \frac{\|\rho_\varepsilon^{X,0}\|_\infty \|\rho_\varepsilon^{Y,0}\|_\infty}{\rho_0^-} e^{\frac{2rt}{\varepsilon}} \left(e^{\frac{rt}{2\varepsilon}} - 1 \right).$$

4. Bound on $\partial_x n_\varepsilon$. We differentiate $P(n_\varepsilon)$ with respect to x to obtain:

$$\begin{cases} \varepsilon\,\partial_t\partial_x n_\varepsilon = \frac{r}{2}\left[\frac{\partial_x\rho_\varepsilon^Y(x)\,\rho_\varepsilon^X(y)}{\rho_\varepsilon} + \partial_x n_\varepsilon(x,y)\right] - \partial_x m(x,y)\,n_\varepsilon - (m+\kappa\,\rho_\varepsilon)\,\partial_x n_\varepsilon, \\ \partial_x n_\varepsilon(0) = \partial_x n_\varepsilon^0. \end{cases}$$

Putting the latter under integral form yields:

$$\partial_x n_\varepsilon = \partial_x n_\varepsilon^0\, e^{-\int_0^t \frac{m+\kappa\,\rho_\varepsilon(s)}{\varepsilon}ds} + \frac{1}{\varepsilon}\int_0^t\left(\frac{r}{2}\left[\frac{\partial_x\rho_\varepsilon^Y(x)\,\rho_\varepsilon^X(y)}{\rho_\varepsilon} + \partial_x n_\varepsilon(x,y)\right] - n_\varepsilon\,\partial_x m\right)e^{-\int_\tau^t \frac{m+\kappa\,\rho_\varepsilon(s)}{\varepsilon}ds}d\tau.$$

Hence, by first using the previous bounds (18) and (19) and next using the Gronwall's inequality on $t\mapsto\|\partial_x n_\varepsilon(t,\cdot,\cdot)\|_\infty$ (second line), we obtain that:

$$\|\partial_x n_\varepsilon(t,\cdot,\cdot)\|_\infty \le \left\|\partial_x n_\varepsilon^0\right\|_\infty + N_{T_M}\frac{t}{\varepsilon}\|\partial_x m\|_\infty + \int_0^t\frac{r}{2\varepsilon}\left[\frac{\left\|\rho_\varepsilon^{X,0}\right\|_\infty |J|}{\rho_0^-}e^{\frac{r\tau}{\varepsilon}} + 1\right]\|\partial_x n_\varepsilon(\tau,\cdot,\cdot)\|_\infty\,d\tau$$

$$\le \left(\|\partial_x n_\varepsilon^0\|_\infty + N_{T_M}\frac{t}{\varepsilon}\|\partial_x m\|_\infty\right)e^{\frac{\left\|\rho_\varepsilon^{X,0}\right\|_\infty |J|}{2\rho_0^-}e^{\frac{r t}{\varepsilon}} + \frac{r t}{2\varepsilon}}.$$

$\square$

B Proof of Lemma 2

Proof of Lemma 2.

1. $\Phi\left(\mathcal{A}_\varepsilon^0\right)\subset\mathcal{A}_\varepsilon^0$. Let us recall the definition of $\mathcal{A}_\varepsilon^0$:

$$\mathcal{A}_\varepsilon^0 = \Big\{n\in C^1([0,T]\times I\times J,\,\mathbb{R}_+)\,|\,n(0,\cdot,\cdot) = n_\varepsilon^0,\quad \rho(n)\in[\rho_0^-,\rho_0^+],$$

$$\rho^X(n)(t,y)\le\left\|\rho_\varepsilon^{X,0}\right\|_\infty e^{r\frac{t}{\varepsilon}},\quad \rho^Y(n)(t,x)\le\left\|\rho_\varepsilon^{Y,0}\right\|_\infty e^{r\frac{t}{\varepsilon}},$$

$$\|n(t,\cdot,\cdot)\|_\infty\le e^{\frac{rt}{2\varepsilon}}\left\|n_\varepsilon^0\right\|_\infty + \frac{\|\rho_\varepsilon^{X,0}\|_\infty\|\rho_\varepsilon^{Y,0}\|_\infty}{\rho_0^-}e^{\frac{2rt}{\varepsilon}}\left(e^{\frac{rt}{2\varepsilon}} - 1\right),$$

$$\|\partial_x n_\varepsilon(t,\cdot,\cdot)\|_\infty\le\left(\|\partial_x n_\varepsilon^0\|_\infty + N_{T_M}\frac{T_M}{\varepsilon}\|\partial_x m\|_\infty\right)e^{\frac{\left\|\rho_\varepsilon^{X,0}\right\|_\infty |J|}{2\rho_0^-}e^{\frac{r t}{\varepsilon}} + \frac{r t}{2\varepsilon}}$$

$$\|\partial_y n_\varepsilon(t,\cdot,\cdot)\|_\infty\le\left(\|\partial_y n_\varepsilon^0\|_\infty + N_{T_M}\frac{T_M}{\varepsilon}\|\partial_y m\|_\infty\right)e^{\frac{\left\|\rho_\varepsilon^{Y,0}\right\|_\infty |I|}{2\rho_0^-}e^{\frac{r t}{\varepsilon}} + \frac{r t}{2\varepsilon}}\Big\}.$$

We consider $n\in\mathcal{A}_\varepsilon^0$. Let us show that $\Phi(n)$ satisfies all the conditions defining $\mathcal{A}_\varepsilon^0$. From H1, H2 and (21), $\Phi(n)$ is in $C^1([0,T]\times I\times J,\,\mathbb{R}_+)$ and $\Phi(n)(0,\cdot,\cdot) = n_\varepsilon^0$. Next, for $t\in[0,T]$, since

$n \in \mathcal{A}_\varepsilon^0$, we use the bounds on $\rho(n), \rho^X(n), \rho^Y(n)$ and we obtain the same bound for $\Phi(n)$:

$$|\Phi(n)(t,\cdot,\cdot)| \le \left\|n_\varepsilon^0\right\|_\infty + \frac{r}{2\varepsilon}\int_0^t \left(\frac{\left\|\rho_\varepsilon^{Y,0}\right\|_\infty \left\|\rho_\varepsilon^{Y,0}\right\|_\infty}{\rho_0^-}\, e^{\frac{2r\tau}{\varepsilon}} + \|n_\varepsilon(\tau,\cdot,\cdot)\|_\infty\right)d\tau$$

$$\le \left\|n_\varepsilon^0\right\|_\infty + \frac{r}{2\varepsilon}\int_0^t \left(\frac{\left\|\rho_\varepsilon^{Y,0}\right\|_\infty \left\|\rho_\varepsilon^{Y,0}\right\|_\infty}{\rho_0^-}\, e^{\frac{2r\tau}{\varepsilon}}\right.$$

$$\left. + e^{\frac{r\tau}{2\varepsilon}}\left\|n_\varepsilon^0\right\|_\infty + e^{\frac{2r\tau}{\varepsilon}}\frac{\left\|\rho_\varepsilon^{X,0}\right\|_\infty \left\|\rho_\varepsilon^{Y,0}\right\|_\infty}{\rho_0^-}\left(e^{\frac{r\tau}{2\varepsilon}} - 1\right)\right)d\tau \qquad (31)$$

$$\le \left\|n_\varepsilon^0\right\|_\infty \left(1 + e^{\frac{rt}{2\varepsilon}} - 1\right) + e^{\frac{2rt}{\varepsilon}}\frac{\left\|\rho_\varepsilon^{Y,0}\right\|_\infty \left\|\rho_\varepsilon^{Y,0}\right\|_\infty}{\rho_0^-}\int_0^t \frac{r}{2\varepsilon}e^{\frac{r\tau}{2\varepsilon}}d\tau$$

$$= \left\|n_\varepsilon^0\right\|_\infty e^{\frac{rt}{2\varepsilon}} + e^{\frac{2rt}{\varepsilon}}\frac{\left\|\rho_\varepsilon^{Y,0}\right\|_\infty \left\|\rho_\varepsilon^{Y,0}\right\|_\infty}{\rho_0^-}\left(e^{\frac{rt}{2\varepsilon}} - 1\right).$$

Next, for $t \in [0,T]$, integrating twice (21) reads:

$$\iint_{I\times J}\Phi(n)(t,x,y)\,dx\,dy = \iint_{I\times J}n_\varepsilon^0\, e^{-\frac{1}{\varepsilon}\int_0^t m(x,y)+\kappa\,\rho(n)(s)\,ds}\,dx\,dy$$

$$+ \frac{r}{\varepsilon}\iint_{I\times J}\int_0^t \frac{1}{2}\left[\frac{\rho^X(n)(\tau,y)\,\rho^Y(\tau,x)}{\rho(n)(\tau)} + n(\tau,x,y)\right]e^{-\frac{1}{\varepsilon}\int_\tau^t m(x,y)+\kappa\,\rho(n)(s)\,ds}\,d\tau\,dx\,dy$$

$$\le \rho_\varepsilon^0\, e^{-\frac{1}{\varepsilon}\int_0^t \kappa\,\rho(n)(s)\,ds} + \frac{r}{\kappa}\int_0^t \frac{\kappa\,\rho(n)(\tau)}{\varepsilon}\, e^{-\frac{1}{\varepsilon}\int_\tau^t \kappa\,\rho(n)(s)\,ds}\,d\tau$$

$$\le \rho_\varepsilon^0\, e^{-\frac{1}{\varepsilon}\int_0^t \kappa\,\rho(n)(s)\,ds} + \frac{r}{\kappa}\left(1 - e^{-\frac{1}{\varepsilon}\int_0^t \kappa\,\rho(n)(s)\,ds}\right) \le \rho_0^+.$$

Similarly, using that $n \in \mathcal{A}_\varepsilon^0$ and thus $\rho(n) \ge \rho_0^-$, we obtain that:

$$\iint_{I\times J}\Phi(n)(t,x,y)\,dx\,dy \ge \rho_\varepsilon^0\, e^{-\frac{1}{\varepsilon}\int_0^t \|m\|_\infty+\kappa\,\rho(n)(s)\,ds} + \frac{r}{\varepsilon}\int_0^t \rho(n)(\tau)\, e^{-\frac{1}{\varepsilon}\int_\tau^t \|m\|_\infty+\kappa\,\rho(n)(s)\,ds}\,d\tau$$

$$\ge \rho_\varepsilon^0\, e^{-\frac{1}{\varepsilon}\int_0^t \left[\frac{\|m\|_\infty}{\rho_0^-}+\kappa\right]\rho(n)(s)\,ds} + \frac{r}{\frac{\|m\|_\infty}{\rho_0^-}+\kappa}\int_0^t \left[\frac{\|m\|_\infty}{\rho_0^-}+\kappa\right]\frac{\rho(n)(\tau)}{\varepsilon}\, e^{-\frac{1}{\varepsilon}\int_\tau^t \left[\frac{\|m\|_\infty}{\rho_0^-}+\kappa\right]\rho(n)(s)\,ds}\,d\tau$$

$$\ge \rho_\varepsilon^0\, e^{-\frac{1}{\varepsilon}\int_0^t \left[\frac{\|m\|_\infty}{\rho_0^-}+\kappa\right]\rho(n)(s)\,ds} + \frac{r}{\frac{\|m\|_\infty}{\rho_0^-}+\kappa}\left(1 - e^{-\frac{1}{\varepsilon}\int_0^t \left[\frac{\|m\|_\infty}{\rho_0^-}+\kappa\right]\rho(n)(s)\,ds}\right)$$

$$\ge \min\left(\rho_\varepsilon^0, \frac{r}{\frac{\|m\|_\infty}{\rho_0^-}+\kappa}\right) = \min\left(\rho_\varepsilon^0, \frac{r}{\frac{\|m\|_\infty}{r-\|m\|_\infty}+\kappa}\right) = \min\left(\rho_\varepsilon^0, \frac{r-\|m\|_\infty}{\kappa}\right) = \rho_0^-.$$

Next, for $y \in J$ and $t \in [0,T]$, we get from (21):

$$\rho^X(\Phi(n))(t,y) = \int_I \Phi(n)(t,x,y)\,dx = \int_I n_\varepsilon^0(x,y)\, e^{-\frac{1}{\varepsilon}\int_0^t m(x,y)+\kappa\,\rho(n)(s)\,ds}\,dx$$

$$+ \frac{r}{\varepsilon}\int_I \int_0^t \frac{1}{2}\left[\frac{\rho^X(n)(\tau,y)\,\rho^Y(\tau,x)}{\rho(n)(\tau)} + n(\tau,x,y)\right]e^{-\frac{1}{\varepsilon}\int_\tau^t m(x,y)+\kappa\,\rho(n)(s)\,ds}\,d\tau\,dx$$

$$\le \rho_\varepsilon^{X,0}(y) + \frac{r}{\varepsilon}\int_0^t \left\|\rho^X(n)(\tau,\cdot)\right\|_\infty d\tau \le \left\|\rho_\varepsilon^{X,0}\right\|_\infty + \frac{r}{\varepsilon}\int_0^t \left\|\rho^{X,0}\right\|_\infty e^{\frac{r\tau}{\varepsilon}}\,d\tau \le \left\|\rho_\varepsilon^{X,0}\right\|_\infty e^{\frac{rt}{\varepsilon}},$$

29

since $n \in \mathcal{A}_\varepsilon^0$. The same holds for $\rho^Y \left(\Phi(n) \right)(t,x) := \int_J \Phi(n)(t,x,y)\, dy$.

Finally, we compute:

$$\partial_x \Phi(n) = \left(\partial_x n_\varepsilon^0 - n_\varepsilon^0 \frac{1}{\varepsilon} \int_0^t \partial_x A\, ds \right) e^{-\frac{1}{\varepsilon} \int_0^t A\, ds} + \frac{1}{\varepsilon} \int_0^t \left(\partial_x B - B \frac{1}{\varepsilon} \int_\tau^t \partial_x A\, ds \right) e^{-\frac{1}{\varepsilon} \int_\tau^t A\, ds}\, d\tau$$

$$= \partial_x n_\varepsilon^0\, e^{-\frac{1}{\varepsilon} \int_0^t A\, ds} + \frac{1}{\varepsilon} \int_0^t \partial_x B\, e^{-\frac{1}{\varepsilon} \int_\tau^t A\, ds}\, d\tau$$

$$- \frac{1}{\varepsilon} \int_0^t \partial_x m \left(n_\varepsilon^0\, e^{-\frac{1}{\varepsilon} \int_0^\tau A\, ds} + B \frac{1}{\varepsilon}(t - \tau) \right) e^{-\frac{1}{\varepsilon} \int_\tau^t A\, ds}\, d\tau.$$

We next consider the following integration by parts:

$$\int_0^t (t - \tau)\, B(\tau)\, e^{-\frac{1}{\varepsilon} \int_\tau^t A(s)\, ds}\, d\tau = 0 + \int_0^t \int_0^\tau B(s)\, e^{-\frac{1}{\varepsilon} \int_s^t A(u)\, du}\, ds\, d\tau,$$

The latter leads to:

$$\partial_x \Phi(n) = \partial_x n_\varepsilon^0\, e^{-\frac{1}{\varepsilon} \int_0^t A\, ds} + \frac{1}{\varepsilon} \int_0^t \partial_x B\, e^{-\frac{1}{\varepsilon} \int_\tau^t A\, ds}\, d\tau$$

$$- \frac{\partial_x m}{\varepsilon} \int_0^t \left(n_\varepsilon^0\, e^{-\frac{1}{\varepsilon} \int_0^\tau A\, ds} + \frac{1}{\varepsilon} \int_0^\tau B(s)\, e^{-\frac{1}{\varepsilon} \int_s^\tau A(u)\, du} \right) e^{-\frac{1}{\varepsilon} \int_\tau^t A\, ds}\, d\tau$$

$$= \partial_x n_\varepsilon^0\, e^{-\frac{1}{\varepsilon} \int_0^t A\, ds} + \frac{1}{\varepsilon} \int_0^t \partial_x B\, e^{-\frac{1}{\varepsilon} \int_\tau^t A\, ds}\, d\tau - \frac{\partial_x m}{\varepsilon} \int_0^t \Phi(n)(\tau)\, e^{-\frac{1}{\varepsilon} \int_\tau^t A\, ds}\, d\tau.$$

Hence, since $n \in \mathcal{A}_\varepsilon^0$, we obtain thanks to (31): $|\Phi(n)(t,\cdot,\cdot)| \leq N_{T_M}$ for $t \in [0,T]$, which implies:

$$\|\partial_x \Phi(n)(t,\cdot,\cdot)\|_\infty$$

$$\leq \left\| \partial_x n_\varepsilon^0 \right\|_\infty + \int_0^t \frac{r}{2\varepsilon} \left[\frac{\left\| \rho_\varepsilon^{X,0} \right\|_\infty |J|}{\rho_0^-}\, e^{\frac{r\tau}{\varepsilon}} + 1 \right] \|\partial_x n_\varepsilon(\tau,\cdot,\cdot)\|_\infty\, d\tau + \frac{t\, \|\partial_x m\|_\infty}{\varepsilon}\, N_{T_M}$$

$$\leq \left\| \partial_x n_\varepsilon^0 \right\|_\infty + \frac{T_M\, \|\partial_x m\|_\infty}{\varepsilon}\, N_{T_M}$$

$$+ \int_0^t \frac{r}{2\varepsilon} \left[\frac{\left\| \rho_\varepsilon^{X,0} \right\|_\infty |J|}{\rho_0^-}\, e^{\frac{r\tau}{\varepsilon}} + 1 \right] \left(\|\partial_x n_\varepsilon^0\|_\infty + N_{T_M} \frac{T_M}{\varepsilon}\, \|\partial_x m\|_\infty \right) e^{\frac{\left\| \rho_\varepsilon^{X,0} \right\|_\infty |J|}{2\rho_0^-}(e^{\frac{r\tau}{\varepsilon}} - 1) + \frac{r\tau}{2\varepsilon}}\, d\tau$$

$$= \left(\left\| \partial_x n_\varepsilon^0 \right\|_\infty + \frac{T_M\, \|\partial_x m\|_\infty}{\varepsilon}\, N_{T_M} \right) \left[1 + \int_0^t \frac{r}{2\varepsilon} \left[\frac{\left\| \rho_\varepsilon^{X,0} \right\|_\infty |J|}{\rho_0^-}\, e^{\frac{r\tau}{\varepsilon}} + 1 \right] e^{\frac{\left\| \rho_\varepsilon^{X,0} \right\|_\infty |J|\, e^{\frac{r\tau}{\varepsilon}}}{\rho_0^-} \cdot \frac{1}{2} + \frac{r\tau}{2\varepsilon}}\, d\tau \right]$$

$$= \left(\left\| \partial_x n_\varepsilon^0 \right\|_\infty + \frac{T_M\, \|\partial_x m\|_\infty}{\varepsilon}\, N_{T_M} \right) \left[1 + \int_0^t \left(e^{\frac{\left\| \rho_\varepsilon^{X,0} \right\|_\infty |J|\, e^{\frac{r\tau}{\varepsilon}}}{\rho_0^-} \cdot \frac{1}{2} + \frac{r\tau}{2\varepsilon}} \right)'\, d\tau \right]$$

$$= \left(\left\| \partial_x n_\varepsilon^0 \right\|_\infty + \frac{T_M\, \|\partial_x m\|_\infty}{\varepsilon}\, N_{T_M} \right) e^{\frac{\left\| \rho_\varepsilon^{X,0} \right\|_\infty |J|}{2\rho_0^-}\, e^{\frac{rt}{\varepsilon}} + \frac{rt}{2\varepsilon}}.$$

The same holds for $\|\partial_y \Phi(n)(t,\cdot,\cdot)\|_\infty$. Hence: $\Phi(n) \in \mathcal{A}_\varepsilon^0$.

2. Φ is a contraction mapping for T small. Let n and $\tilde{n}$ be in $\mathcal{A}_\varepsilon^0$. We have, for all $(t,x,y) \in [0,T] \times I \times J$:

$$\Phi(n)(t,x,y) - \Phi(\tilde{n})(t,x,y) = n_\varepsilon^0(x,y) \left[e^{-\frac{1}{\varepsilon}\int_0^t A(s,x,y)\,ds} - e^{-\frac{1}{\varepsilon}\int_0^t \tilde{A}(s,x,y)\,ds} \right]$$

$$+ \frac{1}{\varepsilon} \left[\int_0^t \left(B(\tau,x,y) - \tilde{B}(\tau,x,y) \right) e^{-\frac{1}{\varepsilon}\int_\tau^t A(s,x,y)ds} \right.$$

$$\left. + \tilde{B}(\tau,x,y) \left(e^{-\frac{1}{\varepsilon}\int_\tau^t A(s,x,y)ds} - e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}(s,x,y)ds} \right) d\tau \right]$$

$$\leq N_{T_M} \left| e^{\frac{1}{\varepsilon}\int_0^t \kappa\,[\rho(s)-\tilde{\rho}(s)]ds} - 1 \right|$$

$$+ \frac{r}{2\varepsilon} \int_0^t \left| \frac{\rho^X \rho^Y}{\rho} - \frac{\tilde{\rho}^X \tilde{\rho}^Y}{\tilde{\rho}} + n - \tilde{n} \right| d\tau$$

$$+ \frac{r}{2\varepsilon} \left[\frac{N_{T_M}^2 |I||J|}{\rho_0^-} + N_{T_M} \right] \int_0^t \left| e^{\frac{1}{\varepsilon}\int_\tau^t \kappa\,[\rho(s)-\tilde{\rho}(s)]ds} - 1 \right| d\tau.$$

Using that $|e^x - 1| \leq |x|\,e^{|x|}$, we get that:

$$\left| e^{\frac{1}{\varepsilon}\int_0^t \kappa\,[\rho(s)-\tilde{\rho}(s)]ds} - 1 \right| \leq \frac{T\,\kappa\,|I||J|}{\varepsilon} e^{\frac{2\,\kappa\,T_M\,\rho_0^+}{\varepsilon}} \|n - \tilde{n}\|_\infty. \tag{32}$$

Furthermore, we have:

$$\frac{r}{2\varepsilon} \int_0^t \left| \frac{\rho^X \rho^Y}{\rho} - \frac{\tilde{\rho}^X \tilde{\rho}^Y}{\tilde{\rho}} \right| d\tau \leq \frac{r}{2\varepsilon} \int_0^t \left| \rho^X - \tilde{\rho}^X \right| \frac{\rho^Y}{\rho} + \tilde{\rho}^X \left| \frac{\rho^Y}{\rho} - \frac{\tilde{\rho}^Y}{\tilde{\rho}} \right| d\tau$$

$$\leq \frac{r\,T}{2\varepsilon} |I| \frac{N_{T_M}|J|}{\rho_0^-} \|n - \tilde{n}\|_\infty + \frac{r\,|I|N_{T_M}}{2\varepsilon} \int_0^t \frac{\rho^Y}{\rho_0^{-2}} |\rho - \tilde{\rho}| + \frac{1}{\rho_0^-} \left| \rho^Y - \tilde{\rho}^Y \right| d\tau \tag{33}$$

$$\leq T \frac{r\,|I||J|N_{T_M}}{2\varepsilon\,\rho_0^-} \left[2 + \frac{N_{T_M}|I||J|}{\rho_0^-} \right] \|n - \tilde{n}\|_\infty.$$

Hence, we have:

$$\|\Phi(n) - \Phi(\tilde{n})\|_\infty \leq T\,k_{T_M,\varepsilon}^1 \|n - \tilde{n}\|_\infty, \tag{34}$$

where $k_{T_M,\varepsilon}^1$ is a constant that does not depend on T.

Moreover, we need to control the difference of the derivatives:

$$\partial_x \Phi(n) - \partial_x \Phi(\tilde{n}) = \partial_x n_\varepsilon^0(x,y) \left[e^{-\frac{1}{\varepsilon}\int_0^t A(s,x,y)\,ds} - e^{-\frac{1}{\varepsilon}\int_0^t \tilde{A}(s,x,y)\,ds} \right]$$

$$+ \frac{1}{\varepsilon} \int_0^t \left(\partial_x B\,e^{-\frac{1}{\varepsilon}\int_\tau^t A\,ds} - \partial_x \tilde{B}\,e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}\,ds} \right) d\tau$$

$$+ \frac{\partial_x m}{\varepsilon} \int_0^t \left(\Phi(\tilde{n})e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}\,ds} - \Phi(n)e^{-\frac{1}{\varepsilon}\int_\tau^t A\,ds} \right) d\tau.$$

Similarly as above (32), the first term is controlled by:

$$\left| \partial_x n_\varepsilon^0(x,y) \left[e^{-\frac{1}{\varepsilon}\int_0^t A(s,x,y)\,ds} - e^{-\frac{1}{\varepsilon}\int_0^t \tilde{A}(s,x,y)\,ds} \right] \right| \leq \left\| \partial_x n_\varepsilon^0 \right\|_\infty \left| e^{\frac{1}{\varepsilon}\int_0^t \kappa\,(\tilde{\rho}(s)-\rho(s))\,ds} - 1 \right|$$

$$\leq T \frac{N_{T_M}^x\,\kappa\,|I||J|}{\varepsilon} e^{\frac{2\,\kappa\,T_M\,\rho_0^+}{\varepsilon}} \|n - \tilde{n}\|_\infty.$$

31

The second term is broken down in two:

$$\frac{1}{\varepsilon}\int_0^t \left(\partial_x B\, e^{-\frac{1}{\varepsilon}\int_\tau^t A\,ds} - \partial_x \tilde{B}\, e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}\,ds}\right) d\tau$$

$$= \frac{1}{\varepsilon}\int_0^t \partial_x B \left(e^{-\frac{1}{\varepsilon}\int_\tau^t A\,ds} - e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}\,ds}\right) d\tau + \frac{1}{\varepsilon}\int_0^t \left(\partial_x B - \partial_x \tilde{B}\right) e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}\,ds}\,d\tau$$

The first part is controlled thanks to (32) and the estimates defining $\mathcal{A}_\varepsilon^0$:

$$\left|\frac{1}{\varepsilon}\int_0^t \partial_x B \left(e^{-\frac{1}{\varepsilon}\int_\tau^t A\,ds} - e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}\,ds}\right) d\tau\right| \leq \int_0^t \frac{r}{2\varepsilon}\left[\frac{\left|\partial_x\rho^Y(n)\right|\rho^X(n)}{\rho_0^-} + |\partial_x n|\right]\left|e^{\frac{1}{\varepsilon}\int_\tau^t \kappa\,(\tilde{\rho}(s)-\rho(s))\,ds} - 1\right|$$

$$\leq \frac{r\,T\,N_{T_M}^x}{2\varepsilon\,\rho_0^-}\left[1 + \frac{N_{T_M}|I||J|}{\rho_0^-}\right]\frac{T_M\,\kappa\,|I||J|}{\varepsilon}\,e^{\frac{2\,\kappa\,T_M\,\rho_0^+}{\varepsilon}}\|n - \tilde{n}\|_\infty$$

$$= T\frac{r\,T_M\,N_{T_M}^x}{2\varepsilon^2\,\rho_0^-}\left[1 + \frac{N_{T_M}|I||J|}{\rho_0^-}\right]\kappa\,|I||J|\,e^{\frac{2\,\kappa\,T_M\,\rho_0^+}{\varepsilon}}\|n - \tilde{n}\|_\infty.$$

The second part is controlled similarly as in (33):

$$\left|\frac{1}{\varepsilon}\int_0^t \left(\partial_x B - \partial_x \tilde{B}\right) e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}\,ds}\,d\tau\right| \leq \frac{1}{\varepsilon}\int_0^t \left|\partial_x B - \partial_x \tilde{B}\right| d\tau$$

$$\leq \frac{r}{2\varepsilon}\int_0^t \left|\partial_x\rho^X - \partial_x\tilde{\rho}^X\right|\frac{\rho^Y}{\rho} + \left|\partial_x\tilde{\rho}^X\right|\left|\frac{\rho^Y}{\rho} - \frac{\tilde{\rho}^Y}{\tilde{\rho}}\right| d\tau$$

$$\leq \frac{r}{2\varepsilon}\left[\frac{T|I||J|N_{T_M}}{\rho_0^-}\|\partial_x n - \partial_x\tilde{n}\|_\infty + |I|N_{T_M}^x\int_0^t \frac{\rho^Y}{\rho_0^{-2}}|\rho - \tilde{\rho}| + \frac{1}{\rho_0^-}\left|\rho^Y - \tilde{\rho}^Y\right|\right]$$

$$\leq \frac{r}{2\varepsilon}\left[\frac{T|I||J|N_{T_M}}{\rho_0^-}\|\partial_x n - \partial_x\tilde{n}\|_\infty + \frac{|I|N_{T_M}^x T|J|\left(1 + \frac{|I||J|N_{T_M}}{\rho_0^-}\right)}{\rho_0^-}\|n - \tilde{n}\|_\infty\right]$$

$$= T\frac{r|I||J|}{2\varepsilon\rho_0^-}\left[\frac{N_{T_M}}{\rho_0^-}\|\partial_x n - \partial_x\tilde{n}\|_\infty + N_{T_M}^x\left(1 + \frac{|I||J|N_{T_M}}{\rho_0^-}\right)\|n - \tilde{n}\|_\infty\right].$$

The last term is controlled thanks to the first part of the proof on $\|\Phi(n) - \Phi(\tilde{n})\|_\infty$ (34) and that $\|\Phi(n)\|_\infty \leq N_{T_M}$, for $\Phi(n) \in \mathcal{A}_0^\varepsilon$:

$$\left|\frac{\partial_x m}{\varepsilon}\int_0^t \left(\Phi(\tilde{n})e^{-\frac{1}{\varepsilon}\int_\tau^t \tilde{A}\,ds} - \Phi(n)e^{-\frac{1}{\varepsilon}\int_\tau^t A\,ds}\right) d\tau\right|$$

$$\leq \frac{\|\partial_x m\|_\infty}{\varepsilon}\int_0^t \|\Phi(n)(\tau,\cdot,\cdot) - \Phi(\tilde{n})(\tau,\cdot,\cdot)\|_\infty + \|\Phi(n)(\tau,\cdot,\cdot)\|_\infty\left|e^{\frac{1}{\varepsilon}\int_\tau^t \kappa\,(\tilde{\rho}(s)-\rho(s))\,ds} - 1\right| d\tau$$

$$\leq T\frac{\|\partial_x m\|_\infty}{\varepsilon}\left(\|\Phi(n) - \Phi(\tilde{n})\|_\infty + N_{T_M}\frac{T_M\,\kappa\,|I||J|}{\varepsilon}\,e^{\frac{2\,\kappa\,T_M\,\rho_0^+}{\varepsilon}}\|n - \tilde{n}\|_\infty\right)$$

$$\leq T\frac{\|\partial_x m\|_\infty}{\varepsilon}\left(T_M k_{T_M,\varepsilon}^1 + N_{T_M}\frac{T_M\,\kappa\,|I||J|}{\varepsilon^2}\,e^{\frac{2\,\kappa\,T_M\,\rho_0^+}{\varepsilon^2}}\right)\|n - \tilde{n}\|_\infty$$

The same controls hold up for $\partial_y \Phi(n) - \partial_y \Phi(\tilde{n})$. Hence:

$$\|\Phi(n) - \Phi(\tilde{n})\|_X \leq T\,k_{T_M,\varepsilon}\,\|n - \tilde{n}\|_X\,,$$

where $k_{T_M,\varepsilon}$ is a constant that does not depend on T.

Hence, we can choose $T > 0$ small enough uniformly on $[0, T_M]$ so that Φ is a contraction mapping. $\qquad\square$

Remark B.1. *Thanks to* (34)*, the uniqueness can be obtained in* $C^0([0, T_M], C^0(I \times J))$.

Acknowledgments

References

[BEV17]   N. H. Barton, A. M. Etheridge, and A. Véber. "The infinitesimal model: Definition, derivation, and implications". *Theor. Popul. Biol.* 118 (2017), pp. 50–73.

[BMP09]   G. Barles, S. Mirrahimi, and B. Perthame. "Concentration in Lotka-Volterra Parabolic or Integral Equations: A General Convergence Result". *Methods and Applications of Analysis* 16.3 (2009), 321–340.

[Bou+17]   T. Bourgeron et al. "Existence of recombination-selection equilibria for sexual populations". *arXiv:1703.09078 [math, q-bio]* (2017). arXiv: 1703.09078.

[Bul80]   M. G. Bulmer. *The Mathematical Theory of Quantitative Genetics*. 1980.

[CGP19]   V. Calvez, J. Garnier, and F. Patout. "Asymptotic analysis of a quantitative genetics model with nonlinear integral operator". *J. de l'École Polytechnique* 6 (2019), pp. 537–579.

[CMM13]   P. Collet, S. Méléard, and J. A. J. Metz. "A rigorous model study of the adaptive dynamics of Mendelian diploids". *Journal of Mathematical Biology* 67.3 (2013), 569–607.

[Dek20]   L. Dekens. "Evolutionary dynamics of complex traits in sexual populations in a strongly heterogeneous environment: how normal?" (2020). arXiv: 2012.10115.

[Die+05]   O. Diekmann et al. "The dynamics of adaptation: An illuminating example and a Hamilton-Jacobi approach". *Theor. Popul. Biol.* 67.4 (2005), pp. 257–271.

[DL21]   L. Dekens and F. Lavigne. "Front Propagation of a Sexual Population with Evolution of Dispersion: A Formal Analysis". *SIAM Journal on Applied Mathematics* (2021).

[DOC21]   L. Dekens, S. P. Otto, and V. Calvez. "The best of both worlds: combining population genetic and quantitative genetic models" (2021). arXiv: 2111.11142.

[FIM18]   S. Figueroa Iglesias and S. Mirrahimi. "Long Time Evolutionary Dynamics of Phenotypically Structured Populations in Time-Periodic Environments". *SIAM Journal on Mathematical Analysis* 50.5 (2018), pp. 5537–5568.

[Fis19]   R. A. Fisher. "The Correlation between Relatives on the Supposition of Mendelian Inheritance." *Transactions of the Royal Society of Edinburgh* 52.2 (1919), pp. 399–433.

[Kim65]   M. Kimura. "A stochastic model concerning the maintenance of genetic variability in quantitative characters". *Proceedings of the National Academy of Sciences* 54.3 (1965), pp. 731–736.

[Lan75]   R. Lande. "The maintenance of genetic variability by mutation in a polygenic character with linked loci". *Genetical Research* 26.3 (1975), 221–235.

[Lan78]   K. Lange. "Central limit theorems of pedigrees". *J. Math. Biol.* 6.1 (1978), pp. 59–66.

[Lat72]   B. Latter. "Selection in Finite Populations with Multiple Alleles. III. Genetic Divergence with Centripetal Selection and Mutation". *Genetics* 70.3 (1972), pp. 475–490.

[Len+20] T. Lenormand et al. "Sex Chromosome Degeneration by Regulatory Evolution". *Current Biology* (2020).

[MG20]   S. Mirrahimi and S. Gandon. "Evolution of Specialization in Heterogeneous Environments: Equilibrium Between Selection, Mutation and Migration". *Genetics* 214.2 (2020), pp. 479–491.

[Mir17]   S. Mirrahimi. "A Hamilton-Jacobi approach to characterize the evolutionary equilibria in heterogeneous environments". *Math. Models Methods Appl. Sci.* 27.13 (2017), pp. 2425–2460.

[MR13]   S. Mirrahimi and G. Raoul. "Dynamics of sexual populations structured by a space variable and a phenotypical trait". *Theor. Popul. Biol.* 84 (2013), pp. 87–103.

[Pat20]   F. Patout. "The Cauchy problem for the infinitesimal model in the regime of small variance". *arXiv:2001.04682 [math]* (2020). arXiv: 2001.04682.

[PB08]   B. Perthame and G. Barles. "Dirac concentrations in Lotka-Volterra parabolic PDEs". *Indiana University Mathematics Journal* 57.7 (2008), pp. 3275–3302.

[PST21]   B. Perthame, M. Strugarek, and C. Taing. "Selection-mutation dynamics with asymmetrical reproduction kernels" (2021).

[Rao17]   G. Raoul. "Macroscopic limit from a structured population model to the Kirkpatrick-Barton model". *arXiv:1706.04094 [math]* (2017). arXiv: 1706.04094.

[Rao21]   G. Raoul. "Exponential convergence to a steady-state for a population genetics model with sexual reproduction and selection" (2021). arXiv: 2104.06089.

[RRG12]   I. G. Romero, I. Ruvinsky, and Y. Gilad. "Comparative studies of gene expression and the evolution of gene regulation". *Nature Reviews Genetics* 13.7 (2012), 505–516.

[TB94]   M. Turelli and N. H. Barton. "Genetic and Statistical Analyses of Strong Selection on PolygenicTraits: What, Me Normal?" *Genetics* (1994), pp. 913–941.

[Tuf00]   J. Tufto. "Quantitative genetic models for the balance between migration and stabilizing selection". *Genetical Research* 76.3 (2000), pp. 285–293.

[Tur17]   M. Turelli. "Commentary: Fisher's infinitesimal model: A story for the ages". 118 (2017), pp. 46–49.