

Selection, mutations, evolution. A population approach

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September 6, 2019

Contents

1	Phenotypically structured population	7
1.1	Distributed growth and mortality rates	8
1.2	Cannibalism	8
1.3	Adults, juveniles	9
1.4	Chemostat	10
1.5	Intra-specific local competition	11
1.6	Chemostat with continuous nutrients distribution	12
1.7	Mating and sexual reproduction	12
1.8	Multispecies models	13
2	Selection only: long time behavior	15
2.1	Single environment: the competitive exclusion principle	15
2.2	Rate of convergence: an explicit computation	20
2.3	A more precise general asymptotics	22
2.4	Two environmental variables	23
2.5	Evolutionary Stable Strategy, several nutrients	25
2.6	Intraspecific competition: example	26
2.7	Intraspecific competition: a condition for monomorphism	28
2.8	Another point of view: change time scale	30
3	Mutations in population models	31
3.1	Mutation kernels	31
3.2	The hyperbolic limit	32
3.3	The parabolic limit	33
4	Branching and transition to dimorphism in models with two environmental unknowns	35
4.1	what is branching?	35

4.2	A simple example	36
4.3	A smoother example	37
4.4	Why does it branch?	38
5	Rare mutations in population models and monomorphism	41
5.1	Integral models for mutations	41
5.2	Parabolic Lotka-Volterra models for mutations	44
5.3	Limit of small mutations (monomorphic case)	45
5.4	Formal asymptotic analysis (parabolic model)	47
5.5	Formal asymptotic analysis (integral model)	48
5.6	The case of systems	50
5.7	The relation with canonical equations	50
5.8	Convergence Stable Strategy and ESS	52
6	Local competition and polymorphism	55
6.1	The nonlocal Fisher equation; relation to Turing instability	55
6.2	The nonlocal Fisher equation; polymorphism	58
6.3	Continuous vs individual based models	60
6.4	Survival thresholds	61
.1	From population genetics to continuous models	64
.2	The replicator dynamics	65
.3	Interpolation of \dot{u} between u and \ddot{u}	66

Forewords

The question of assessing Darwin's explanation of evolution ([42]) by mean of mathematical modeling is certainly challenging. It is indeed based on very few and simple principles: food limited growth, natural selection and 'variations' or 'mutations' from mothers to off-springs. This is certainly the reason why several mathematical approaches have been proposed. Game theory and optimal strategies were introduced by John Maynard Smith [77] and mathematical developments can be found in the books of J. Hofbauer and K. Zygmund [65, 66]. This approach is based on population dynamics and can be derived from individual based stochastic models in the limit of large populations (see [45, 35, 33, 34] and the references therein). The analysis can also be made through a particular stability analysis of steady states in dynamical systems and was developed for several biologically relevant examples by [58, 59, 78, 46].

The populational point of view still uses a different aproach based on an intrinsic modeling of all the processes at the population level and was initiated in [30, 29, 25]. It leads us to consider integral and parabolic partial differential equations of Lotka-Volterra type as it is usually done in population biology ([86, 88, 79, 102]) but the nonlocal aspect is here fundamental for the solution behaviour. An important ingredient is that mutations should be rare or lead to small variations, therefore a small parameter should be present. A possible rescaling was first introduced in [47], leading to for a new qualitative analysis : solutions concentrate as moving Dirac masses. To tackle the asymptotic analysis, the idea was introduced of using a Hopf-Cole transform and leads to a new system of PDEs: constrained Hamilton-Jacobi equations. Therefore the approach presented here relies on asymptotic analysis of PDEs. In this framework it presents how one can interpret both the natural selection and mutations.

For mathematics, the main target in this asymptotic populational approach is to understand the concentration phenomena to Dirac masses. The monomorphism situation, that is a single Dirac mass, is well understood and a form of canonical equation can be established in smoothness regimes. Our understanding of polymorphic cases is much lower, a weak limit is proved in [36] for the chemostat but a classical theory is not available in opposition to the monomorphic

case [74]. In particular the branching from a monomorphic to a dimorphic solution requires to solve the so-called 'tail problem' that is too small populations should not survive [12, 68] to arrive to smooth branching. This question also opens the question of other possible rescalings as performed by the probabilistic school departing from a stochastic description of finite populations.

Other issues are also little touched in this approach: fluctuations in the environmental variables, evolution in systems of interacting species as cooperative systems and the various possible strength of interactions. On the application side several topics are arising from present developments in biology; a typical question is to model epigenetic mutations, an emerging topic is the understanding of resistance to therapy, in particular in cancer treatment, by principles based on adaptation or mutations of tumor cells [53, 103, 73].

These notes are a compilation of several papers and book chapters already published independently. They have been slightly modified in order to be self contained with unified notations. But the original and main content is completely taken from [47, 90, 9, 10, 55]. They have been put together as a support for the CRM Advanced Course in Mathematical Biology held during the first semester 2009. I would like to thank the CRM and the organizing committee for this opportunity to give the course and to put together these notes.

Belle-Ile en Mer
July 2008

Notations

- $x_- = \max(0, -x)$ is the negative part of x . Therefore $x = x_+ - x_-$ and $|x| = x_+ + x_-$.
In the same way $x_- = -\operatorname{sgn}_-(x) x$ and $\operatorname{sgn}_-(x) \geq 0$.
- The space of continuous functions is denoted by C^0 , the space of differentiable functions with continuous derivative is denoted by C^1 ...
- The space of continuous functions on \mathbb{R}^d vanishing at infinity is denoted $C_0(\mathbb{R}^d)$.
- Measures on \mathbb{R}^d are seen as the dual space of $C_0(\mathbb{R}^d)$. Integration of C_0 functions against a measure μ is denoted as that of L^1 functions by $\int_{\mathbb{R}^d} \varphi(x) \mu(x) dx$.
- Also $\mu_n \xrightarrow{n \rightarrow \infty} \mu$ means that $\int_{\mathbb{R}^d} \varphi(x) \mu_n(x) dx \rightarrow \int_{\mathbb{R}^d} \varphi(x) \mu(x) dx$, as $n \rightarrow \infty$, for all functions $\varphi \in C_0(\mathbb{R}^d)$.
- Dirac masses at a point a are denoted as $\delta_a(x) = \delta(x - a) = \delta(x = a)$.
- The Sobolev space $W^{2,\infty}(\mathbb{R}^d)$ is the space of C^1 functions which are bounded, with a bounded and Lipschitz continuous derivative.

Chapter 1

Phenotypically structured population

Population biology always faces a fundamental difficulty, the heterogeneity of populations. All individuals do not respond to their environment with exactly the same laws. In order to take into account this fact, population models can be structured by a parameter (always denoted by x below). The theory of structured population dynamics deals with the related questions and is now well established [79, 41, 102, 90]. The most classical examples of structuring parameters are the size of individuals, their age. These evolve during the life of individuals and are not under consideration in these notes.

Phenotypical parameters represent traits that individuals inherit from their parents and refer to their value for adults. They are considered here as much as they describe the ability of the adult individuals to use the environment (resources) for their reproduction. This Chapter presents examples of phenotypically structured populations. The most important other ingredient in the theory, namely *mutation* is also presented later in this chapter.

Various effects have been studied based on the emergence of a fittest trait in a structured population. We give here several example which are all described by the general formalism

$$\frac{\partial}{\partial t}n(t, x) = n(t, x) R(x, [n(t, \cdot)], I_1(t), \dots, I_K(t)) \quad (1.1)$$

with the I_j 's are unknowns which describe the environment (nutrients for instance) and which can be also solution of differential equations. Roughly $n(t, x)$ denotes the density of individuals with trait x and $R(\dots)$ represents the growth (and death) rates. The growth rate $R(x, [n(t, \cdot)], I_1(t), \dots, I_K(t))$ also depends generally on the full population whatever is the trait x because everybody is in

competition for the nutrients. This is the meaning of the notation $[n(t, \cdot)]$. The rate $R(x, \dots)$ is usually called the fitness of individuals with trait x in the environment $I_1(t), \dots, I_K(t)$.

1.1 Distributed growth and mortality rates

The formalism covers several examples, the simplest general subclass being as follows

$$\begin{cases} \frac{\partial}{\partial t} n(t, x) = n(t, x) R(x, I_1(t), \dots, I_K(t)), & x \in \mathbb{R}^d, t \geq 0, \\ I_k(t) = \int \psi_k(x) n(t, x) dx. \end{cases} \quad (1.2)$$

A family of models, see [1, 90], is based on growth and death rates depending on a parameter $x \in \mathbb{R}^d$ (that describes resources allocation for instance). The model under consideration is then defined by

$$R(x, I) = b(x)Q_1(\varrho(t)) - d(x)Q_2(\varrho(t)), \quad \varrho(t) = \int n(t, x) dx, \quad (1.3)$$

with $Q_i \in C^1(\mathbb{R})$ for $i = 1, 2$, and

$$Q'_1(\cdot) < 0, \quad Q'_2(\cdot) > 0, \quad Q_i > 0. \quad (1.4)$$

$$b \geq b_m > 0, \quad d \geq d_m > 0 \text{ and } b, d \in L^\infty(\mathbb{R}^d). \quad (1.5)$$

With these assumptions, the long time behavior of such equations is studied in Section 2.1.

Resistance to chemotherapy is an example which is closely related, [73, 81, 95]. The trait x represents the level of resistance to drugs and the fitness is defined as

$$R(x, I) = \frac{b(x)}{1 + c_S(t)} - c(x)\varrho(t) - d(x)(1 + c_T(t)),$$

where c_S and c_T represent the concentrations of cytostatic and cytotoxic drugs and $c(x)$ the competition between cells (for space or oxygen).

1.2 Cannibalism

See [46, 90]. Here, the trait $x \geq 0$ under consideration is the degree of cannibalism, and $0 < \alpha \leq 1$ denotes the efficiency in offspring production from intraspecific predation, also called rendering factor. To begin with, consider two species with population density $n_1(t)$ and $n_2(t)$ and with different levels of cannibalism x_1 and x_2 . We write the differential system

$$\frac{d}{dt} n_1(t) = (r + \alpha x_1 n_2(t) - x_2 n_2(t)) n_1(t),$$

$$\frac{d}{dt}n_2(t) = (r + \alpha x_2 n_1(t) - x_1 n_1(t))n_2(t).$$

For the equation on n_1 , the parameter r represents the growth rate in the absence of cannibalism (and we have substracted the death rate to simplify). The term $\alpha x_1 n_2$ is the growth rate induced from predation on n_2 and $-x_2 n_2$ the death rate from predation by species n_2 .

And one can see that cannibalism acts as a negative feedback. The global growth rate of the population is indeed lower than the logistic rate r (eventhough the more cannibalistic individuals perform better and thus there is a selective advantage to be more cannibalistic) since

$$\frac{d}{dt} \int_0^\infty n(t, x) = \int_0^\infty n(t, x) [r - (1 - \alpha) \int_0^\infty x n(t, x)] \leq r \int_0^\infty n(t, x). \quad (1.6)$$

Rather than two values of x , consider that the predation parameter x is continous, we write

$$\frac{\partial}{\partial t} n(x, t) = (r + \alpha x \int_0^\infty n(y, t) dy - \int_0^\infty y n(y, t) dy) n(t, x).$$

Therefore, we recover the general equation (1.2) with the growth rate

$$R(x, I_1, I_2) = r + \alpha x \int_0^\infty n(y, t) dy - \int_0^\infty y n(y, t) dy. \quad (1.7)$$

Here two global environmental quantities arise that represent respectively the total population and the total cannibalistic behavior,

$$I_1(t) = \int_0^\infty n(y, t) dy, \quad I_2(t) = \int_0^\infty y n(y, t) dy.$$

For results concerning the long time behavior, and in particular extinction, we refer to [90].

1.3 Adults, juveniles

See [26, 25, 27, 32]. Systems of equations may also arise. This is the case for a population distributed into two groups of age introduced in [27]. Let $n(t, x)$ and $p(t, x)$ denote the density of young and adult individuals (respectively) with respect to the phenotypic trait $x = \frac{1}{T} \in (0, \infty)$ where T is the expected duration of the juvenile state. As in [26, 27] we assume that the maturation age is an exponentially distributed random variable so that the per capita transition rate from juveniles with trait x to adults is exactly x . As long as birth occurs from adults with the same trait as the newborn (with a rate $b(x)$), we obtain a structured population model

$$\begin{cases} \frac{\partial}{\partial t} n(t, x) &= b(x)p(t, x) - m_1(S_1(t))n(t, x) - xn(t, x), \\ \frac{\partial}{\partial t} p(t, x) &= xn(t, x) - m_2(S_2(t))p(t, x), \end{cases} \quad (1.8)$$

with

$$\begin{cases} S_1(t) = \int_0^\infty [\omega_{11}(x) n(t, x) + \omega_{12}(x) p(t, x)] dx, \\ S_2(t) = \int_0^\infty [\omega_{21}(x) n(t, x) + \omega_{22}(x) p(t, x)] dx. \end{cases} \quad (1.9)$$

Here we have followed again [26, 27] to include nonlinear mortality rates m_1, m_2 that are known to control the total population.

1.4 Chemostat

One of the most classical model from ecology arises in laboratory experiments. A *chemostat* contains nutrients S_k , $k = 1, 2, \dots, I$, and micro-organisms (the example of *Daphnia* is frequent) which uses the nutrients to grow. The modeling is particularly simple because $S_k(t)$ can measure the mass of chemical constituents that are either free in the chemostat or absorbed by the micro-organisms with density by $n(t, x)$ which is structured for instance by their size x . Therefore we can write an exact balance equation

$$\begin{cases} \frac{d}{dt} S_k(t) = R[S_{0k} - S_k(t)] - S_k(t) \int \psi_k(x) n(t, x) dx, \\ \frac{d}{dt} n(t, x) = n(t, x) \left(\sum_{k=1}^I S_k(t) \eta_k(x) - R \right). \end{cases} \quad (1.10)$$

Here the vector with positive coefficients $(S_{0k})_{k=1, \dots, I}$ represents the inflow of 'pure' nutrients and the terms $-RS_k(t)$ and $-Rn(t, x)$ represent the outflow of the mixture with rate $R > 0$. The quadratic term, as usual, represents the uptake, with rate $\psi_k(x) > 0$, of the constituent S_k , and its restitution rate η_k . As we can see, the only effect of the variable x is on the uptake and restitution coefficients. It is usual to use $\psi_k = \eta_k$, at least they are naturally strongly related.

When $\psi_k = \eta_k$, this system contains a fundamental balance law for the total biomass $M(t)$ of constituents (free or absorbed) defined by

$$\begin{aligned} M(t) &= \sum_{k=1}^I S_k(t) + \int n(t, x) dx, \\ \frac{d}{dt} M(t) &= R \left(\sum_{k=1}^I S_{0k} - M(t) \right), \quad \forall t \geq 0. \end{aligned} \quad (1.11)$$

The long time behavior of this type of systems has attracted much attention and is not entirely known. See [100, 65, 66, 90].

To fit the general equations we deal with, it is better to consider that the time scale for nutrients is much faster than that for the population $n(t, x)$. This means that the terms $\frac{d}{dt}S_k$ are neglected. In physics this is called the 'adiabatic' assumption. Then we arrive to

$$\begin{cases} S_k(t) = \frac{RS_{0k}}{R + \int \psi_k(x)n(t, x)dx}, \\ \frac{d}{dt}n(t, x) = n(t, x) \left(\sum_{k=1}^I S_k(t)\eta_k(x) - R \right). \end{cases} \quad (1.12)$$

With the notation $I_k = 1/S_k$, this falls obviously in the general case of system (1.1).

1.5 Intra-specific local competition

See [78, 57, 56, 55]. Several models in evolution biology suppose that the competition is higher between individuals of closer traits because they feed on the same preys, see [54]. The simpler examples of equations that arise in this context use quadratic death rates given by an integral kernel $C(x, y)$,

$$\frac{\partial}{\partial t}n(t, x) = n(t, x) \left(S(x) - \int C(x, y)n(t, y)dy \right), \quad (1.13)$$

with $S(x) \geq$ the net growth rate and $C(\cdot)$ the competition kernel.

This type of modelling is rather general. For instance it contains a limiting case of the chemostat. We follow P.E. Jabin (adiabatic assumption and linearization)

$$S_k(t) \approx S_{0k} \left(1 - \int \psi(y)n(t, y)dy \right).$$

Then the fitness in the chemostat model (1.10) becomes

$$R = \sum_{k=1}^I$$

A particular case is related to the non-local Fisher equation and is written

$$\frac{\partial}{\partial t}n(t, x) = n(t, x) \left(1 - \int K(x - y)n(t, y)dy \right).$$

The typical example is a convolution $(K * n(t, \cdot))(x) = \int K(x - y)n(t, y)dy$ which shows the difficulties of this problem.

There might be smooth steady states (example of the gaussians) and Dirac mass steady states.

1.6 Chemostat with continuous nutrients distribution

In nature, it is more often observed indirect competition. The different individuals compete for a common resource. We can imagine the situation of girafs which can reach leaves (which mathematical description gives a repartition structured by their height y) as long as they are lower than their size (the other structuring parameter).

Modeling this type of situation leads to extend the chemostat to a continuous resource

$$\begin{cases} \frac{\partial}{\partial t} S(t, y) = S_{\text{input}}(y) - R S(t, y) - S(t, y) \int \eta(x) K(x - y) n(t, x) dx, \\ \frac{\partial}{\partial t} n(t, x) = n(t, x) \left(-R + \eta(x) \int K(x - y) S(t, y) dy \right), \end{cases} \quad (1.14)$$

where, to simplify the mathematical setting, we have used $x, y \in \mathbb{R}$. The food input $S_{\text{input}}(y)$ is a given function as well as the uptake function $\eta(x)$.

Again the basic property of this model is a balance law

$$\frac{d}{dt} \left[\int S(t, y) dy + \int n(t, x) dx \right] = R \left[\int S_{\text{input}}(y) dy - \int n(t, x) dx \right].$$

1.7 Mating and sexual reproduction

We take the model from [44, 49]. Given gaussian like distributions $A(y, z)$ (probability of mating between individuals of trait y and z), $B(x - \frac{y+z}{2})$ is the repartition of traits after mating individuals of traits y and z . The total amount of mating that phenotype y participates in is given by

$$N(y) = \int A(y, z) n(z) dz.$$

Then, the probability distribution of offspring with phenotype x produced by phenotype y is

$$\frac{1}{N(y)} \int A(y, z) B(x - \frac{y+z}{2}) n(z) dz$$

Finally the total density of offsprings at phenotype x resulting from all possible matings is given by

$$\beta(x) = \int \left[\frac{1}{N(y)} \int A(y, z) B(x - \frac{y+z}{2}) n(z) dz \right] n(y) dy$$

Denoting by $r(x)$ is the basic reproduction rate, this motivates the dynamics of phenotype distributions in sexual populations given by the equation

$$\frac{\partial}{\partial t} n(t, x) = r(x) \beta(x) - \frac{r(x)}{K(x)} n(t, x) K * n(t).$$

Because new traits are generated through mating, this equation does not enter in the general structure (1.1).

1.8 Multispecies models

In [96], the authors treat of the multispecies problem

$$\begin{cases} \frac{\partial n_i(t,x)}{\partial t} = \left(r_i(x) - d_i(x) \sum_{j=1}^N a_{ij} \varrho_j(t) \right) n_i(t,x), & i = 1, \dots, N, \\ \varrho_i(t) = \int n_i(t,x) dx. \end{cases}$$

As in usual ecology problem, see [91] for instance, the matrix a_{ij} describes the type of interactions between the species.

Chapter 2

Selection only: long time behavior

The immediate consequence of the formalism is natural selection. If the resources are limited, this induces that the fittest individuals take over the rest of the population which is lead to extinction by lack of resources. This phenomena is also called *competitive exclusion principle*.

The competitive exclusion principle, first formulated by Gause¹ refers to the observation that two species competing for the same resource cannot coexist (in a stable way). The *paradox of the plankton* gives an example where this rule seems to be violated; a wide variety of plankton species use only light and minerals as nutrients.

A further consequence, when a single resource is used is *mutual exclusion*. This refers to the situation when there is a unique trait represented, i.e. a single Dirac mass in the limit in the formalism of this Chapter.

We base our analysis on [1, 90, 10, 43, 69].

2.1 Single environment: the competitive exclusion principle

The simplest model (a single population density and a single environmental variable) can be studied under fairly general assumptions. The simplest model under consideration here is

$$\begin{cases} \frac{\partial}{\partial t} n(t, x) = n(t, x) R(x, I(t)), & x \in \mathbb{R}^d, t \geq 0, \\ n(t = 0) = n^0 \in L^1(\mathbb{R}^d), & n^0 \geq 0, \end{cases} \quad (2.1)$$

$$I(t) = \int_{\mathbb{R}^d} n(t, x) dx. \quad (2.2)$$

We have decided to state the problem in \mathbb{R}^d for later purposes but it would me more natural at this stage to use a bounded subset and, more generally, only a measurable space.

¹Gause, G. F. (1934) The struggle for existence. Baltimore, MD: Williams and Wilkins

Our purpose is to show that, under various assumptions on the growth rate $R(x, I)$, the population n concentrates as a Dirac mass (or a sum of Dirac masses) in long times, i.e., $t \rightarrow \infty$, a mathematical way to express that a well identified species emerge from the adaptive landscape defined by the rate R . This is the natural selection occuring in such models.

The quantity $R(x, I)$ is sometimes called the *invasion exponent* because it describes the ability of the individuals of trait x to invade the population with environmental state I . It is negative for certain traits and positive for others.

We assume that $R(x, I)$ is C^1 and that there are constants $0 < I_m < I_M < \infty$ and $0 < \bar{R} < \infty$ such that

$$\min_{x \in \mathbb{R}^d} R(x, I_m) = 0, \quad \max_{x \in \mathbb{R}^d} R(x, I_M) = 0, \quad (2.3)$$

$$\max_{x \in \mathbb{R}^d} R(x, I) \leq \bar{R}, \quad \forall I \in [I_m, I_M], \quad (2.4)$$

and that there is a constant $K_- > 0$ such that,

$$\frac{\partial R}{\partial I}(x, I) < -K_- < 0, \quad \forall x \in \mathbb{R}^d, \quad I \in [I_m, I_M]. \quad (2.5)$$

These mean that in the environmental conditions $I_m < I < I_M$ some traits decay but not all, and that the environmental conditions $I > I_M$ are so defavorable that the whole population decreases whatever the trait.

We will also use the assumption

$$n^0 \in L^1 \cap L^\infty(\mathbb{R}^d) \quad \text{and} \quad I_m \leq \int_{\mathbb{R}^d} n^0(x) dx \leq I_M. \quad (2.6)$$

We do not prove existence of solutions which follows from usual Cauchy-Lipschitz theory and yields

Theorem 2.1 *With the assumptions (2.3), (2.4) and (2.6), there is a unique solution $n \in C(\mathbb{R}^+; L^1(\mathbb{R}^d))$, $n \geq 0$, to equation (2.1)–(2.2), and it satisfies,*

$$I_m \leq I(t) \leq I_M, \quad \forall t \geq 0. \quad (2.7)$$

$$\int_0^T \int_{\mathbb{R}^d} R_-(x, I(t)) n(t, x) dx dt < I^0 + \bar{R} I_M T. \quad (2.8)$$

Here, we just indicate the derivation of the upper bound in (2.7). We first have from equation (2.1)

$$\frac{d}{dt} \int_{\mathbb{R}^d} n(t, x) dx = \int_{\mathbb{R}^d} n(t, x) R(x, I(t)) dx \leq \int_{\mathbb{R}^d} n(t, x) dx \max_{x \in \mathbb{R}^d} R(x, I(t)),$$

and thus

$$\frac{dI(t)}{dt} \leq \overline{R} I(t).$$

This proves that $I(t)$, i.e., the L^1 norm of n remains bounded in finite time. But it also proves that if $I(t)$ reaches I_M , then $\frac{dI(t)}{dt} \leq 0$ which means that $I(t) \leq I_M$ for all times.

Next, we have

$$\frac{dI(t)}{dt} dx \geq \int_{\mathbb{R}^d} n(t, x) dx \min_{x \in \mathbb{R}^d} R(x, I(t)),$$

and, as before this proves that $I(t) \geq I_m$.

Finally, we have, by integration in time and x of equation (2.1)

$$\int_{\mathbb{R}^d} [n(T, x) - n^0(x)] dx = \int_0^T \int_{\mathbb{R}^d} R_+(x, I(t)) n(t, x) dx dt - \int_0^T \int_{\mathbb{R}^d} R_-(x, I(t)) n(t, x) dx dt,$$

from which we deduce

$$\int_0^T \int_{\mathbb{R}^d} R_-(x, I(t)) n(t, x) dx dt \leq \overline{R} T I_M + \int_{\mathbb{R}^d} n^0(x) dx.$$

Better results with weaker assumptions can be found in [43], and statements in the space of measures can be found in [1].

There are many singular steady states to equation (2.1)–(2.2). For $I_m \leq I \leq I_M$ we can choose the Dirac measures

$$\bar{n}(x) = I(y) \delta(x - y), \quad R(y, I(y)) = 0.$$

Among them, only one is attained for positive initial data, because we have

Theorem 2.2 (*Competitive exclusion principle*) *We assume (2.3)–(2.5) and that $n^0 > 0$. Then, the solution to equation (2.1)–(2.2) satisfies,*

$$I(t) \xrightarrow[t \rightarrow \infty]{} I_M. \tag{2.9}$$

Furthermore, if there is a unique $\bar{x} \in \mathbb{R}^d$ such that

$$R(\bar{x}, I_M) = \max_{x \in \mathbb{R}^d} R(x, I_M) = 0,$$

and for some $A > 0$, $\sup_{|x| \geq A} R(x, I_M) < 0$, then we have

$$n(t, x) \xrightarrow[t \rightarrow \infty]{} I_M \delta(x - \bar{x}). \tag{2.10}$$

One sometimes refers to the *pessimization principle* ([87]) to express that the final population has used the environment in such a way that no possible growth is ever possible

$$R(\bar{x}, I_M) = 0.$$

This result was first proved in [1]. The proof we give here is based on different arguments due to [90, 10]. Before proving it, we need another fundamental estimate, namely a *BV* estimate that we prove first.

Theorem 2.3 *With the assumptions (2.3)–(2.5), the solutions to equation (2.1) also satisfy the uniform L^∞ bound (2.7), the BV and sub-Lipschitz bounds*

$$\begin{aligned} \frac{dI(t)}{dt} &\geq -e^{-K-I_m t} \left(\int n^0(x) R(x, I^0) dx \right)_-, \\ \int_0^\infty \left| \frac{dI(t)}{dt} \right| dt &\leq I_M + \frac{2}{K-I_m} \left(\int n^0(x) R(x, I^0) dx \right)_- \\ \int_0^\infty \int n(t, x) R(x, I(t))^2 dx &< \infty. \end{aligned}$$

Proof. We first integrate the equation (2.1) over \mathbb{R}^d , this yields

$$\frac{d}{dt} I(t) = \mathcal{J}(t), \tag{2.11}$$

with $\mathcal{J}(t)$ defined by

$$\mathcal{J}(t) = \int n(t, x) R(x, I(t)) dx.$$

The result relies on an estimate on $\mathcal{J}(t)$. In the same way as before, we have

$$\frac{d}{dt} \mathcal{J}(t) = \int n(t, x) R(x, I(t))^2 dx + \int n(t, x) \frac{\partial}{\partial I} R(x, I(t)) dx \frac{dI(t)}{dt}. \tag{2.12}$$

Now we use (2.11) to replace $\frac{d}{dt} I(t)$ by $\mathcal{J}(t)$ in the last term. Therefore,

$$\frac{d}{dt} \mathcal{J}(t) = \int n(t, x) R(x, I(t))^2 dx + \int n(t, x) \frac{\partial}{\partial I} R(x, I(t)) dx \mathcal{J}(t). \tag{2.13}$$

But we have, using (2.5),

$$\int n(t, x) \frac{\partial}{\partial I} R(x, I(t)) dx \leq -K_- \int n(t, x) \leq -K_- I_m < 0.$$

We multiply equation (2.13) by $-\text{sgn}_- \mathcal{J}(t) (\leq 0)$ and we obtain

$$\frac{d}{dt} (\mathcal{J}(t))_- \leq -K_- I_m (\mathcal{J}(t))_-.$$

From this differential inequality, we deduce the announced sub-lipschitz inequality

$$(\mathcal{J}(t))_- \leq (\mathcal{J}(0))_- e^{-K_- I_m t}. \quad (2.14)$$

Additionally, this already proves a BV bound on $(\mathcal{J}(t))_-$ since

$$\int_0^\infty (\mathcal{J}(t))_- dt \leq \frac{(\mathcal{J}(0))_-}{K_- I_m}. \quad (2.15)$$

In order to conclude the TV bound, we argue as follows. We have from (2.11)

$$\int_0^T \mathcal{J}(t) dt = I(T) - I(0) \leq I_M. \quad (2.16)$$

Therefore

$$\int_0^T (\mathcal{J}(t))_+ dt \leq I_M + \int_0^T (\mathcal{J}(t))_- dt,$$

and the BV bound follows.

The last statement is a consequence of (2.12) once we know that I is TV and $\frac{dT}{dt}$ is integrable.

□

Proof of Theorem 2.2. We can now conclude the derivation of the long time behavior of $n(t, x)$ in equation (2.1).

1st step. Limit of $I(t)$. From the BV bound in Theorem 2.3, we deduce that there is a limit

$$I(t) \xrightarrow[t \rightarrow \infty]{} \bar{I}.$$

2nd step. $\bar{I} = I_M$. Suppose by contradiction that $\max_{x \in R^d} R(x, \bar{I}) := 2M > 0$. Then, for $\varepsilon > 0$ small enough, there is a ball B_ε where $R(x, \bar{I} - \varepsilon) \geq M$. From the first step, there is T_ε such that $I(t) \geq \bar{I} - \varepsilon$ for $t \geq T_\varepsilon$. This gives, solving equation (2.1) explicitly for $t > T_\varepsilon$,

$$n(t, x) = n(T_\varepsilon, x) \exp \left(\int_{T_\varepsilon}^t R(x, I(s)) ds \right) \geq n(T_\varepsilon, x) \exp((t - T_\varepsilon)M), \quad \forall x \in B_\varepsilon.$$

As $t \rightarrow \infty$ this proves that $n(t, x) \rightarrow \infty$ on B_ε and this is a contradiction with the boundness of $I(t)$. Therefore $\max_{x \in R^d} R(x, \bar{I}) = 0$ and by the strict monotonicity of $R(x, I)$ in I , this proves that $\bar{I} = I_M$.

3rd step. Limit of $n(t)$. Equi-integrability. Because $n(t)$ is a bounded measure, we can extract a subsequence $n(t_k)$ such that $n(t) \xrightarrow[t \rightarrow \infty]{} \bar{n}$, a bounded nonnegative measure with total mass less

than I_M . Our first purpose is to prove that $\int_{\mathbb{R}^d} \bar{n}(x)dx = I_M$ (we denote the integration of measures with dx as for functions). This follows from the assumption (2.5) because for T large enough

$$\sup_{t \geq T, |x| \geq A} R(x, I(t)) < 0.$$

This implies that for all $\varepsilon > 0$, we may find $A_\varepsilon > A$ such that

$$\sup_{t \geq T} \int_{|x| \geq A_\varepsilon} n(t, x)dx \leq \varepsilon,$$

and thus that for all $\varepsilon > 0$,

$$\int \bar{n}(x)dx \geq \lim_{k \rightarrow \infty} \int_{|x| \leq A_\varepsilon} n(t_k, x)dx \geq I_M - \varepsilon.$$

This proves our claim for the total mass of \bar{n} .

4th step. Identifying the measure \bar{n} . It also follows from the explicit formula for $n(t, x)$ in step 2, that \bar{n} can only be supported by points where $R(x, I_M)$ vanishes and thus, with our strong assumption that its support is reduced to \bar{x} thus proving our last claim.

One can also give a more quantitative estimate on the convergence rate. To do that, we use again the equality (2.13) and assumption (2.5) to arrive, for $S > T > 0$, at

$$\int_T^S \int_{\mathbb{R}^d} n(t, x) R(x, I(t))^2 dx dt \leq \mathcal{J}(S) - \mathcal{J}(T) + K_+ I_M \int_T^S (\mathcal{J}(t))_+ dt.$$

Because $\mathcal{J}(t)$ is integrable, there is a sequence $S_n \rightarrow \infty$ such that $\mathcal{J}(S_n) \rightarrow 0$. Choosing this sequence in the above inequality and passing to the limit we obtain

$$\begin{aligned} \int_T^\infty \int n(t, x) R(x, I(t))^2 dx dt &\leq -\mathcal{J}(T) + K_+ I_M \int_T^\infty (\mathcal{J}(t))_+ dt \\ &\leq (\mathcal{J}(0))_- e^{-K_- I_M T} + I_M \int_T^\infty (\mathcal{J}(t))_+ dt \\ &\longrightarrow 0, \quad \text{as } T \rightarrow \infty \end{aligned}$$

thanks to the estimate (2.14). \square

2.2 Rate of convergence: an explicit computation

We wish to precise the convergence rate and thus consider a simple variant of Verhulst's logistic equation which we structure with a trait $x \in [x_m, x_M]$

$$\begin{cases} \frac{\partial}{\partial t} n(t, x) &= b(x)n(t, x) - \varrho(t)n(t, x), \\ \varrho(t) &= \int_{x_m}^{x_M} n(t, x)dx, \\ n(t=0) &= n^0(x) > 0 \text{ for } x \in [x_m, x_M]. \end{cases} \quad (2.17)$$

Also to make things very clear, we assume

$$n^0 \in C^2([x_m, x_M]), \quad n^{0''}(0) \neq 0, \quad n^0 > 0, \quad (2.18)$$

$$b \in C^2([x_m, x_M]), \quad \bar{b} := b(0) > 0, \quad B := b''(0) < 0, \quad b(x) < \bar{b} \quad \forall x \neq 0. \quad (2.19)$$

In this situation we know the fittest trait $\bar{x} = 0$ (highest reproduction rate here) is selected

$$\varrho(t) \rightarrow \bar{b}, \quad n(t, x) \rightarrow \bar{b} \delta(x) \quad \text{as } t \rightarrow \infty. \quad (2.20)$$

We wish to go further and describe the measure through a 'potential' φ defined by

$$n(t, x) = e^{\varphi(t, x)}.$$

We expect a description of $n(t)$ analogous to the convergence of gaussians $\frac{\sqrt{t}}{\sqrt{2\pi}} e^{-t\frac{|x|^2}{2T}}$ towards the Dirac mass. We expect that $\varphi(t, x) \approx -t\frac{|x|^2}{2T} + \frac{1}{2} \ln\left(\frac{t}{2\pi T}\right)$ near $x = 0$ (for some T) but far away there is no reason to think that this quadratic shape is appropriate. Anyhow, the knowledge near $x = 0$ describes accurately the concentration of the measure (what proportion of mass stays in a given neighborhood of 0).

The equation on φ is simple

$$\frac{\partial}{\partial t} \varphi(t, x) = b(x) - \varrho(t), \quad (2.21)$$

and we can prove from it that

Theorem 2.4 *Assume (2.18), (2.19). Then, the solution to (2.17) satisfies*

$$\varphi(t, x) = -[b(0) - b(x)]t + \frac{1}{2} \ln(t) - \ln\left(\sqrt{2\pi B} \frac{n^0(0)}{b(0)}\right) + O\left(\frac{1}{t}\right). \quad (2.22)$$

As a consequence, we deduce the expected expansion near 0

$$\varphi(t, x) \approx -B\frac{|x|^2}{2}t + \frac{1}{2} \ln(t) - \ln\left(\sqrt{2\pi B} \frac{n^0(0)}{b(0)}\right).$$

Proof. The proof relies on an explicit computation which allows us to compute the convergence rate of $\varrho(t)$ to $b(0)$. We integrate equation (2.17) and find successively

$$n(t, x) = n^0(x) e^{b(x)t - \int_0^t \varrho(s) ds}, \quad \varrho(t) e^{\int_0^t \varrho(s) ds} = \int_{x_m}^{x_M} n^0(x) e^{b(x)t},$$

$$\frac{d}{dt} e^{\int_0^t \varrho(s) ds} = \varrho(t) e^{\int_0^t \varrho(s) ds} = \int_{x_m}^{x_M} n^0(x) e^{b(x)t} dx,$$

$$e^{\int_0^t \varrho(s) ds} = \int_{x_m}^{x_M} \frac{n^0(x)}{b(x)} e^{b(x)t} dx + K, \quad K = 1 - \int_{x_m}^{x_M} \frac{n^0(x)}{b(x)} dx.$$

Therefore we conclude

$$\int_0^t \varrho(s) ds = \ln \left(\int_{x_m}^{x_M} \frac{n^0(x)}{b(x)} e^{b(x)t} dx + K \right), \quad (2.23)$$

$$\varrho(t) = \int_{x_m}^{x_M} n^0(x) e^{b(x)t} dx / \left[\int_{x_m}^{x_M} \frac{n^0(x)}{b(x)} e^{b(x)t} dx + K \right], \quad (2.24)$$

and we notice that the constant K may be negative but the denominator is larger than 1.

These formula are based on Laplace integrals and we recall that , with $B = b''(0)$,

$$\int_{x_m}^{x_M} f(x) e^{b(x)t} dx = \sqrt{\frac{2\pi B}{t}} e^{b(0)t} \left[f(0) + \frac{f''(0)}{2Bt} + o\left(\frac{1}{t}\right) \right].$$

Therefore, from equation (2.23),

$$\begin{aligned} \int_0^t [\varrho(s) - \bar{b}] ds &= \ln \left(\sqrt{\frac{2\pi B}{t}} e^{b(0)t} \left[\frac{n^0(0)}{b(0)} + \frac{(n^0/b)''(0)}{2Bt} + o\left(\frac{1}{t}\right) \right] + K \right) - b(0)t \\ &= -\frac{1}{2} \ln(t) + \ln \left(\sqrt{2\pi B} \left[\frac{n^0(0)}{b(0)} + O\left(\frac{1}{t}\right) \right] \right) \\ &= -\frac{1}{2} \ln(t) + \ln \left(\sqrt{2\pi B} \frac{n^0(0)}{b(0)} \right) + O\left(\frac{1}{t}\right). \end{aligned}$$

And the claim (2.22) on $\varphi(t, x)$ follows from this formula.

2.3 A more precise general asymptotics

We come back to the general model (2.1)–(2.2). We have proved the weak convergence of the population density to a Dirac mass, in the sense of measures. Following the exact computation in Section 2.2, it can also be made general.

The rigorous statement is the following corollary of the proof of Theorem 2.2

Corollary 2.5 *With the assumptions of Theorem 2.2 and writing the solution to equation (2.1)–(2.2) as $n(t, x) = e^{\varphi(t, x)}$, we have*

$$\frac{\varphi(t, x)}{t} \rightarrow R(x, \bar{I}), \quad \forall x \in \mathbb{R}^d. \quad (2.25)$$

Notice that this is a very weak statement which does not tell the details on the convergence rate of $I(t)$ for instance.

Proof. The equation (2.1) yields

$$\frac{d\varphi(t, x)}{dt} = R(x, I(t)).$$

For a given $\varepsilon > 0$, we choose a T large enough so that $|R(x, I(t)) - R(x, \bar{I})| \leq \varepsilon$. Therefore we have

$$\varphi(t, x) = \varphi(T, x) + \int_T^t R(x, I(s)) ds = \varphi(T, x) + (t - T)[R(x, \bar{I}) + O(\varepsilon)],$$

$$\frac{\varphi(t, x)}{t} = \frac{\varphi(T, x) - TR(x, \bar{I})}{t} + R(x, \bar{I}) + O(\varepsilon).$$

The result follows immediately. \square

2.4 Two environmental variables

When several environmental variables are present the results are more difficult to establish. In particular, the afore examples show that the quantities I_k may have different effects on the population (increased growth, or increased death). Here we treat the case of equation (1.1) with two variables, when they increase the pressure on the population,

$$\begin{cases} \frac{\partial}{\partial t} n(t, x) = n(t, x) R(x, I_1(t), I_2(t)), & x \in \mathbb{R}^d, t \geq 0, \\ I_k(t) = \int \psi_k(x) n(t, x) dx, & k = 1, 2, \end{cases} \quad (2.26)$$

with the following extension of the assumptions (2.3)–(2.5): there are constants $0 < I_m^k < I_M^k < \infty$ and $0 < \bar{R} < \infty$ such that for all I

$$\begin{cases} \min_{x \in \mathbb{R}^d} R(x, I_m^1, I) \geq 0, & \max_{x \in \mathbb{R}^d} R(x, I_M^1, I) \leq 0, \\ \min_{x \in \mathbb{R}^d} R(x, I, I_m^2) \geq 0, & \max_{x \in \mathbb{R}^d} R(x, I, I_M^2) \leq 0, \end{cases} \quad (2.27)$$

$$\max_{x \in \mathbb{R}^d} R(x, I_1, I_2) \leq \bar{R}, \quad \forall I_k \in [I_m^k, I_M^k], \quad (2.28)$$

and that there are constants $K_-^k < K_+^k$ such that,

$$-K_+^1 \leq \frac{\partial R}{\partial I_1}(x, I_1, I_2) < -K_-^1 < 0, \quad -K_+^2 \leq \frac{\partial R}{\partial I_2}(x, I_1, I_2) < -K_-^2 < 0, \quad (2.29)$$

$$n^0 \in L^1 \cap L^\infty(\mathbb{R}^d), \quad n^0 \geq 0 \quad \text{and} \quad I_m^k \leq \int_{\mathbb{R}^d} \psi_k(x) n^0(x) dx \leq I_M^k. \quad (2.30)$$

As before, we first mention the

Theorem 2.6 *With the assumptions (2.27), (2.28) and (2.30), there is a unique solution $n \in C(\mathbb{R}^+; L^1(\mathbb{R}^d))$, $n \geq 0$, to equation (2.26), and it satisfies,*

$$I_m^k \leq I_k(t) \leq I_M^k, \quad \forall t \geq 0, k = 1, 2. \quad (2.31)$$

$$\int_0^T \int_{\mathbb{R}^d} R_-(x, I(t)) n(t, x) dx dt < I^0 + \bar{R} I_M T. \quad (2.32)$$

The long time behavior uses more elaborate ingredients similar to the previous sections

Theorem 2.7 *With the assumptions (2.27)–(2.30), there are limits as $t \rightarrow \infty$,*

$$I_k(t) \rightarrow I_k^\infty, \quad k = 1, 2,$$

and $n(t, x)$ concentrates on points x^∞ such that

$$R(x^\infty, I_1^\infty, I_2^\infty) = 0.$$

Proof. As before we define

$$\frac{dI_k(t)}{dt} = \mathcal{J}_k(t) := \int_{\mathbb{R}^d} \psi_k(x) R(x, I_1(t), I_2(t)) n(t, x) dx. \quad (2.33)$$

The proof is based again on the differential relations

$$\frac{d\mathcal{J}_k(t)}{dt} = S_k(t) - A_k^1(t) \mathcal{J}_1(t) - A_k^2(t) \mathcal{J}_2(t), \quad (2.34)$$

with

$$\begin{aligned} S_k(t) &:= \int_{\mathbb{R}^d} \psi_k(x) R^2(x, I_1(t), I_2(t)) n(t, x) dx > 0, \\ A_k^j(t) &:= - \int_{\mathbb{R}^d} \psi_k(x) \frac{\partial R(x, I_1(t), I_2(t))}{\partial I_j} n(t, x) dx \geq K_-^j \int_{\mathbb{R}^d} \psi_k(x) n(t, x) dx \geq K_-^j I_m^k > 0. \end{aligned}$$

Lemma 2.8 *Set $\alpha = \min_{1 \leq j, k \leq 2} K_-^j I_m^k$, then*

$$\max(\mathcal{J}_1(t), \mathcal{J}_2(t))_- \leq \max(\mathcal{J}_1(0), \mathcal{J}_2(0))_- e^{-\alpha t}$$

Proof. Set $\mathcal{J} = \max(\mathcal{J}_1, \mathcal{J}_2)$. We have, for the times where this max is attained by $\mathcal{J}_1(t)$,

$$\frac{d\mathcal{J}(t)}{dt} \geq -A_1^1(t) \mathcal{J}_1(t) - A_1^2(t) \mathcal{J}_2(t),$$

and thus

$$\frac{d(\mathcal{J}(t))_-}{dt} \leq -A_1^1(t)(\mathcal{J}(t))_- + A_1^2(t)\mathcal{J}_2(t)\text{sgn}_-(\mathcal{J}(t))$$

When $\text{sgn}_-(\mathcal{J}(t)) \neq 0$, this means $\mathcal{J}_2(t) \leq \mathcal{J}_1(t) < 0$ and thus

$$\frac{d(\mathcal{J}(t))_-}{dt} \leq -A_1^1(t)(\mathcal{J}(t))_- \leq -\alpha(\mathcal{J}(t))_-.$$

The same argument leads to the same inequality in case the max is attained by $\mathcal{J}_2(t)$ and leads to the result of the lemma.

The end of the proof of Theorem 2.7 is as before. \square

2.5 Evolutionary Stable Strategy, several nutrients

It is much more difficult to prove general convergence results for structured population models with several environmental unknowns as

$$\begin{cases} \frac{\partial}{\partial t} n(t, x) = n(t, x) R(x, I_1(t), \dots, I_K(t)), & x \in \mathbb{R}^d, t \geq 0, \\ I_k(t) = \int \psi_k(x) n(t, x) dx, & k = 1, \dots, K. \end{cases} \quad (2.35)$$

Because it is natural that $R(x, \cdot)$ has only isolated zeros, the steady states can only be Dirac masses. These are characterized by the relations

$$\begin{cases} \bar{n}(x) = \sum_{i=1}^I \varrho_i \delta(x - \bar{x}_i), \\ R(\bar{x}_i, \bar{I}_1, \dots, \bar{I}_K) = 0, & i = 1, \dots, I, \\ \bar{I}_k = \sum_{i=1}^I \varrho_i \psi_k(\bar{x}_i), & k = 1, \dots, K. \end{cases} \quad (2.36)$$

Notice that there are many steady states in general. If we consider the case of a single environmental variable $K = 1$ treated in section 2.1, for each $I_m < I \leq I_M$ there is at least one Dirac mass steady state $\varrho(I) \delta(x - \bar{x}(I))$ at least. Indeed, we can find the possible traits $x(I)$ by the relation

$$R(\bar{x}(I), I) = 0. \quad (2.37)$$

In adaptive dynamics jargon, such a state $(\bar{x}(I), I)$ is called a *singular point*. And such a singular point always exists for $I_m < I \leq I_M$ because

$$\min_x R(x, I) < 0, \quad \max_x R(x, I) > 0,$$

as a consequence of assumptions (2.3), (2.5). Then the weight $\varrho(I) = I$ fits the definition of I from n . But we have seen that only one of them is reached in long time.

This means that not all these states in (2.36) are stable in the sense that some initial data with $n^0(x) > 0$ for all x will converge to such a state. To see this we can ask a weaker requirement, namely that \bar{n} is *Evolutionary Stable*. This means that, given the environmental state $(\bar{I}_1, \dots, \bar{I}_K)$, a small perturbation of \bar{n} with $n^0(x) > 0$ will go back to \bar{n} . This requires that other traits than the \bar{x}_i are decaying, i.e., $R(x, \bar{I}_1, \dots, \bar{I}_K) < 0$ for $x \neq \bar{x}_i$, this means

$$\max_x R(x, \bar{I}_1, \dots, \bar{I}_K) = 0 = R(\bar{x}_i, \bar{I}_1, \dots, \bar{I}_K), \quad i = 1, \dots, I, \quad (2.38)$$

this is again the pessimization principle.

Two consequences are noticeable which are the first and second variations conditions for a maximum,

$$\nabla_x R(\bar{x}_i, \bar{I}_1, \dots, \bar{I}_K) = 0, \quad i = 1, \dots, I, \quad (2.39)$$

$$D_{xx}^2 R(x, \bar{I}_1, \dots, \bar{I}_K) \leq 0, \quad i = 1, \dots, I. \quad (2.40)$$

Notice that (2.38) is indeed a necessary condition for the stability of \bar{n} among measure solutions to the dynamics (2.35). To prove such a statement requires some material, as measure solutions and we refer the reader interested in details to [39, 43], and more precise notions of stability as Continuously Stable Strategy in [1]. This statement is however rather intuitive. If (2.38) did not hold, then an initial perturbation with $\delta n^0(x) > 0$ for $x \in B_\varepsilon$ a small ball of traits such that $R(x, \bar{I}_1, \dots, \bar{I}_K) > 0$, would further increase.

We conclude with underlying a shortcoming of the presentation we have adopted up to this point. We have assumed that all the traits are represented initially in the population. Any advantageous trait, in a certain environment due to the full population, can emerge and take over the rest of the population. This is certainly realistic for a lake where many species of bacteria are present, maybe undetectable, and one of them will develop very quickly if the conditions become favorables. This is not what we have in mind when the word 'evolution' is used. Then the population is fixed and mutations can create new traits. Assuming these mutations have a small effect on the trait, only small variations of the dominant trait \bar{x} are possible. Therefore the local conditions (2.39), (2.40) are more realistic.

2.6 Intraspecific competition: example

Consider the model

$$\frac{\partial n(t, x)}{\partial t} = n(t, x) \left(r(x) - \int K(x - y) n(t, y) dy \right), \quad (2.41)$$

with

$$K \in C(\mathbb{R}), \quad K(\cdot) \geq 0, \quad \int K(z)dz = 1.$$

There are many Dirac steady states, namely $\varrho(z)\delta(x-z)$ for all $r(z) = \varrho(z)K(0)$. Most of them are unstable because nearby z we can find values of x such that $r(x) - \varrho(z)K(x-z) > 0$ (and the corresponding initial value $n^0(x) > 0$ will grow exponentially. In other word all those z are unstable if

$$\exists x \text{ such that } \frac{r(x)}{r(z)} > \frac{K(x-z)}{K(0)}.$$

The condition for a stable Dirac steady state $N(x) = \bar{\varrho}\delta(x - \bar{x})$ is

$$r(\bar{x}) = \bar{\varrho}K(0),$$

$$r(x) < \bar{\varrho}K(x - \bar{x}) \quad \forall x \neq \bar{x},$$

or, replacing $\bar{\varrho}$ from the first condition

$$\frac{r(x)}{r(\bar{x})} < \frac{K(x - \bar{x})}{K(0)} \quad \forall x \neq \bar{x}.$$

Combining it with the unstability condition we arrive at the *min-max* condition that \bar{x} realizes the min over z in

$$\min_z \max_x \left[\frac{r(x)}{r(z)} - \frac{K(x-z)}{K(0)} \right] = 0 = \max_x \left[\frac{r(x)}{r(\bar{x})} - \frac{K(x-\bar{x})}{K(0)} \right].$$

This makes a direct relation with game theory.

We illustrate this on the case of gaussian coefficients

$$r(x) = \frac{1}{\sqrt{2\pi}\sigma_1} e^{-\frac{|x|^2}{2\sigma_1^2}}, \quad K(z) = \frac{1}{\sqrt{2\pi}\sigma_2} e^{-\frac{|z|^2}{2\sigma_2^2}}.$$

We have the

Proposition 2.9 *For $\sigma_1 > \sigma_2$ there is a smooth steady state to (2.41) with gaussian coefficients given by*

$$N(x) = \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{|x|^2}{2\sigma^2}}, \quad \sigma = \sigma_1 - \sigma_2,$$

and Dirac masses are not stable steady states.

For $\sigma_1 < \sigma_2$ the Dirac mass $\bar{\varrho}\delta(x)$ is a stable steady state (and only the Dirac mass at 0 is stable).

We refer to [69] for a proof.

2.7 Intraspecific competition: a condition for monomorphism

We give a general condition leading to this case that is an extension of a case treated in [43]

The model is again

$$\frac{\partial n(t, x)}{\partial t} = n(t, x) \left(r(x) - \int c(x, y) n(t, y) dy \right), \quad (2.42)$$

with an initial data satisfying

$$n^0 \geq 0, \quad n^0(x) > 0, \quad \forall x \in B(0) \quad \text{a ball centered at 0.} \quad (2.43)$$

We use the following notations and assumptions

$$\sup_y \frac{c_x(x, y)}{c(x, y)} := q(x), \quad (2.44)$$

$$r(0) > 0, \quad (2.45)$$

$$r'(x) - q_+(x) r(x) := p(x) \begin{cases} \geq P|x| & \text{for } x < 0, \\ \leq -Px & \text{for } x > 0, \end{cases} \quad (2.46)$$

for some constant $P > 0$.

This assumption means that $r(x)$ has a maximum at 0 sufficiently peaked compared to c . And a weaker condition is needed in fact which is given in the proof below.

Theorem 2.10 *With the notations and assumptions (2.44)–(2.46) (or more generally (2.48) below in place of (2.46)), we have*

$$n(t, x) \xrightarrow[t \rightarrow \infty]{} \bar{\rho} \delta(x),$$

for all bounded and closed intervals I that do not contain 0, there is a constant C such that

$$\int_I n(t, x) dx \leq e^{-Ct},$$

finally there is $\bar{\varphi} > 0$ such that for t large enough

$$\varphi(t, x) \leq \bar{\varphi} \ln t.$$

The weight of the Dirac mass is given by the singular point condition $R = 0$, that is

$$r(0) = \bar{\rho} b(0, 0).$$

Proof. Step 1. We first prove that the total population satisfies

$$0 < \varrho_- \leq \varrho(t) = \int_{\mathbb{R}} n(t, x) dx \leq \varrho_+ < \infty. \quad (2.47)$$

We integrate equation (2.43) and find

$$\begin{aligned} \frac{d}{dt} \varrho(t) &= \int_{\mathbb{R}} r(x) n(t, x) dx - \int_{\mathbb{R}^2} b(x, y) n(t, y) n(t, x) dy dx \\ &\leq \varrho(t) [\max r - \min b \varrho(t)]. \end{aligned}$$

Consequently, we obtain

$$\varrho(t) \leq (\varrho(0), \frac{\max r}{\min b}) := \varrho_+.$$

and also

$$\begin{aligned} \frac{d}{dt} \varrho(t) &= \int_{\mathbb{R}} r(x) n(t, x) dx - \int_{\mathbb{R}^2} b(x, y) n(t, y) n(t, x) dy dx \\ &\geq \varrho(t) [r_m - b_M \varrho(t)]. \end{aligned}$$

Step 2. Then, we set $\varphi = \ln(n)$ and write as usual

$$\frac{\partial}{\partial t} \varphi(t, x) = r(x) - \int c(x, y) n(t, y) dy.$$

We prove that

$$\varphi(t, 0) \leq \bar{\varphi} \ln t \quad \forall t \geq t_0.$$

Step 3. We compute for $x < 0$,

$$\begin{aligned} \frac{\partial}{\partial t} \varphi_x(t, x) &= r'(x) - \int c_c(x, y) n(t, y) dy \\ &= r'(x) - \int \frac{c_c(x, y)}{c(x, y)} c(x, y) n(t, y) dy \\ &\geq r'(x) - \sup_y \frac{c_c(x, y)}{c(x, y)} \int c(x, y) n(t, y) dy \\ &\geq r'(x) - q_+(x) \int c(x, y) n(t, y) dy \\ &\geq r'(x) + q_+(x) \left[\frac{\partial}{\partial t} \varphi(t, x) - r(x) \right]. \end{aligned}$$

We now use the notations $Q_+(x) = \int_0^x q_+(y) dy$ and the precise assumption

$$\Pi(x) := - \int_0^x p(y) e^{Q_+(y)} dy > 0 \quad \forall x \neq 0. \quad (2.48)$$

Then, this can be written, still for $x < 0$,

$$\begin{aligned} \frac{\partial}{\partial t} (\varphi_x(t, x) - q_+(x) \varphi) &\geq p(x), \\ \frac{\partial}{\partial t} (\varphi(t, x) e^{-Q_+(x)})_x &\geq p(x) e^{-Q_+(x)}, \end{aligned}$$

$$\left(\varphi(t, x)e^{-Q_+(x)}\right)_x \geq \left(\varphi^0(x)e^{-Q_+(x)}\right)_x + t p(x)e^{-Q_+(x)}.$$

Integrating between $x < 0$ and 0, we obtain

$$\varphi(t, x)e^{-Q_+(x)} - \varphi(t, 0) \leq \varphi^0(x)e^{-Q_+(x)} - \varphi^0(0) - t \Pi(x),$$

$$\varphi(t, x) \leq \varphi^0(x) + e^{Q_+(x)} [\varphi(t, 0) - \varphi^0(0) - t \Pi(x)].$$

Because we know a priori the bound

$$\varphi(t, x) \leq \bar{\varphi},$$

we conclude that

$$\varphi(t, x)e^{Q_+(x)} \leq C(x) - t \Pi(x).$$

This clearly implies the second statement of the Theorem.

It remains to conclude that the total mass converges.

2.8 Another point of view: change time scale

One can also consider another point of view, using a rescaling in time

$$\begin{cases} \varepsilon \frac{\partial}{\partial t} n_\varepsilon(t, x) = n_\varepsilon(t, x) R(x, I_\varepsilon(t)), & x \in \mathbb{R}^d, t \geq 0, \\ n_\varepsilon(t = 0) = n_\varepsilon^0 \in L_+^1(\mathbb{R}^d), \\ I_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t, x) dx. \end{cases} \quad (2.49)$$

We assume

$$\begin{cases} n_\varepsilon^0 \rightarrow n^0 & \text{in } L^1(\mathbb{R}^d), \\ n_\varepsilon^0(x) = e^{\frac{u_\varepsilon^0(x)}{\varepsilon}}, \quad u_\varepsilon^0(x) \rightarrow u^0(x) & \text{uniformly.} \end{cases}$$

Theorem 2.11 *With these notations $n_\varepsilon(t, x) = e^{\frac{u_\varepsilon(t, x)}{\varepsilon}}$ and $u_\varepsilon(t, x) \rightarrow u(t, x), I_\varepsilon(t) \rightarrow I(t)$ a.e. and u satisfies*

$$\begin{cases} \frac{\partial u}{\partial t} = R(x, I(t)) \\ \max_x u(t, x) = 0 & \text{a.e. } t \end{cases}$$

Some assumptions are needed of course, which should guarantee that $I_\varepsilon(t) \rightarrow I(t)$ a.e. by the same BV technique as before.

Chapter 3

Mutations in population models

Mutations can easily be included in the population models we have encountered so far. We present here several aspects of the formalism. The most natural formalism consists in an integral term which represents how much a mother of trait x may give an off-spring of trait y with a certain probability. If the phenotypical changes are taken as very small, the mutation term becomes a differential term. This is what we explain now.

3.1 Mutation kernels

The most natural formalism consists in an integral term which represents how much a mother of trait x may give an off-spring of trait y with a certain probability. This is not the only possible formalism. Indeed differential terms can also represent mutations, depending on the microscopic models under consideration. The rigorous derivation of the equations we write in this Chapter can be performed from Individual Based Stochastic Models and can be found for instance in [24, 45, 35, 33, 34].

Consider a mutation probability $\mu \in [0, 1]$, then we introduce in equation (1.1) an additional term representing mutations from the trait y to x and write

$$\frac{\partial}{\partial t} n(t, x) = (1 - \mu) n(t, x) R(x, [n(t, \cdot)]) + \mu \int M(y, x) b(y) n(t, y) dy. \quad (3.1)$$

Here $b(\cdot)$ represents the birth rate in case of a mutation and $M(y, x)$ the mutation rate from y to x .

Our purpose is to show that this model is closely related to another formalism, namely

$$\frac{\partial}{\partial t} n(t, x) = (1 - \mu) n(t, x) R(x, [n(t, \cdot)]) + \mu \Delta n(t, x). \quad (3.2)$$

3.2 The hyperbolic limit

In order to present scalings of the mutation terms, we depart from a generic and simpler formalism, namely

$$\frac{\partial}{\partial t}n(t, x) + k(x)n(t, x) = \int K(y, x - y)n(t, y)dy. \quad (3.3)$$

It is a conservative model under the condition

$$\int K(y, z)dz = k(y). \quad (3.4)$$

For the hyperbolic limit, we rescale the equation as

$$\frac{\partial}{\partial t}n_\varepsilon(t, x) + \frac{1}{\varepsilon} \left[k(x)n_\varepsilon(t, x) - \int \frac{1}{\varepsilon} K(y, \frac{x-y}{\varepsilon})n_\varepsilon(t, y)dy \right] = 0. \quad (3.5)$$

Theorem 3.1 *The hyperbolic limit model is*

$$\frac{\partial}{\partial t}n(t, x) + \operatorname{div}[V(x)n(t, x)] = 0,$$

$$V(x) = \int zK(x, z).$$

Proof. We change variables $y \rightarrow z = \frac{x-y}{\varepsilon}$ and we write it as

$$\frac{\partial}{\partial t}n_\varepsilon(t, x) + \frac{1}{\varepsilon} \left[k(x)n_\varepsilon(t, x) - \int K(x - \varepsilon z, z)n_\varepsilon(t, x - \varepsilon z)dz \right] = 0,$$

$$\frac{\partial}{\partial t}n_\varepsilon(t, x) + \int \frac{1}{\varepsilon} \left[K(x, z)n_\varepsilon(t, x) - K(x - \varepsilon z, z)n_\varepsilon(t, x - \varepsilon z) \right] dz = 0,$$

The limit in distributions is obtained using a test function (in x only to simplify the formulas)

$$\frac{\partial}{\partial t} \int n_\varepsilon(t, x)\Phi(x)dx + \int \int \frac{1}{\varepsilon} [\Phi(x) - \Phi(x + \varepsilon z)] zK(x, z)n_\varepsilon(t, x)dz dx = 0,$$

$$\frac{\partial}{\partial t} \int n_\varepsilon(t, x)\Phi(x)dx - \int \int z \cdot \nabla \Phi(x) K(x, z)n_\varepsilon(t, x)dz dx = O(\varepsilon).$$

In the limit, this is a weak formulation of

$$\frac{\partial}{\partial t}n(t, x) + \operatorname{div} \left[\int zK(x, z)n(t, x) \right] = 0.$$

and the result is proved. \square

3.3 The parabolic limit

A more general equation in the limit can be obtained with another scaling

$$\frac{\partial}{\partial t} n_\varepsilon(t, x) + \frac{1}{\varepsilon^2} \left[k(x) n_\varepsilon(t, x) - \int \frac{1}{\varepsilon} K_\varepsilon(y, \frac{x-y}{\varepsilon}) n_\varepsilon(t, y) dy \right] = 0. \quad (3.6)$$

Then we assume

$$\int K_\varepsilon(y, z) dz = k(y), \quad \int z K_\varepsilon(y, z) dz = \varepsilon V(y), \quad \int z_i z_j K_\varepsilon(y, z) dz = 2A_{ij}(y). \quad (3.7)$$

Theorem 3.2 *The parabolic limit model is*

$$\frac{\partial}{\partial t} n(t, x) - \frac{\partial^2}{\partial x_i \partial x_j} [A_{ij}(x) n(t, x)] + \operatorname{div} [V(x) n(t, x)] = 0.$$

Proof. As before, we have

$$\frac{\partial}{\partial t} n_\varepsilon(t, x) + \int \frac{1}{\varepsilon^2} [K_\varepsilon(x, z) n_\varepsilon(t, x) - K_\varepsilon(x - \varepsilon z, z) n_\varepsilon(t, x - \varepsilon z)] dz = 0.$$

As before, we introduce a test function $\Phi(x)$ and find

$$\begin{aligned} \frac{d}{dt} \int \Phi(t, x) n_\varepsilon(t, x) + \int n_\varepsilon(t, x) \int K_\varepsilon(x, z) \frac{\Phi(t, x) - \Phi(t, x + \varepsilon z)}{\varepsilon^2} dz dx &= 0, \\ \frac{d}{dt} \int \Phi(t, x) n_\varepsilon(t, x) + \int n_\varepsilon(t, x) \int K_\varepsilon(x, z) \left[-\frac{z \cdot \nabla \Phi(t, x)}{\varepsilon} + \frac{z_i z_j}{2} D_{ij}^2 \Phi(t, x) \right] dz dx &= O(\varepsilon). \end{aligned}$$

And thus, we arrive at the announced limit. \square

Chapter 4

Branching and transition to dimorphism in models with two environmental unknowns

The formalism leading to monomorphic populations, as described in Chapter 5, is based on a single environmental unknown $I(t)$. It allows us to understand how dimorphism can occur when the model contains two environmental functions along with Section 2.4. The equation is written as

$$\begin{aligned} \frac{\partial}{\partial t} n(t, x) &= n(t, x) R(x, I_1(t), I_2(t)) \\ I_1(t) &= \int \psi_1(x) n(t, x) dx, \quad I_2(t) = \int \psi_2(x) n(t, x) dx \end{aligned}$$

4.1 what is branching?

It may happen that, at a certain time t^* a monomorphic population

$$n(x, t) \approx \varrho(t) \delta(x - \bar{x}(t)), \quad t \leq t^*,$$

can evolve towards a point where suddenly there is an adaptive advantage to split in two co-existing subpopulations. In analytical terms this means

$$n(x, t) \approx \varrho_1(t) \delta(x - \bar{x}_1(t)) + \varrho_2(t) \delta(x - \bar{x}_2(t)), \quad t \geq t^*,$$

with $\bar{x}_1(t) \neq \bar{x}_2(t)$ for $t > t^*$.

A desirable property is continuity at the branching time, say t^* , i.e.

$$\bar{x}_1(t^*) = \bar{x}_2(t^*) = \bar{x}(t^*), \quad \varrho(t^*) = \varrho_1(t^*) + \varrho_2(t^*).$$

To be a convergent point for a monomorphic population the branching point should satisfy

$$R(x^b, I_1^b, I_2^b) = 0, \quad \frac{\partial}{\partial x} R(x^b, I_1^b, I_2^b) = 0. \quad (4.1)$$

To sustain a divergent dimorphic population, we should have

$$\frac{\partial^2}{\partial x^2} R(x^b, I_1^b, I_2^b) > 0. \quad (4.2)$$

It is not completely obvious to build models undergoing smooth branching, neither to run numerical simulations exhibiting them. The reason is that mutations are needed to depart from a monomorphic attractive point; however the mutation rate should be small enough to observe well localized populations, this also means many grid points should be used.

4.2 A simple example

To build a simple model with quadratic convex nonlinearities according to (4.2), we take the simpler choice

$$R(x, I_1, I_2) = 1 - d_1(x)I_1 - d_2(x)I_2, \quad 0 < x < 1, \\ d_1(x) = 1 - x^2, \quad d_2(x) = 1 - (1 - x)^2.$$

We also choose $x_b = 1/2$ and conditions on the weights ψ_i are determined in our analysis below.

We consider a monomorphic dynamics $n = \bar{\varrho}(t)\delta(x - \bar{x}(t))$, these satisfy the relation between density and position as

$$R(x, \varrho_x \psi_1(x), \varrho_x \psi_2(x)) = 0, \quad (\text{defines } \varrho_x \text{ for a given } x).$$

Next, we write the conditions to reach a stationary state at x^b from a point $\bar{x}(t) < x^b$ (and these include (4.1))

$$\frac{\partial}{\partial x} R(x, \varrho_x \psi_1(x), \varrho_x \psi_2(x)) > 0, \quad \frac{\partial}{\partial x} R(x^b, \varrho^b \psi_1(x^b), \varrho^b \psi_2(x^b)) = 0.$$

The second condition is simple to impose; because $x_b = 1/2$ and $d_1'(x^b) = -d_2'(x^b)$, this implies that (the second equality below is a choice of normalisation)

$$\psi_1(x^b) = \psi_2(x^b) = 1.$$

It remains to impose the first condition, that is for some $x < x^b$, the selection gradient should be positive that is

$$d_1'(x)\psi_1(x) + d_2'(x)\psi_2(x) < 0.$$

Because this quantity vanishes at x^b this is a second order condition

$$d_1''(x^b)\psi_1(x^b) + d_1'(x^b)\psi_1'(x^b) + d_2''(x^b)\psi_2(x^b) + d_2'(x^b)\psi_2'(x^b) > 0$$

and writing explicitly the numbers

$$4 - \psi_1'(x^b) + \psi_2'(x^b) > 0.$$

We have taken

$$\psi_1'(x) = \frac{1}{4} + 3(1-x)^2, \quad \psi_2'(x) = \frac{1}{4} + 3x^2.$$

4.3 A smoother example

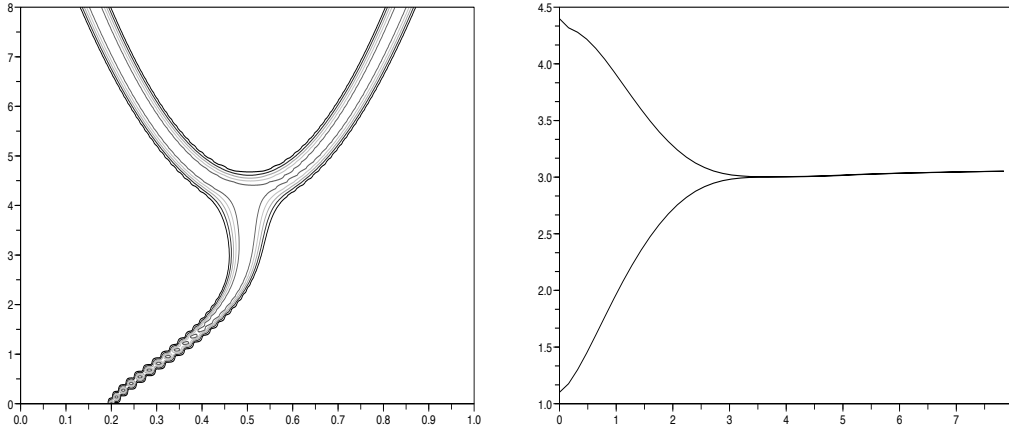


Figure 4.1: LEFT: ISOVALUES OF THE POPULATION DENSITY $n(x, t)$ COMPUTED WITH THE MODEL (4.3)–(4.4). THE MONOMORPHIC POPULATION EXHIBITS BRANCHING AT TIME (y AXIS) $t^* = 4.5$. RIGHT: THE ENVIRONMENTAL UNKNOWN $I_1(t)$ AND $I_2(t) > I_1(t)$. SEE FIGURE 4.2 FOR PROFILES AT DIFFERENT TIMES.

We present a simple example that is set for $x \in (0, 1)$ and which is symmetric with respect to the point $x = .5$ for the equation

$$\frac{\partial}{\partial t}n - \varepsilon \Delta n = nR(x, I_1(t), I_2(t)),$$

completed with Neumann boundary conditions at $x = 0$ and $x = 1$.

Consider the growth rate

$$R(x, I_1, I_2) := \frac{x}{1 + I_1} + \frac{1 - x}{1 + I_2} - 0.25 + \frac{(x - .5)^2}{[1 + 10(x - .5)^2](1 + I_1)(1 + I_2)}, \quad (4.3)$$

$$I_1(t) = \int_0^1 xn(x, t)dx, \quad I_2(t) = \int_0^1 (1 - x)n(x, t)dx. \quad (4.4)$$

Numerical simulations are run with $\varepsilon = 2 \cdot 10^{-4}$, 6000 grid points and initial data $n = \exp\left(-2 \frac{(x-.2)^2}{\varepsilon}\right)$. Isovalues of the population density $n(x, t)$ are presented in Figure 4.1 together with the two function $sI_1(t)$ and $I_2(t)$. Snapshots at three different times of the evolution are presented in Figure 4.2 before (monomorphic), during and after (dimorphic) branching. The final time is $t = 8$.

To assert that the grid is fine enough, we have run the code with 12000 points and we have obtained the same results. With 3000 grid points, the global picture is the same but branching occurs a little forward of $\bar{x}(t^*) = 1/2$ and the asymmetry of the early two branches is a little stronger.

4.4 Why does it branch?

In the example above, the branching point has been chosen at $\bar{x}^b = .5$. The initial population density approximates the Dirac mass at $x = .2$ and all along the monomorphic branch $\bar{x}(t) < 1/2$. For this reason

$$I_1(t) < I_2(t) \quad \text{for } t < t^*,$$

as can be observed in Figure 4.1 (picture on the right). According with the canonical equation we have, with $M(t) = (D^2\varphi(\bar{x}(t), t))^{-1} > 0$,

$$\frac{d\bar{x}(t)}{dt} = M(t)\nabla_x R(\bar{x}(t), t) > 0,$$

and this is mainly due to the first two terms in R , namely $\frac{x}{1+I_1} + \frac{1-x}{1+I_2} - 0.25$, that run the dynamics in this monomorphic regime. This can be seen in the upper right picture in Figure 4.2 which shows R to be almost affine increasing.

Thus $\bar{x}(t)$ increases until it reaches $\bar{x}(t^*) = 1/2$. At that time t^* , by symmetry we obtain $I_1(t^*) = I_2(t^*)$. The singular point $\bar{x}^b = .5$ is characterized by

$$\bar{I}_1^b = \bar{\varrho}^b \bar{x}^b, \quad \bar{I}_2^b = \bar{\varrho}^b (1 - \bar{x}^b),$$

$$R(\bar{x}^b, \bar{I}_1^b, \bar{I}_2^b) = 0, \quad i.e., \quad \bar{\varrho}^b = 6,$$

$$\nabla R(\bar{x}^b, \bar{I}_1^b, \bar{I}_2^b) = 0 = \frac{1}{1 + \bar{I}_1^b} - \frac{1}{1 + \bar{I}_2^b}, \quad (\text{satisfied}).$$

After reaching this point, the dynamics is continued with $\bar{I}_1(t) = \bar{I}_2(t) > \bar{I}_1^b = \bar{I}_2^b = 3$. Then, the last term $\frac{(x-.5)^2}{[1+10(x-.5)^2](1+I_1)(1+I_2)}$ becomes dominant and for which we have two roots of $R = 0$, i.e., of

$$\frac{(x-.5)^2}{[1+10(x-.5)^2](1+I_1)(1+I_2)} = .25 - \frac{1}{1+I(t)}.$$

Notice that the denominator is not essential and has only been chosen so as to smooth out the branching by penalizing $x = 0$ and $x = 1$ which are attractive. The factor $(1 + I_1)(1 + I_2)$ normalizes the first two terms in R with this last term.

But the singular point is strictly repulsive because

$$D_{xx}^2 R(\bar{x}^b, \bar{I}_1^b, \bar{I}_2^b) = \frac{2}{(1 + I_1)(1 + I_2)} > 0.$$

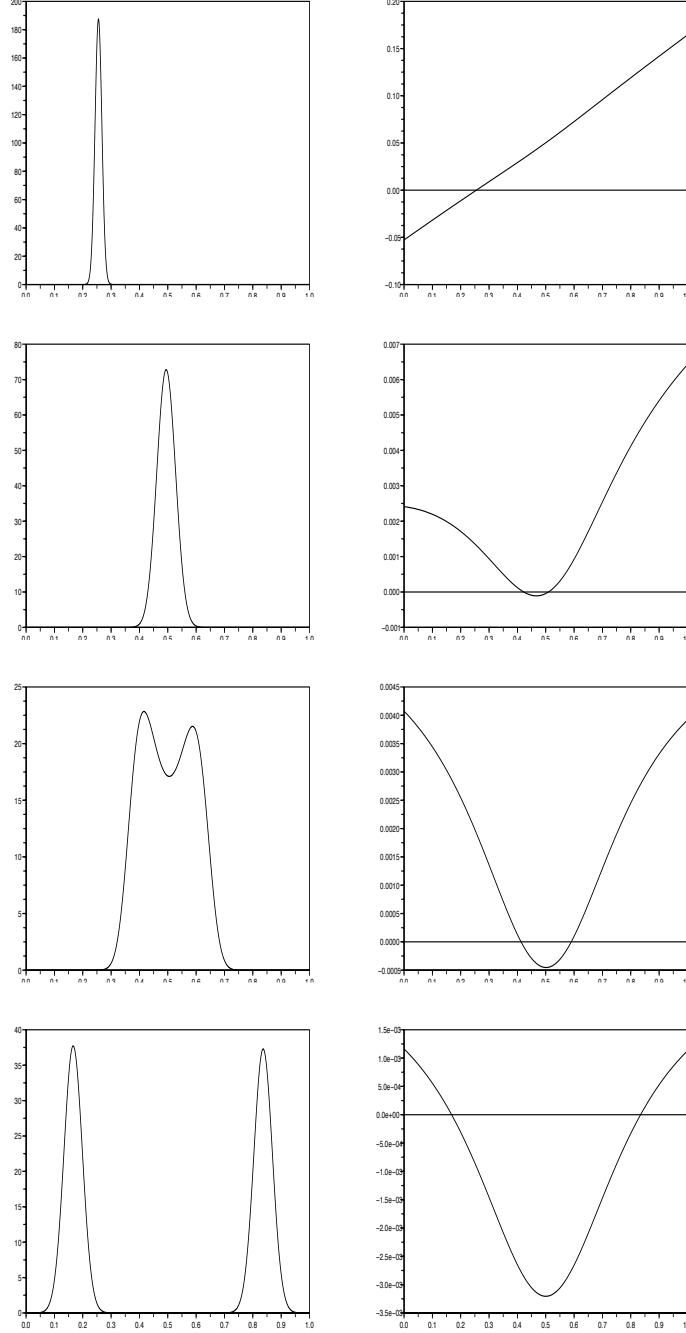


Figure 4.2: Snapshots at three different times of the evolution corresponding to the isovalues in Figure 4.1. We show the profiles before (monomorphic), during and after (dimorphic) branching. LEFT: THE POPULATION DENSITY $n(\cdot, t)$. RIGHT: THE ADAPTATIVE LANDSCAPE $R(x, I_1(t), I_2(t))$.

Chapter 5

Rare mutations in population models and monomorphism

We now present a scaled version of the model. We introduce a small parameter $\varepsilon > 0$ which represents the average size of mutations. It is also used to rescale time so as to consider the population on a long time scale compared to the time scale of a generation. In other words we use the evolutionary time scale rather than the demographic timescale. The main assumption behind this rescaling is that only small mutations of the phenotypical trait are possible (or more precisely on its influence on environment and population growth).

The asymptotic analysis is performed later. Here we just mention uniform estimates as $\varepsilon \rightarrow 0$.

5.1 Integral models for mutations

The most natural models for describing mutations consists in including a rate of mutations in birth terms and a probability of mutation from the trait x to y . Here, we only present the case of the example 1 of our general presentation in Chapter 1, namely equation (1.3). Including mutations, we arrive to the following type of equation for the density $n(t, x)$ of individuals with trait x ,

$$\left\{ \begin{array}{l} \varepsilon \frac{\partial}{\partial t} n_\varepsilon(t, x) = \left[\frac{b(x)}{1+I_\varepsilon(t)} - (1 + I_\varepsilon(t))d(x) \right] n_\varepsilon(t, x) + \frac{1}{1+I_\varepsilon(t)} \int \frac{1}{\varepsilon} K\left(\frac{x-y}{\varepsilon}\right) \beta(y) n_\varepsilon(t, y) dy, \\ I_\varepsilon(t) = \int n_\varepsilon(t, x) dx, \\ n_\varepsilon(t = 0, x) = n_\varepsilon^0(x) \geq 0, \quad n_\varepsilon^0 \in L^1 \cap L^\infty(\mathbb{R}). \end{array} \right. \quad (5.1)$$

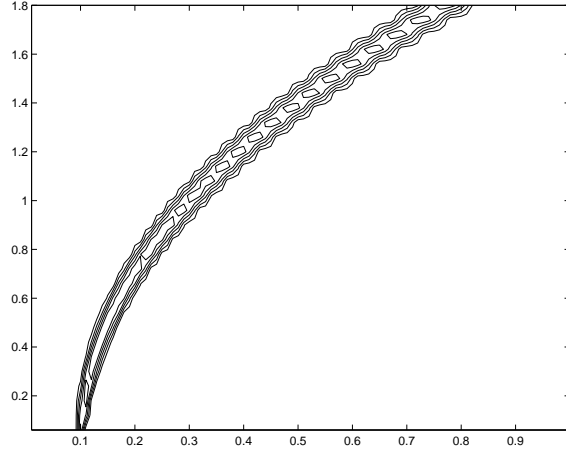


Figure 5.1: EVOLUTION OF THE TRAIT $x \in (0, 1)$ AS A FUNCTION OF TIME (y AXIS) FOR THE MODEL (??) WITH $b(x) = 1 + 3x$, $d = \beta = 1$. THE PARAMETER VALUE FOR ε IS $3 \cdot 10^{-3}$. THIS FIGURE SHOWS THE ISOVALUES OF $n(t, x)$ AND A PLOT OF n IS PRESENTED IN FIGURE 5.2.

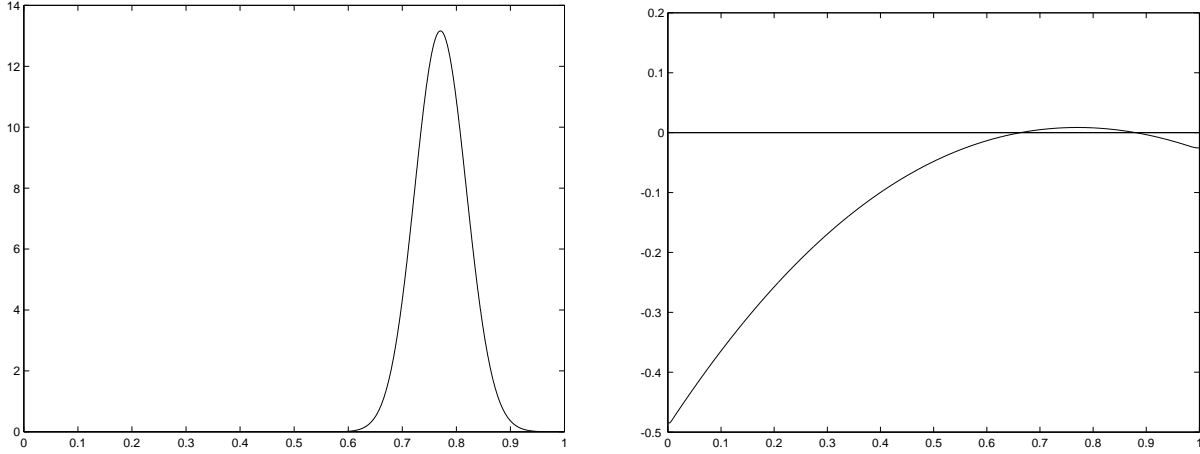


Figure 5.2: FINAL TIME OF THE SIMULATION SHOWN IN FIGURE 5.1. PLOT OF THE POPULATION DENSITY $n_\varepsilon(t, \cdot)$ (LEFT) AND THE PHASE FUNCTION $\varphi_\varepsilon(t, \cdot)$ (RIGHT) AS INTRODUCED IN (5.19).

The parameter ε in front of the time derivatives just indicates that we have rescaled time to consider the long time behavior on the scale ε . We also have used two different birth rates for neutral births (rate $b(x)$) and for the births arising with mutations (rate $\beta(x)$). Both are limited by a factor depending upon the total population size $I_\varepsilon(t)$, as special case of the model (1.3), (1.4). The probability kernel $K(\cdot)$ describes the mutation rate and we assume that

$$K(\cdot) \geq 0, \quad \int K(z) dz = 1, \quad \int K(z) e^{|z|^2} dz < \infty. \quad (5.2)$$

We need that a population described by such a model does not explode neither get extinct. For that we assume, still in accordance with (1.3), (1.4), (1.5),

$$b, d, d' \text{ and } \beta \text{ are Lipschitz continuous.} \quad (5.3)$$

$$0 < b_m \leq b(x) + \beta(x) \leq b_M < \infty, \quad 0 < d_m \leq d(x) \leq d_M < \infty, \quad (5.4)$$

with the following assumption and notations

$$I_m = \sqrt{\frac{b_m}{d_M}} - 1 > 0, \quad I_M = \sqrt{\frac{b_M}{d_m}} - 1. \quad (5.5)$$

A numerical simulation of this equation is exhibited in Figures 5.1 and 5.2. The value $x \in (0, 1)$ has been discretized with 1500 points and $\varepsilon = 1/300$, this is a small mutation rate and we can already guess that solutions to the system (??) are highly concentrated.

The existence of solutions is a classical matter (see [90, 43] for instance). An example of existence result with uniform bounds is as follows (we drop the dependency of n and I upon ε which is not relevant here)

Theorem 5.1 *With the assumptions (5.2)–(5.5), the system (??) has a unique nonnegative solution such that $n, \frac{\partial}{\partial t}n \in C(\mathbb{R}^+; L^1 \cap L^\infty(\mathbb{R}))$. Assume also that $I^0 := I(t = 0)$, satisfies $I_m \leq I^0 \leq I_M$, then we have for all $t \geq 0$*

$$I_m \leq I(t) \leq I_M. \quad (5.6)$$

Proof. We do not provide a complete proof of this theorem but just mention that the lower and upper bounds on $I(t)$ are easily deduced, integrating in x the equation (??) which gives

$$\varepsilon \frac{d}{dt} I(t) = \int \left[(1 + I(t)) (b(x) + \beta(x)) - \frac{d(x)}{1 + I(t)} \right] n(t, x) dx$$

and thus

$$\varepsilon \frac{d}{dt} I(t) \leq I(t) \left[(1 + I(t)) b_M - \frac{d_m}{1 + I(t)} \right],$$

and whenever $I(t)$ attains the value I_M then $\frac{\partial}{\partial t} I(t)$ vanishes and thus this value is never over-passed.

A similar argument gives the lower bound. □

Population models of this type have been studied by several authors, and in particular possible steady states. See [24, 26, 27, 32, 30, 47, 43] and the references therein.

5.2 Parabolic Lotka-Volterra models for mutations

It is also standard to describe the mutations by a Laplace term. Analysis and derivation of this model, in particular from stochastic individual based systems, can be found in [78, 24, 33, 35, 43].

More generally, differential models are also useful for describing mutations, see [24, 29, 75]. In the case of a differential model, it is possible to state and study mutation equations in the spirit of the general model treated in Section 2.1. This yields a particularly simple formalism

$$\begin{cases} \frac{\partial}{\partial t} n_\varepsilon - \varepsilon \Delta n_\varepsilon = \frac{n_\varepsilon}{\varepsilon} R(x, I_\varepsilon(t)), & x \in \mathbb{R}^d, t \geq 0, \\ n_\varepsilon(t=0) = n_\varepsilon^0 \in L^1(\mathbb{R}^d), & n_\varepsilon^0 \geq 0, \end{cases} \quad (5.7)$$

$$I_\varepsilon(t) = \int_{\mathbb{R}^d} \psi(x) n_\varepsilon(t, x) dx. \quad (5.8)$$

The neutral mutations are now modeled by the Laplace term (this is a price to pay simplicity, the corresponding birth rate is not included here). The function ψ is given and measures the uptake of individuals with trait x on the environment. Notice that this makes a difference in this model while it did not for the pure selection model in Section 2.1 where we can always change $n(t, x)$ to $\psi(x)n(t, x)$ in order to include such a term without changing the equation.

We assume that there are two constants ψ_m, ψ_M such that

$$0 < \psi_m \leq \psi \leq \psi_M < \infty, \quad \psi \in W^{2,\infty}(\mathbb{R}^d). \quad (5.9)$$

The quantity R is called the *invasion exponent* because it describes the ability of the individuals of trait x to invade the population with environmental state $I(t)$. It is negative for certain traits and positive for others. We assume that there are two constants $0 < I_m \leq I_M < \infty$ such that

$$\min_{x \in \mathbb{R}^d} R(x, I_m) = 0, \quad \max_{x \in \mathbb{R}^d} R(x, I_M) = 0, \quad (5.10)$$

and that there exists a constant $K > 0$ such that, for any $x \in \mathbb{R}^d, I \in \mathbb{R}$,

$$-K \leq \frac{\partial R}{\partial I}(x, I) < -K^{-1} < 0, \quad \sup_{I_m/2 \leq I \leq 2I_M} \|R(\cdot, I)\|_{W^{2,\infty}(\mathbb{R}^d)} \leq K. \quad (5.11)$$

These mean that in the environmental conditions $I_m < I < I_M$ some traits decay but not all, and that the environmental condition I_M is so defavorable that the whole population decreases.

We will also use the assumption

$$n_\varepsilon^0 \in L^\infty(\mathbb{R}^d), \quad \nabla n_\varepsilon^0 \in L^1(\mathbb{R}^d) \quad \text{and} \quad I_m \leq \int_{\mathbb{R}^d} \psi(x) n_\varepsilon^0(x) dx \leq I_M, \quad (5.12)$$

and the notation

$$\varrho_\varepsilon(t) = \int_{\mathbb{R}^d} n_\varepsilon(t, x) dx. \quad (5.13)$$

Notice that the assumption (5.9) and the bound $I_m \leq \int_{\mathbb{R}^d} \psi(x) n_\varepsilon(t, x) dx \leq I_M$ imply

$$\frac{I_m}{\psi_M} =: \varrho_m \leq \int_{\mathbb{R}^d} n_\varepsilon(t, x) dx \leq \varrho_M := \frac{I_M}{\psi_m}.$$

We recall that we have the following existence result and a priori bounds (here C denotes various constants which maybe different from line to line)

Theorem 5.2 *With the assumptions (5.9)–(5.12) and $I_m - C\varepsilon^2 \leq I_\varepsilon(0) \leq I_M + C\varepsilon^2$, there is a unique solution $n_\varepsilon \in C(\mathbb{R}^+; L^1(\mathbb{R}^d))$, to equation (5.7)–(5.8), and it satisfies,*

$$I_m - C\varepsilon^2 \leq I_\varepsilon(t) \leq I_M + C\varepsilon^2. \quad (5.14)$$

Again, we do not recall the proof of existence of this non-local Lotka-Volterra parabolic equation which falls in a class that has been largely studied. Improvements are possible, e.g., according to [43] the lower bound is unessential because they are indirect ways to guarantee non-extinction a posteriori, we keep it here for the sake of simplicity. Section ?? gives another and stronger uniform bound in time, a uniform BV bound on $I_\varepsilon(t)$. Here, we just indicate the derivation of the upper bound in (5.14). We have

$$\begin{aligned} \frac{d}{dt} \int_{\mathbb{R}^d} \psi(x) n_\varepsilon(t, x) dx &= \varepsilon \int_{\mathbb{R}^d} n_\varepsilon(t, x) \Delta \psi dx + \frac{1}{\varepsilon} \int_{\mathbb{R}^d} \psi(x) n_\varepsilon(t, x) R(x, I_\varepsilon(t)) \\ &\leq C_1 \varepsilon I_\varepsilon(t) + \frac{1}{\varepsilon} I_\varepsilon(t) \max_{x \in \mathbb{R}^d} R(x, I_\varepsilon(t)), \end{aligned}$$

and, from the assumption (2.5), the right hand side becomes negative as soon as $I_\varepsilon(t)$ overpasses $I_M + \frac{C_1}{K} \varepsilon^2$ and the result follows.

5.3 Limit of small mutations (monomorphic case)

We can state a very typical and simple asymptotic result proved in [10] and which explains the numerical results already depicted in Figures 5.1 and 5.2. It deals with the case when dimension d is equal to 1 and when the function $R(x, I)$ is also monotone in x . It uses, along with the precised asymptotics in Section 2.3, the logarithmic change of unknown. This is the reason why we assume

$$\varphi_\varepsilon^0 := \varepsilon \log n_\varepsilon^0 \quad \text{is bounded in } W^{1,\infty}(\mathbb{R}), \quad \varphi_\varepsilon^0 \xrightarrow{\varepsilon \rightarrow 0} \varphi^0 \leq 0 \quad \text{uniformly.} \quad (5.15)$$

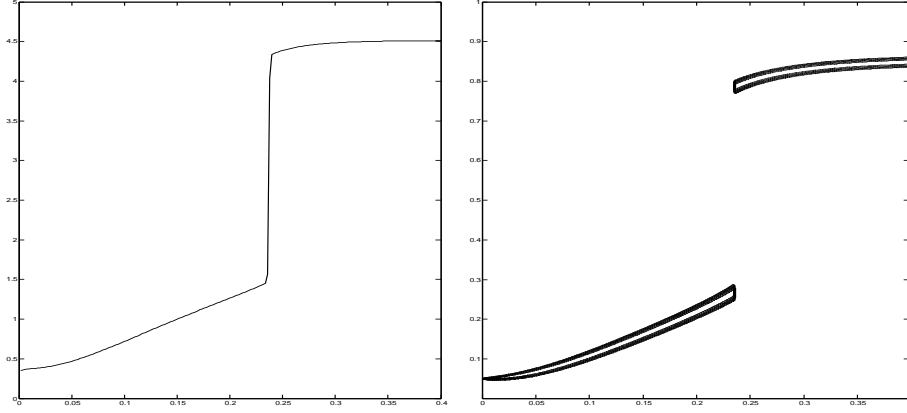


Figure 5.3: A NUMERICAL EXAMPLE OF DISCONTINUOUS SOLUTION IN THE LIMIT $\varepsilon \rightarrow 0$ OF EQUATION (5.7)–(5.8). THE ABSCISSAE IS TIME. (LEFT) THE POPULATION DENSITY $\varrho(t)$. (RIGHT) THE CONCENTRATION POINT $\bar{x}(t)$ (IN FACT ISOVALUES OF THE DENSITY $n_\varepsilon(t, x)$). FIGURE TAKEN FROM [10].

Theorem 5.3 (Dimension $d = 1$) *We assume (5.9)–(5.12), (5.15), and*

$$\forall I_m < I < I_M \text{ there is a unique } X(I) \in \mathbb{R} \text{ such that } R(X(I), I) = 0. \quad (5.16)$$

Then, after extraction of a subsequence, the solution $n_\varepsilon(t)$ to equation (5.7)–(5.8) converges in the weak sense of measures to a dirac mass

$$n_{\varepsilon_k}(t) \xrightarrow{\varepsilon \rightarrow 0} \varrho(t) \delta(x - \bar{x}(t)), \quad (5.17)$$

and we have

$$\bar{x}(t) = X(I(t)), \quad R(\bar{x}(t), I(t)) = 0,$$

and the pair $(\bar{x}(t), I(t))$ satisfies the constrained Hamilton-Jacobi equation given later on.

Such a population is called *monomorphic* because a single trait is represented asymptotically. This is the general situation with a single environmental variable $I(t)$ (this is called the Competitive Exclusion Principle, [46]).

Notice that this limit, for a nonlocal Volterra equation is very different from the asymptotic, under similar rescaling, for reaction diffusion equations. In the later case, the limit is described by a propagating front (typically fresh and consumed chemicals). See [8, 14, 101]. For nonlocal equations, the concentration as Dirac masses seems a general asymptotic behavior, see [56, 55].

Finally, the maps $t \mapsto X(t)$ and $t \mapsto \varrho(t)$ are not very regular, in particular they can be discontinuous (see the example in Figure 5.3. One can prove *BV* regularity but not more. Also an interesting point here is that these maps cannot be described in a simple manner, by ordinary differential equations, by opposition to the case of ‘canonical equations’ introduced in [45].

The proof of Theorem 5.3 is given in [10] and follows earlier ideas from [47]. We recall below the main ideas of a formal derivation.

5.4 Formal asymptotic analysis (parabolic model)

It is rather easy to guess why Dirac concentrations should appear in the limit $\varepsilon \rightarrow 0$ in the parabolic equation (5.7)–(5.8). On the one hand, multiplying the equation by ε , we find

$$n_\varepsilon(t, x)R(x, I_\varepsilon(t)) = O(\varepsilon),$$

and the formal limit gives

$$n(t, x)R(x, I(t)) = 0.$$

On the other hand, from the $L^1(\mathbb{R}^d)$ bound on $n(t, \cdot)$, this limit $n(t, x)$ in a bounded measure, which is therefore supported by the zeros of $R(x, I)$. From our assumptions this is an isolated point $X(I)$. Therefore we should have

$$n(t, x) = \bar{\varrho}(t)\delta(x - \bar{x}(t)), \quad \text{with} \quad \bar{x}(t) = X(I(t)). \quad (5.18)$$

This is the result announced in Theorem 5.3.

Of course there are many difficulties to make this argument rigorous

- the quantity $n_\varepsilon(t, x)R(x, I_\varepsilon(t))$ does not pass to the limit so easily because $I_\varepsilon(t)$ does not converge uniformly to $I(t)$,
- one should first prove that $I_\varepsilon(t)$ converges a.e. to $I(t)$ to have a chance to pass to the limit,
- a differential information on the limit $I(t)$ or $n(t, x)$ should come out to use that the mutations occur according to the term Δn or something else; the limit should see this specific form. For instance replacing Δn by $2\Delta n$ should have an influence on the limit.

A step in this direction is to follow the argument leading to the precise asymptotics in Section 2.3. This means that we introduce again the change of unknowns

$$n_\varepsilon(t, x) = e^{\varphi_\varepsilon(t, x)/\varepsilon}. \quad (5.19)$$

A direct computation shows that it satisfies the following equation, equivalent to (5.7),

$$\begin{cases} \frac{\partial}{\partial t}\varphi_\varepsilon(t, x) = |\nabla\varphi_\varepsilon|^2 + R(x, I_\varepsilon(t)) + \varepsilon\Delta\varphi_\varepsilon, \\ \varphi_\varepsilon(t=0, x) = \varphi_\varepsilon^0(x) := \varepsilon \ln n_\varepsilon^0. \end{cases} \quad (5.20)$$

This is a classical viscous Hamilton-Jacobi equation. The recent theory developed by Crandall and Lions (see [38, 6, 50]) allows to study the limit as $\varepsilon \rightarrow 0$ and to define the so-called *viscosity solutions*. To explain in a few words the interest of this concept, we can say the following: one cannot hope that the solutions to an Hamilton-Jacobi equation are C^1 but Lipschitz continuity is natural from the structure of the equation. The viscosity solution is usually unique while the

almost everywhere solution is not.

Following [47, 9, 10], in the limit $\varepsilon \rightarrow 0$, we obtain a viscosity solution to the *constrained Hamilton-Jacobi equation*

$$\begin{cases} \frac{\partial}{\partial t} \varphi(t, x) = R(x, I(t)) + |\nabla \varphi|^2, \\ \max_{x \in \mathbb{R}} \varphi(t, x) = 0, \quad \forall t > 0, \\ \varphi(t = 0, x) = \varphi^0(x). \end{cases} \quad (5.21)$$

The new feature of this equation, compared to the standard Hamilton-Jacobi equation, is that its solution is the pair $(\varphi(t, x); I(t))$. The quantity $I(t)$ is a Lagrange multiplier associated with the constraint $\max_{x \in \mathbb{R}} \varphi(t, x) = 0$.

This constraint follows from the uniform a priori bounds proved in Theorem 5.2, stating that the total mass of n_ε neither explode neither vanishes. This proves that we cannot have $\varphi(t_0, x_0) > 0$ at any point (t_0, x_0) , otherwise this is also true uniformly for n_ε and the total mass explodes as $\varepsilon \rightarrow 0$. This also proves that we cannot have $\varphi(t, x) < -a < 0$ otherwise this is also true uniformly for n_ε and the total mass vanishes as $\varepsilon \rightarrow 0$. Therefore, we should have $\max_{x \in \mathbb{R}} \varphi(t, x) = 0$.

Back to the relation between n_ε and φ_ε in (5.19), we see that the Dirac mass in (5.18) is now related to φ by

$$\varphi(t, \bar{x}(t)) = 0. \quad (5.22)$$

Also because the equation (5.21) gives us $I(t)$ we can recover the weight of the Dirac mass by

$$I(t) = \int_{\mathbb{R}^d} \psi(x) n(t, x) dx = \varrho(t) \psi(\bar{x}(t)).$$

5.5 Formal asymptotic analysis (integral model)

We can hope for the similar concentration effect, and similar theoretical results, for the limit $\varepsilon \rightarrow 0$ in the integral equation (??). We explain why in this section.

Since, in the weak measure sense $\frac{1}{\varepsilon} K(\frac{\cdot}{\varepsilon}) \rightarrow \delta(\cdot)$, the mutations are not a first-order effect (and act only in the present time scale) therefore we can think of the model as close to

$$\frac{\partial}{\partial t} n(t, x) = \left[\frac{b(x) + \beta(x)}{1 + \varrho(t)} - (1 + \varrho(t)) d(x) \right] n(t, x), \quad \varrho(t) = \int n(t, x) dx$$

which concentrates to a Dirac mass for long times as proved in Section 2.1:

$$n(t, x) \rightarrow \varrho_l \delta(x = x_l) \quad \text{as } t \rightarrow \infty,$$

at least if $\sqrt{\frac{b(x)+\beta(x)}{d(x)}} - 1$ attains its maximum ϱ_l at a single point x_l .

For this reason one expects the same type of concentration for $n_\varepsilon(t, x)$ but with varying weights and positions

$$n_\varepsilon(t, x) \rightarrow \bar{\varrho}(t) \delta(x = \bar{x}(t)) \quad \text{as } \varepsilon \rightarrow 0, \quad (5.23)$$

In order to describe these concentrations, and following again [47] and the motivations in Section 5.4, an asymptotic calculation is needed which we now perform, still in a formal way. We consider again the ansatz (5.19), namely

$$n_\varepsilon(t, x) = e^{\varphi_\varepsilon(t, x)/\varepsilon},$$

and obtain from equation (??)

$$\frac{\partial}{\partial t} \varphi_\varepsilon(t, x) = \left[\frac{b(x)}{1 + \varrho_\varepsilon(t)} - (1 + \varrho_\varepsilon(t))d(x) \right] + \frac{1}{1 + \varrho_\varepsilon(t)} \int K(z) \beta(x + \varepsilon z) e^{(\varphi_\varepsilon(t, x + \varepsilon z) - \varphi_\varepsilon(t, x))/\varepsilon} dz,$$

after changing y to $z = (x - y)/\varepsilon$. The limit $\varepsilon \rightarrow 0$ is now clear. We set

$$H(p) := \int K(z) e^{zp} dz, \quad (5.24)$$

a convex Hamiltonian, that arises naturally in jump processes (see [93] for instance).

And, we obtain for the limit

$$\frac{\partial}{\partial t} \varphi(t, x) = \frac{b(x)}{1 + \varrho(t)} - (1 + \varrho(t))d(x) + \frac{1}{1 + \varrho(t)} \beta(x) H\left(\frac{\partial}{\partial x} \varphi(t, x)\right). \quad (5.25)$$

On the other hand, the a priori bound in Theorem 5.1 tells us that n_ε , in total mass, does not explode neither vanishes. Therefore $\varphi(t, x)$ has to be nonpositive (otherwise n_ε blows up), but cannot be everywhere negative (otherwise n_ε would get extinct). Therefore we arrive at the conclusion that

$$\max_{x \in \mathbb{R}} \varphi(t, x) = 0 \quad \forall t > 0. \quad (5.26)$$

If this maximum is attained at a single point, $\bar{x}(t)$ we arrive at the conclusion that (5.23) indeed holds true and the mass can be recovered by the fact that

$$\frac{\partial}{\partial t} \varphi(t, \bar{x}(t)) = \frac{\partial}{\partial q} \varphi(t, \bar{x}(t)) = 0,$$

which implies that the growth rate vanishes (this is the so-called pessimization principle, cf. [87, 46]). This gives the characterization of the limiting parameters

$$\begin{cases} \varphi(t, \bar{x}(t)) = 0 & (\text{defines } \bar{x}(t)), \\ \frac{b(\bar{x}(t)) + \beta(\bar{x}(t))}{1 + \varrho(t)} = (1 + \varrho(t))d(\bar{x}(t)) & (\text{defines } \bar{\varrho}(t)). \end{cases}$$

Again, we recall that from a PDE point of view the system (5.25), (5.26) is a constrained H.-J. equation which has to be solved for $\varphi(t, x)$ and $\varrho(t)$. the parameter $\varrho(t)$ is a Lagrange multiplier associated with the constraint (5.26). This makes the originality and difficulty of this problem.

5.6 The case of systems

Systems of equations are important for applications. One can wonder whether the concentration effect still holds true and if the asymptotic method described above, and based on Hamilton-Jacobi equations, can be extended.

An typical example is the classical example of juveniles and adults already introduced in Section ???. Following [40, 25], this system with mutations reads after rescaling the system can be written as

$$\begin{cases} \varepsilon \frac{d}{dt} n_\varepsilon(t, x) = \int_0^\infty b(y) \beta_\varepsilon(x, y) p_\varepsilon(t, y) dy - m_1(S_{1\varepsilon}(t)) n_\varepsilon(t, x) - x n_\varepsilon(t, x), \\ \varepsilon \frac{d}{dt} p_\varepsilon(t, x) = x n_\varepsilon(t, x) - m_2(S_{2\varepsilon}(t)) p_\varepsilon(t, x). \end{cases} \quad (5.27)$$

The asymptotic analysis is performed in [32], and the main new qualitative aspect, compared to Theorem 5.2, is that dimorphism is possible (even though not asymptotically stable). Another new aspect is that the Hamiltonian arising in the Hamilton-Jacobi equation is more complicated compared to (5.24). This relies on a known and interesting general theory that one can find for front propagation in [8].

5.7 The relation with canonical equations

In the case of individual based stochastic models, it is possible to write an ordinary differential equation for the dynamics of the fittest trait $\bar{x}(t)$ arising in the formula (5.17). See [45, 34]. The denomination *canonical equation* usually refers to such a differential equation for the position of the dominant trait in trait space.

In the context of the asymptotic theory presented above in Theorem 5.3, we can also derive an analog of the canonical equation from the constrained Hamilton-Jacobi equation. We argue with a computation that holds true in C^2 regularity regions for the solution $\varphi(t, x)$ and for the fittest trait $\bar{x}(t)$, to both equations (5.21) and (5.25). In order to present both computations together, we consider the more general case of the solution $(\varphi(t, x), I(t))$ to

$$\begin{cases} \frac{\partial}{\partial t} \varphi(t, x) = R(x, I(t)) + H(x, I(t), \nabla \varphi(t, x)), & t \geq 0, x \in \mathbb{R}^d, \\ \max_{x \in \mathbb{R}} \varphi(t, x) = 0, & \forall t > 0, \end{cases} \quad (5.28)$$

with $R(x, I)$ defined such that the Hamiltonian $H(x, I, p)$ satisfies

$$H(x, I, 0) = 0, \quad \forall x, I. \quad (5.29)$$

When the mutation kernel is symmetric in (5.25), we also find that

$$\nabla_p H(x, I(t), 0) = 0, \quad \forall x, I. \quad (5.30)$$

Finally we complete, still according to the theories developed in Sections 5.4 and 5.5, by a C^2 curve $\bar{x}(t)$ such that

$$\varphi(t, \bar{x}(t)) = 0. \quad (5.31)$$

We are going to prove the following *alternative for the canonical equation*:

Proposition 5.4 *Consider a hamiltonian $H(x, I, p)$ satisfying (5.29), (5.30). For a C^2 function $\varphi(t, x)$, and a C^1 curve $\bar{x}(t)$ satisfying (5.28), (5.31), we have*

$$R(\bar{x}(t), I(t)) = 0, \quad (5.32)$$

$$\frac{d\bar{x}(t)}{dt} = \left(-D_{xx}^2 \varphi(t, \bar{x}(t)) \right)^{-1} \cdot \nabla_x R(\bar{x}(t), I(t)). \quad (5.33)$$

Notice that $-D_{xx}^2 \varphi$ is a nonnegative matrix because $\bar{x}(t)$ corresponds to a maximum of $\varphi(t, \cdot)$. Therefore, in one dimension, one can read the direction in which $\bar{x}(t)$ moves off from (5.33) and in fact from the selection gradient (also sometimes called fitness gradient) $\nabla_x R(x, I(t))$.

Proof. On the one hand, we can use that (5.31) defines a maximum of φ according to the constraint in equation (5.29), to infer (here and in the following we omit the argument $(t, \bar{x}(t))$)

$$\frac{\partial \varphi}{\partial t} = 0, \quad \nabla_x \varphi = 0.$$

Using this information in (5.29), we directly find the equality (5.32). And we can also differentiate (5.31) with respect to t and we obtain,

$$\frac{\partial^2 \varphi}{\partial t \partial x} + D_{xx}^2 \varphi \cdot \frac{d\bar{x}}{dt} = 0 \quad (5.34)$$

On the other hand, differentiating (5.28) with respect to x we find, in general

$$\begin{aligned} \frac{\partial^2 \varphi}{\partial t \partial x}(t, x) = & \nabla_x R(x, I(t)) + \nabla_x H(x, I(t), \nabla \varphi(t, x)) \\ & + \nabla_p H(x, I(t), \nabla \varphi(t, x)) \cdot D_{xx}^2 \varphi(t, x). \end{aligned} \quad (5.35)$$

But if we specialise to $x = \bar{x}(t)$ then, since $H(x, I, 0) = 0$ from (5.29) and $\nabla_p H(x, I, 0) = 0$ from (5.30), this boils down to

$$\frac{\partial^2 \varphi}{\partial t \partial x} = \nabla_x R(\bar{x}(t), I(t)). \quad (5.36)$$

Combining (5.34) and (5.36) we obtain (5.33). \square

Because the matrix $D_{xx}^2 \varphi$ is not known a priori (one need to solve the Hamilton-Jacobi equation), we may try to go further and differentiate (5.35) once more with respect to x and subsequently put $x = \bar{x}(t)$. We restrict ourself to one dimension for a simpler analysis of the outcome. Using again (5.29), (5.30), we obtain the differential equation

$$\frac{\partial}{\partial t} \left(\frac{\partial^2 \varphi}{\partial x^2}(t, x) \right) = \frac{\partial^2 R}{\partial x^2}(\bar{x}(t), I(t)) + H_{pp}(\bar{x}(t), I(t), 0) \left(\frac{\partial^2 \varphi}{\partial x^2}(t, x) \right)^2. \quad (5.37)$$

Along the path $(t, \bar{x}(t))$ we obtain

$$\frac{d}{dt} \left(\frac{\partial^2 \varphi}{\partial x^2} \right) = \frac{\partial^2 R}{\partial x^2}(\bar{x}(t), I(t)) + H_{pp}(\bar{x}(t), I(t), 0) \left(\frac{\partial^2 \varphi}{\partial x^2} \right)^2 + \frac{\partial^3 \varphi}{\partial x^3} \frac{d\bar{x}}{dt}. \quad (5.38)$$

Continuing this process to recover $\frac{\partial^3 \varphi}{\partial x^3}$, we need a fourth derivative of φ and so on. We directly see that the Hamilton-Jacobi system boils down to an infinite system of ODEs and no finite closure can describe entirely the adaptive dynamic system for $\bar{x}(t)$.

5.8 Convergence Stable Strategy and ESS

We still consider the general formalism of Section 5.6, and we focus on the ODE (5.33) describing a monomorphic population and analyze the possible limits as $t \rightarrow \infty$.

We begin with the steady states $(\bar{x}_\infty, \bar{I}_\infty)$. They should satisfy, taking also into account (5.32),

$$R(\bar{x}_\infty, \bar{I}_\infty) = 0, \quad \nabla_x R(\bar{x}_\infty, \bar{I}_\infty) = 0, \quad (5.39)$$

or, in AD jargon, \bar{x}_∞ should be a *singular point*.

Not all of them can be reached by the dynamics departing from a neighboring point, i.e.,

$$(\bar{x}_\infty, \bar{I}_\infty) = \lim_{t \rightarrow \infty} (\bar{x}(t), I(t)).$$

To analyze the stability, we need the sign of $\frac{d\bar{x}}{dt}$ near $t = \infty$, and thus we consider the second derivative of $\bar{x}(t)$ at the point \bar{x}_∞ . From (5.33) we find, using (5.39),

$$\frac{d^2\bar{x}(t)}{dt^2} = \left(-D_{xx}^2\varphi(t, \bar{x}_\infty) \right)^{-1} \cdot \frac{d}{dt} \nabla_x R(\bar{x}(t), I(t)) \Big|_{t=\infty}.$$

Define, as usual, (see [46])

$$c_{22} = \frac{\partial^2 R}{\partial x^2}(\bar{x}_\infty, \bar{I}_\infty), \quad (5.40)$$

$$c_{12} = \frac{\partial^2 R}{\partial x \partial I}(\bar{x}_\infty, \bar{I}_\infty) \frac{dI}{dx}(\bar{x}_\infty), \quad (5.41)$$

and note that (since $D_{xx}^2\varphi$ “enters” the differential equation for $\bar{x}(t)$ only via a signed factor) whether or not $\bar{x}(t)$ moves to or from the singular point is completely determined by the sign of $c_{22} + c_{12}$. In particular the movement is towards the singular point precisely when

$$c_{22} + c_{12} < 0 \quad (5.42)$$

or, in the jargon of adaptive dynamics, when the singular point is *Convergence Stable*.

Note also that, thanks to (5.32), we have

$$0 = \frac{\partial R}{\partial x} \frac{d\bar{x}(t)}{dt} + \frac{\partial R}{\partial I} \frac{dI(t)}{dt},$$

which allows to compute along the path $(\bar{x}(t), I(t))$

$$\frac{dI}{dx} = -\frac{R_x}{R_I}(\bar{x}(t), I(t))$$

Using (5.39), we conclude that $\frac{dI}{dx}(\bar{x}_\infty) = 0$. Therefore, for the model with a single nutrient, the stability is to say that

$$c_{22} < 0.$$

We can also perform the analysis directly from the Hamilton-Jacobi equation, without referring to the canonical equation. The steady state equation corresponding to (5.28) reads

$$\begin{cases} H(x, \bar{I}_\infty, \frac{\partial \varphi}{\partial x}(x)) = -R(x, \bar{I}_\infty), \\ \max_x \varphi(x) = 0, \quad \varphi(\bar{x}_\infty) = 0. \end{cases} \quad (5.43)$$

Since we can assume also $H \geq 0$ (for the cases derived so far), there can be a solution only if the condition $R(x, \bar{I}_\infty) \leq 0$ holds for all x . Since $\frac{\partial}{\partial x} \varphi(\bar{x}_\infty) = 0$ is a singular point, from (5.29) we find $R(\bar{x}_\infty, \bar{I}_\infty) = 0$. Then, we find the condition

$$\max_x R(x, \bar{I}_\infty) = 0 = R(\bar{x}_\infty, \bar{I}_\infty), \quad (5.44)$$

and subsequently, again we recover

$$c_{22} < 0. \quad (5.45)$$

Or, in other words, with a singular point one can associate a steady state only when it is an Evolutionary Stable Strategy in accordance with the case without mutations in (2.38). The population state $((\bar{x}_\infty, \bar{I}_\infty))$ corresponds to an unbeatable strategy. No mutant can invade such a population since its growth rate will be negative.

Chapter 6

Local competition and polymorphism

The models we have used so far suppose that all the only interactions through individuals arise through the environment, shared by all the population, whatever the trait. This creates a global interaction. In many cases this assumption is too restrictive. For instance predation is mostly from larger individuals on smaller ones. Also, individuals that are characterized by closer traits might use similar resources while very different individuals might use different foods.

These are the reasons to introduce local competitions. This creates a new and completely different situation that we explain now. We begin with the non-local Fisher equation, a model that can be interpreted both in terms of adaptive dynamics along with [57], or in terms of ecology and make the relation to Turing patterns following [57].

Then we treat a more natural parabolic Lotka-Volterra model that we borrow from [78] along with the analysis in [55].

6.1 The nonlocal Fisher equation; relation to Turing instability

As a simple nonlinear example to explain what is Turing instability, we consider the non-local Fisher equation

$$\frac{\partial}{\partial t}n - \nu \frac{\partial^2}{\partial x^2}n = r n(1 - K * n), \quad t \geq 0, x \in \mathbb{R}, \quad (6.1)$$

still with $\nu > 0$, $r > 0$ given parameters and the convolution kernel K is a smooth probability density function

$$K(\cdot) \geq 0, \quad \int_{\mathbb{R}} K(x)dx = 1, \quad K \in L^\infty(\mathbb{R}) \quad (\text{at least}).$$



Figure 6.1: AN EXAMPLE OF TIGER BUSH IN NIGER, SEE [72].

Compared to the Fisher equation it takes into account that competition for resources can be of long range (the size of the support of K) and not just local.

It has been proposed in ecology as an improvement of the Fisher equation that takes into account long range competition for resources [23, 61]. In semi-arid regions the roots of the trees, in competition for water, can cover up ten times the external size of the tree itself (while in temperate regions the ratio is roughly one to one). This leads to the so-called 'tiger bush' landscape [72], see Figure 6.1.

It has also been proposed as a simple model of adaptive evolution to take account for higher competition between closer trait [57]; x represents a physiological trait, the Laplace term represents mutations and the right hand side growth and competition. The convolution kernel means that competition between individuals of closer phenotypical traits is higher than between more different traits.

The convolution term has a drastic effect on solutions; it can induce that solutions exhibit a behavior quite different from those to the Fisher equation. The reason is mainly that the maximum principle is lost with the non-local term. Again we notice that the steady state $n \equiv 0$ is unstable, that $n \gg 1$ is also unstable because it induces a strong decay. In one dimension, for a general reaction function $f(n)$ the conditions reads $f(0) = 0$, $f'(0) > 0$ and $f(n) < 0$ for n large; consequently there is a point n_0 satisfying (generically) $f(n_0) = 0$, $f'(n_0) < 0$, i.e. a stable steady state should be in between the unstable ones. This is the case of the nonlinearities arising in Fisher equation that we have encountered.

Here the steady state $n \equiv 1$ may satisfy a condition only possible because we have the variable x at hand, namely

Definition 6.1 *The steady state $n^0 \equiv 1$ is called linearly unstable if there are perturbations of n^0 such that the linearized system has exponential growth in time.*

Definition 6.2 *A steady state n^0 is said Turing unstable if*

- (i) it is between two unstable states as above (no blow-up, no extinction),
- (ii) it is linearly unstable,
- (iii) the corresponding growth modes are bounded (no high frequency oscillations).

Obviously when Turing instability occurs, solutions should exhibit strange behaviors because they remain bounded away from the two extreme steady states, cannot converge to u^0 and cannot oscillate rapidly. In other words, they should exhibit Turing patterns. See Figure 6.2 for a numerical solution to (6.1).

In practice, to check linear instability we use spectral functions. In compact domains the concept can be handled using eigenfunctions of the Laplace operator as we see it later. On the full line, we may use the generalized eigenfunctions which are the Fourier modes. We define the Fourier transform as

$$\widehat{u}(\xi) = \int_{\mathbb{R}} u(x) e^{-ix\xi} dx.$$

Theorem 6.3 *Assume the condition*

$$\exists \xi_0 \quad \text{such that } \widehat{K}(\xi_0) < 0, \quad (6.2)$$

and ν/r small enough (depending on ξ_0 and $K(\xi_0)$), then the non-local Fisher equation (6.1) is Turing unstable.

A practical consequence of this Theorem is that solutions should create so-called Turing patterns. This can easily be seen on numerical simulations, Figure 6.2.

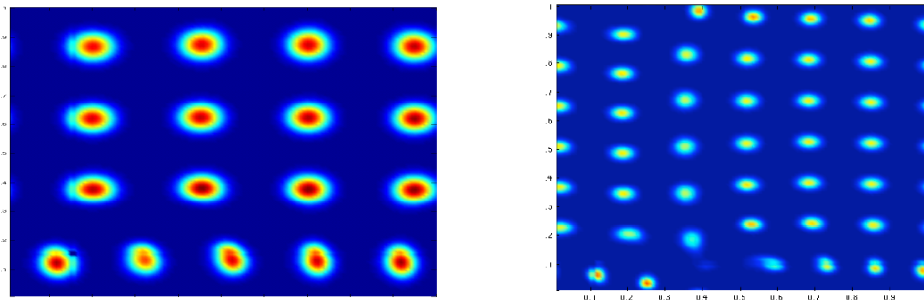


Figure 6.2: STEADY STATE SOLUTIONS OF THE NONLOCAL FISHER EQUATION (6.1) IN 2 DIMENSIONS WITH DIFFERENT DIFFUSION COEFFICIENTS.

Proof. (i) The state $u \equiv 0$ and $u \equiv \infty$ are clearly both unstable.

(ii) The linearized equation around $n \equiv 1$ is obtained setting $n = 1 + \tilde{u}$ and keeping the first order terms, we obtain

$$\frac{\partial}{\partial t} \tilde{u} - \nu \frac{\partial^2}{\partial x^2} \tilde{u} = -r K * \tilde{u}.$$

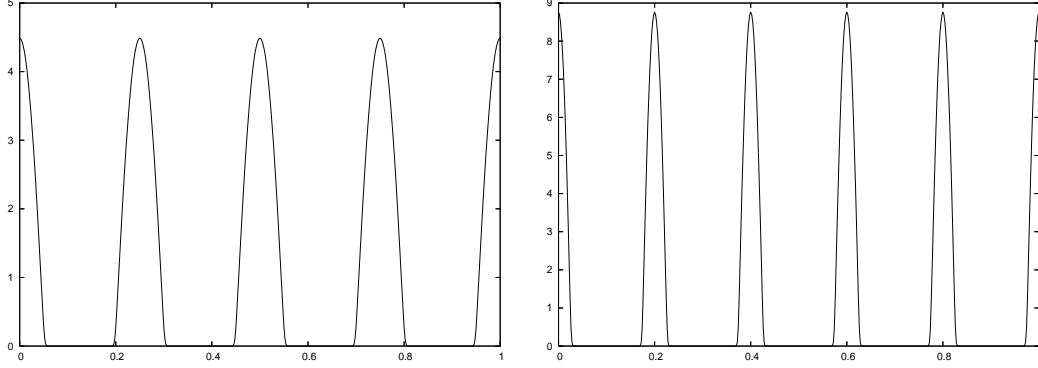


Figure 6.3: Rectangular kernel (6.8), $\varepsilon = 10^{-4}$. Initial conditions are: 4 peaks evenly spaced (left), 5 peaks evenly spaced (right). These are examples of 'smooth' steady states.

And we look for solutions of the form $\tilde{u}(t, x) = e^{\lambda t} v(x)$ with $\lambda > 0$. This means that we should find eigenvectors associated with the positive eigenvalue λ to

$$\lambda v - \nu \frac{\partial^2}{\partial x^2} v = -r K * v.$$

We look for a possible Fourier mode $v(x) = e^{ix \xi_1}$ that we insert in the previous equation. Then we obtain the condition

$$\lambda + \nu \xi_1^2 = -r \widehat{K}(\xi_1), \quad \text{for some } \lambda > 0. \quad (6.3)$$

And it is indeed possible to such a λ and a $\xi_1 = \xi_0$ under the conditions of the Theorem.

(ii) The possible unstable modes ξ_0 are obviously bounded because \widehat{K} is bounded as the Fourier transform of a L^1 function. \square

6.2 The nonlocal Fisher equation; polymorphism

It is rather difficult to characterize the steady states solutions to (6.1) (and thus the long time behaviour to the dynamics). However the case of small diffusion and the Hamilton-Jacobi analysis, give a hint on the reason which solutions may exhibit polymorphisms (concentration as several Dirac masses)

To do so we may follow [56] and consider the steady states

$$-\varepsilon^2 \frac{\partial^2}{\partial x^2} n_\varepsilon = n_\varepsilon (1 - K * n_\varepsilon), \quad x \in \mathbb{R}, \quad (6.4)$$

and look for solutions that behaves as

$$n_\varepsilon \xrightarrow{\varepsilon \rightarrow 0} \sum_{i=1}^I \varrho_i \delta(x - x_i).$$

We use again the ansatz

$$n_\varepsilon = e^{\frac{\varphi_\varepsilon}{\varepsilon}}$$

and insert it in equation (6.4) to obtain

$$-\varepsilon \frac{\partial^2}{\partial x^2} \varphi_\varepsilon - \left| \frac{\partial}{\partial x} \varphi_\varepsilon \right|^2 = 1 - K * n_\varepsilon,$$

and in the limit (see section (5.4)), we arrive at

$$\begin{cases} -\left| \frac{\partial}{\partial x} \varphi \right|^2 = 1 - \sum_{i=1}^I \varrho_i K(x - x_i), \\ \max_x \varphi(x) = 0 = \varphi(x_i) \quad i = 1, \dots, I. \end{cases} \quad (6.5)$$

We can draw immediate consequences. Because $\frac{\partial}{\partial x} \varphi(x_j) = 0$, we have

$$\sum_{i=1}^I \varrho_i K(x_j - x_i) = 1 \quad j = 1, \dots, I, \quad (6.6)$$

this is the pessimization principle. And since

$$\sum_{i=1}^I \varrho_i K(x - x_i) \geq 1, \quad (6.7)$$

we also find, after differentiating equation (6.4), that the selection gradient vanishes at x_j

$$\sum_{i=1}^I \varrho_i K'(x_j - x_i) = 0 \quad j = 1, \dots, I.$$

It is easy to see that the conditions (6.6)–(6.7) are enough to build a viscosity solution to (6.5).

Example. Consider the case of the rectangular kernel

$$K(x) = \frac{1}{2b} \mathbf{1}_{\{|x| \leq b\}}. \quad (6.8)$$

This is the simplest example of a kernel generating Turing instability along with Section 6.2. We see that many steady states are possible. The simplest is, for $c \in [0, b)$, to reconstruct the unit function as

$$\varrho_j = 1, \quad x_j = ac + bj, \quad \varphi = 0.$$

But one may pile-up two (or more) elementary blocs and use, for all d with $\frac{b}{2} < d < b$,

$$\varrho_j = 1, \quad x_j = c + dj, \quad \varphi \neq 0.$$

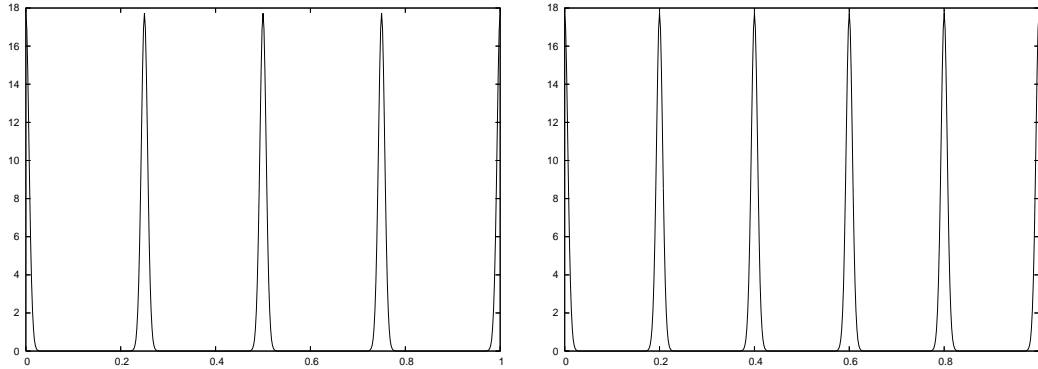


Figure 6.4: M-shape kernel (6.9) with $a = 0.015$, $b = 0.15$, $\varepsilon = 10^{-4}$. Initial conditions are: 4 peaks evenly spaced (left), 5 peaks evenly spaced (right).

Many more steady states are easy to built (with $\varrho_j = \frac{1}{2}$ for instance). The number and diversity of these steady states explain that the dynamics is hardly predictable and long time patterns can undergo high complexity. In particular smooth (uniformly in ε) steady states may exist for rectangular kernels. See Figure 6.3 (borrowed from [56]) for a direct numerical solution giving rise to this type of steady state.

Example. The case of M-shaped kernels

$$K(x) = K(0) \left(1 + a \frac{|x|}{b}\right) \mathbf{1}_{\{|x| \leq b\}}, \quad \int K = 1, \quad (6.9)$$

seems to be give rise solely to Dirac concentrations in the limit $\varepsilon \rightarrow 0$ by opposition to rectangular kernels. It also enters the class of kernels with Turing instability. The 'simple' class of weights and locations for the Dirac is now given, for $c \in \mathbb{R}$, $\frac{b}{2} < d < b$,

$$\varrho_j = \frac{1}{a}, \quad x_j = c + dj, \quad \varphi = 0.$$

Figure 6.4, still borrowed from [56]) shows numerical solutions that indeed concentration on points according to this rule. Again several different steady states can be reached depending on the initial data.

6.3 Continuous vs individual based models

In [99, 22] the authors pose clearly the question of finite size effects that create patterns when the corresponding continuous model does not, it is (6.1) with a gaussian kernel. Because the Fourier transform of a gaussian is still a gaussian and thus positive it cannot fulfill the instability condition (6.2). See Figure 6.5.

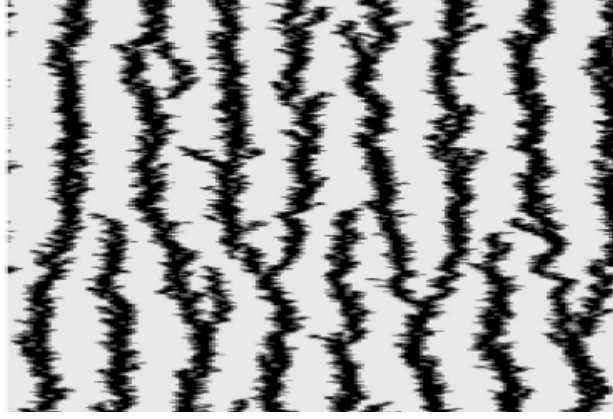


Figure 6.5: TIME EVOLUTION OF A POPULATION BY AN INDIVIDUAL BASED MODEL. THE GAUSSIAN KERNEL USED HERE DOES NOT ALLOW FOR SPECIATION IN A CONTINUOUS MODEL. SEE [99, 22].

6.4 Survival thresholds

The population models we have considered so far have a bad property in terms of biological observations. The density $n_\varepsilon(t, x)$ has a tail which makes that for all x there are individuals with this traits, even with low number. In favorable circumstances, it can increase very quickly and create a new Dirac mass separated from the present population. This phenomenon has been already observed on much simpler models in Section 5.3. This is unrealistic for several reasons; one of them is that in practice there is a limit of one individual which settles a minimal density. Another are statistical effects that make that small populations can die out due to external events. The notion of demographic stochasticity is used in stochastic simulations to take into account such effects. At the population level we may use the notion of survival thresholds as introduced in [55]. This is a way to add an extra death rate that acts particularly strongly on small populations and avoids the undesirable tails with too few individuals.

We consider now general differential models following [29, 75, 78]. More specifically we use the so-called 'Lotka-Volterra' model for intra-specific competition in a deterministic population, with the selection term of the form $\left(R(x) - (K_\sigma * n(t, \cdot))(x)\right)$ and the mutation term set as $\varepsilon^2 \Delta n(t, x)$. Incorporating the survival threshold, we get:

$$\varepsilon \frac{\partial}{\partial t} n(t, x) = \left(R(x) - (K_\sigma * n(t, \cdot))(x)\right) n(t, x) - \sqrt{\bar{n} n(t, x)} + \varepsilon^2 \Delta n(t, x). \quad (6.10)$$

the meaning of the different terms is as follows.

- The first term of the selection, $R(x)$, describes the density independent part of the invasion exponent. A typical example, that we borrow from [78] and use in numerical solutions, is given

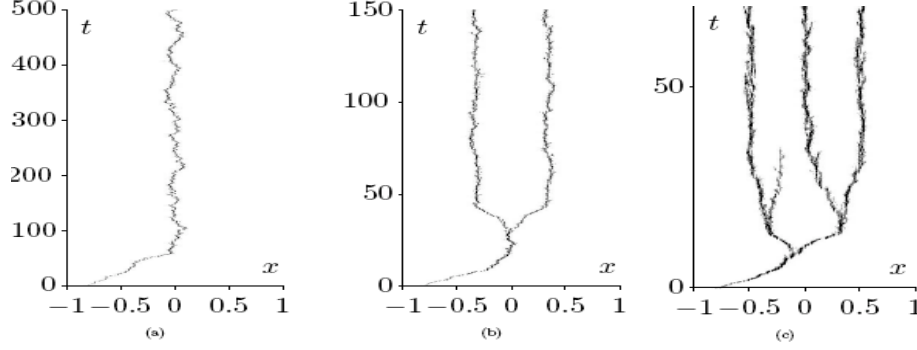


Figure 6.6: Typical stochastic simulations of individuals based model of evolutionary dynamics compatible with the population model (6.10). Different values of b have been chosen.

by

$$R(x) = 1 - x^2. \quad (6.11)$$

- The square root enables the population to vanish for some traits when the population density is too low, thus mimicking the extinction probability due to demographic stochasticity in small sub-populations. At the extreme it means that we do not want to have densities corresponding to less than one individual.
- The localized convolution kernel K_σ describes the competition between similar individuals in terms of x . Typically, we choose it, still following [78], as a gaussian

$$K_\sigma(x) = \frac{1}{\sqrt{2\pi}\sigma} e^{-|x|^2/(2\sigma)}. \quad (6.12)$$

The capability of the survival threshold (but certainly other modeling of demographic stochasticity would do the same job) is shown in Figure 6.6 (stochastic simulations) and Figure 6.7 (deterministic simulations).

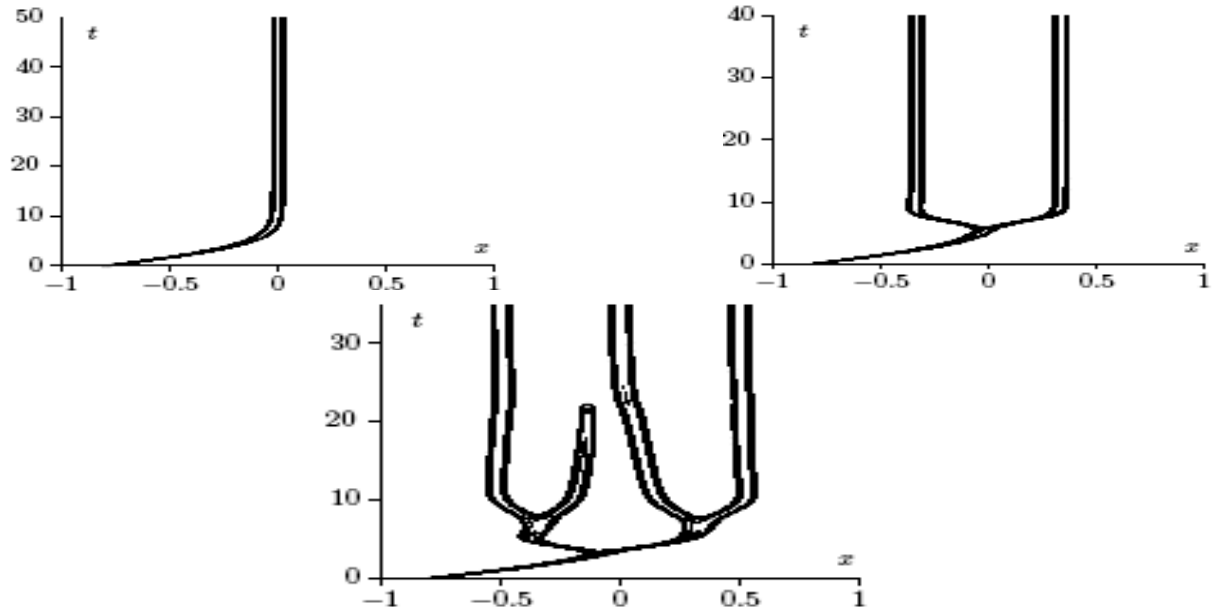


Figure 6.7: Direct simulation of the population model (6.10). Different values of b have been chosen.

APPENDICES

.1 From population genetics to continuous models

Population genetics treats of the probability $p_i(t)$ to find a gene in a population and the discrete aspect of genes is central. A simple and intrinsic way to derive the simplest equation is to consider I genes (or species). The individuals with this gene have their own logistic growth rate $r_i \in \mathbb{R}$

$$\frac{dn_i(t)}{dt} = r_i n_i(t), \quad 1 \leq i \leq I.$$

We can now consider the probability to find the gene i in the total population

$$p_i(t) = \frac{n_i(t)}{\sum_j n_j(t)}.$$

This simple example has the property that the p_i s satisfy a close system of coupled differential equations

$$\frac{dp_i(t)}{dt} = p_i(t) \left(r_i - \sum_{j=1}^I r_j p_j(t) \right), \quad 1 \leq i \leq I.$$

The main asymptotic properties of this system are summarized in the

Lemma .4 *For an initial data satisfying $p_j^0 \geq 0$ then $\sum_{j=1}^I p_j^0 = 1$, then one has $\sum_{j=1}^I p_j(t) = 1$ for all times.*

Assume additionally that the $r_i \in \mathbb{R}$ are all different. Then as $t \rightarrow \infty$, we have

$$\sum_{i=1}^I r_i p_i(t) \rightarrow \bar{r} := \max_{1 \leq i \leq I} r_i = r_{i_0},$$

$$p_i(t) \rightarrow 0 \text{ for } i \text{ such that } r_i < \bar{r}, \quad p_{i_0}(t) \rightarrow 1.$$

Proof. Indeed, we compute directly

$$\frac{d}{dt} \sum_{i=1}^I p_i(t) = \sum_{j=1}^I r_j p_j(t) \left[1 - \sum_{i=1}^I p_i(t) \right],$$

which proves that $(p_i(t))$ are probability measures.

Also, we compute using the Cauchy-Schwarz inequality

$$\frac{d}{dt} \sum_{i=1}^I r_i p_i(t) = \sum_{i=1}^I r_i^2 p_i(t) - \left(\sum_{i=1}^I r_i p_i(t) \right)^2$$

$$= \sum_{i=1}^I p_i(t) \left(r_i - \sum_{i=1}^I r_i p_i(t) \right)^2 \geq 0.$$

this proves that, as $t \rightarrow \infty$, $\sum_{i=1}^I r_i p_i(t) \searrow \tilde{r}$ for some limit that remains to identify.

The differential equation on p_i yields directly $\tilde{r} = \bar{r}$, otherwise p_{i_0} would have an exponential growth which contradicts $p_{i_0} \leq 1$. The end of the proof follows clearly. \square

The continuous version of it enters the class given by (1.1)

$$\frac{\partial n(t, x)}{\partial t} = n(t, x) \left(r(x) - \int_0^\infty r(y) n(t, y) dy \right), \quad x \geq 0.$$

Assuming that the initial data is a probability measure, we also have

$$\int_0^\infty n(t, x) dx = 1, \quad \forall t \geq 0,$$

because

$$\frac{d}{dt} \int_0^\infty n(t, x) dx = \int_0^\infty r(x) n(t, x) dx \left[1 - \int_0^\infty n(t, y) dy \right].$$

.2 The replicator dynamics

A more elaborate model of gene propagation in a population is the replicator equation

$$\frac{dp_i(t)}{dt} = p_i(t) \left(\sum_{j=1}^I a_{ij} p_j(t) - \Phi(t) \right), \quad \Phi(t) = \sum_{i,j=1}^I a_{ij} p_i(t) p_j(t).$$

Again, it satisfies

$$\sum_{i=1}^I p_i(t) = \sum_{i=1}^I p_i^0 = 1$$

because

$$\frac{d}{dt} \sum_{i=1}^I p_i(t) = \sum_{i,j=1}^I a_{ij} p_i(t) p_j(t) - \sum_{i=1}^I p_i(t) \Phi(t) = \Phi(t) \left(1 - \sum_{i=1}^I p_i(t) \right).$$

A remarkable property of this dynamics is that

$$\begin{aligned} \frac{d\Phi(t)}{dt} &= \sum_{i,j=1}^I a_{ij} \frac{dp_i(t)}{dt} p_j(t) + \sum_{i,j=1}^I a_{ij} p_i(t) \frac{dp_j(t)}{dt} \\ &= \sum_{i,j=1}^I a_{ij} p_i(t) p_j(t) \left(\sum_{k=1}^I a_{ik} p_k(t) - \Phi(t) \right) + \sum_{i,j=1}^I a_{ij} p_i(t) p_j(t) \left(\sum_{k=1}^I a_{jk} p_k(t) - \Phi(t) \right) \\ &= \sum_{i=1}^I p_i(t) \left(\sum_{j=1}^I a_{ij} p_j(t) \right)^2 + \sum_{i=1}^I p_i(t) \left(\sum_{k=1}^I a_{ki} p_k(t) \right)^2 - 2\Phi(t)^2 \geq 0 \end{aligned}$$

thanks to the Cauchy-Schwarz inequality.

The continuous version is

$$\begin{cases} \frac{\partial n(t, x)}{\partial t} = n(t, x) \left(\int_0^\infty a(x, y) n(t, y) dy - \Phi(t) \right), & x \geq 0, \\ \Phi(t) = \int_0^\infty \int_0^\infty a(x, y) n(t, y) n(t, x) dx dy, \end{cases}$$

which still describes a probability density

$$\int_0^\infty n(t, x) dx = 1, \quad \forall t \geq 0,$$

because

$$\frac{d}{dt} \int_0^\infty n(t, x) dx = \int_0^\infty \int_0^\infty a(x, y) n(t, y) n(t, x) dx dy \left[1 - \int_0^\infty n(t, x) dx \right].$$

As in the discrete form, one has

$$\frac{d\Phi(t)}{dt} = \int n(t, x) \left(\int a(x, y) n(y, t) \right)^2 + \int n(t, x) \left(\int a(y, x) n(y, t) \right)^2 - 2\Phi(t)^2 \geq 0.$$

The long time behaviour is much more complicated and diverse. See [66]. stable steady states characterized by the ESS condition that there is Lagrange multiplier φ such that

$$\begin{cases} \int a(x, y) n(y, t) = \varphi & \text{for } x \in \text{supp}(n), \\ \int a(x, y) n(y, t) \leq \varphi. \end{cases}$$

.3 Interpolation of \dot{u} between u and \ddot{u}

Proposition .5 *For a function $u \in C^2(\mathbb{R})$ one has*

$$|\dot{u}(t)| \leq \left(\sup_{s \geq t} |u(s)| \sup_{s \geq t} |\ddot{u}(s)| \right)^{1/2}.$$

Proof. For any $\tau > 0$,

$$\dot{u}(t) = \dot{u}(t + \tau) - \int_t^{t+\tau} \ddot{u}(s) ds.$$

For $A > 0$ to be chosen later, one has

$$A\dot{u}(t) = \int_0^A \dot{u}(t + \tau) d\tau - \int_0^A \int_t^{t+\tau} \ddot{u}(s) ds d\tau.$$

Consequently, one deduces

$$A|\dot{u}(t)| \leq |u(t+A) - u(t)| + \int_0^A \int_t^{t+\tau} |\ddot{u}(s)| ds d\tau,$$

$$A|\dot{u}(t)| \leq 2 \sup_{s \geq t} |u(s)| + \sup_{s \geq t} |\ddot{u}(s)| \int_0^A \int_t^{t+\tau} ds d\tau,$$

$$|\dot{u}(t)| \leq \frac{2}{A} \sup_{s \geq t} |\dot{u}(s)| + \frac{A}{2} \sup_{s \geq t} |\ddot{u}(s)|.$$

The result follows choosing the optimal value of A in this inequality. \square

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Index

Adaptative landscape, 36
Adaptive evolution, 54

Balance law (equation), 12

Cannibalism, 10
Chemostat, 11
Competitive exclusion principle, 15
Convergence Stable, 51

Ecology, 11

Fisher equation, 53–55
Fitness, 8
Fitness gradient, 49

Instability, 53, 55

Laplace integral, 22
Logistic growth, 11

Mutual exclusion, 15

Nonlocal Fisher equation, 55

Perturbation, 54

Selection gradient, 49
Singular point, 25, 28, 51, 52
Speciation, 59

Tiger bush, 54
Turing (instability, pattern,...), 54, 55