

# The dynamics of adaptation: An illuminating example and a Hamilton–Jacobi approach

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## Abstract

Our starting point is a selection–mutation equation describing the adaptive dynamics of a quantitative trait under the influence of an ecological feedback loop. Based on the assumption of small (but frequent) mutations we employ asymptotic analysis to derive a Hamilton–Jacobi equation. Well-established and powerful numerical tools for solving the Hamilton–Jacobi equations then allow us to easily compute the evolution of the trait in a monomorphic population when this evolution is continuous but also when the trait exhibits a jump. By adapting the numerical method we can, at the expense of a significantly increased computing time, also capture the branching event in which a monomorphic population turns dimorphic and subsequently follow the evolution of the two traits in the dimorphic population.

From the beginning we concentrate on a caricatural yet interesting model for competition for two resources. This provides the perhaps simplest example of branching and has the great advantage that it can be analyzed and understood in detail.

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*Keywords:* Adaptive dynamics; Selection–mutation process; Hamilton–Jacobi equation

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## 1. Introduction

Biological evolution is driven by selection and mutation. When the environmental conditions are fixed once and for all one can try to describe the end result in terms of optimality and derive estimates for the speed of adaptation of a quantitative trait from a selection–mutation equation (Bürger, 2000, Chapter V). If, however, an ecological feedback loop is taken into account, the environmental conditions necessarily co-evolve and accordingly the spectrum of possible dynamical behavior becomes a lot richer. The theory which focusses on phenotypic evolution driven by *rare* mutations, while ignoring both sex and genes, is known by the name Adaptive Dynamics, see Metz et al. (1996), Geritz et al. (1998), Diekmann and Law (1996), Dercole (2002), Dercole et al. (2003), Diekmann (2004), Calcina and Cuadrado (2004) and the references given there. Particularly intriguing is the possibility of “branching”, a change from a monomorphic to a dimorphic population. Under the assumption, that mutations are not only rare but also very small, one can derive the so-called “canonical equation” (Diekmann and Law, 1996; Champagnat et al., 2001) which describes both the speed and the direction of adaptive movement in trait space. The canonical equation does not capture the branching phenomenon, however. (So the switch from a description of the monomorphic population to a description of the dimorphic population has to be effectuated by hand, see e.g. Dercole, 2002.)

The present paper has two aims. One is to present a rather simple example of branching (in fact so simple that all of the relevant information can be obtained via a pen and paper analysis. The other is to derive, by a limiting procedure, a Hamilton–Jacobi equation from a selection–mutation equation in which it is incorporated that mutations are not necessarily rare but are certainly very small. The link between these two items is that we show that a numerical implementation of the Hamilton–Jacobi description of the example is able to capture both the continuous or jump evolutions of the dominant trait in a monomorphic population, and also the branching phenomenon when a population becomes dimorphic. This leads to our main message: the Hamilton–Jacobi formalism offers a promising tool for analyzing more complicated problems from Adaptive Dynamics numerically.

The organization of the paper is as follows. In Section 2 we introduce the ecological setting for the example, viz. competition for two substitutable resources. Consumers are characterized by a trait  $x$  which takes values in  $[0,1]$ . The two end-points correspond to specialists which ingest only one of the two substrates. The up-take rates for general  $x$  embody a trade-off. In principle this can work both way: either generalists may be less efficient or, on the contrary, there may be a price to specialization.

In Section 3 we model a distributed, with respect to  $x$ , population of consumers. Incorporating the possibility of mutation, we arrive at a selection–mutation equation in which the ecological feedback loop via the resources is explicitly taken into account. Assuming that mutations are very small we derive (by a formal limiting procedure in which time is rescaled in order to capture the slow process of substantial change in predominant trait) the Hamilton–Jacobi equation with constraints that is the main subject of this paper.

What adaptive dynamics should we expect? How does this depend on the trade-off? If we assume that mutations are rare, we can employ the methods of the Adaptive Dynamics references cited above to answer these questions. This we do in Section 4. Focussing at first on a monomorphic population we introduce the invasion exponent, the selection gradient and the notion of mutual invasibility. Next we embark on a search for singular points (i.e., points at which the selection gradient vanishes). Singular points can be classified according to their attraction/repulsion properties with respect to the adaptive dynamics. A key feature is that a singular point may be an attractor for monomorphisms, yet a repeller for dimorphisms. Such a point is called a “branching point”. We deduce conditions which guarantee that the utmost generalist trait  $x = \frac{1}{2}$  corresponds to a branching point. We also present a graphical method, due to Rueffler et al. (2004), for analyzing the adaptive dynamics of dimorphisms, including a characterization of the pair of points at which evolution will come to a halt. As in the context of our example plurimorphisms involving more than two points are impossible, our results give a rather complete qualitative picture of the adaptive dynamics in dependence on qualitative (and quantitative) features of the trade-off. Additional quantitative information about the *speed* of adaptive movement is embodied in the canonical equation which, much as the Hamilton–Jacobi equation,

describes trait change on a very long time scale when mutations are, by assumption, very small.

In Section 5 we explain how the Hamilton–Jacobi equation leads to an alternative canonical equation. It is an ODE that relates the selection gradient to the direction in which the dominant trait moves.

Section 6 gives a rigorous justification of the limiting procedure leading to the Hamilton–Jacobi formulation in the context of a slightly simplified model.

Section 7 deals with the numerical implementation of the Hamilton–Jacobi equation. To test its performance, we compare the results with both the qualitative and quantitative insights derived in Section 4 and with a direct numerical simulation of the full selection–mutation equation. The tests are a signal success for the Hamilton–Jacobi algorithm.

## 2. Competition for two resources

Consider an organism that has access to two resources which provide energy and comparable materials (such resources are called “substitutable”). Let  $S_1$  and  $S_2$  denote the concentrations of these resources in a chemostat, cf [Smith and Waltman \(1984\)](#). Then the vector

$$I = \begin{pmatrix} S_1 \\ S_2 \end{pmatrix} \tag{2.1}$$

constitutes the environmental condition (in the sense of [Diekmann et al., 2001, 2003](#)) for the consumer.

The organisms can specialize to various degrees in consuming, given  $I$ , more or less of either of the two resources. We capture this in a trait, which we denote by  $x$  and which varies continuously between 0 and 1. If the trait is 0 only resource 2 is consumed and when the trait equals 1 only resource 1 is consumed. The general effect of the trait is incorporated in the two up-take coefficients  $\eta(x)$  and  $\zeta(x)$ , which are such that the per capita ingestion rate of an organism with trait  $x$  equals, respectively,  $\eta(x)S_1$  and  $\zeta(x)S_2$  (so we assume mass action kinetics and ignore saturation effects).

In case of a monomorphic consumer population, the ecological dynamics is then generated by the system of differential equations

$$\begin{cases} \frac{dS_1}{dt} = S_{01} - S_1 - \eta(x)S_1X, \\ \frac{dS_2}{dt} = S_{02} - S_2 - \zeta(x)S_2X, \\ \frac{dX}{dt} = -X + \eta(x)S_1X + \zeta(x)S_2X, \end{cases} \tag{2.2}$$

where  $X$  denotes the density of the consumer population and  $S_{0i}$  is the concentration of resource  $i$  in the inflowing medium (note that the variables have been scaled to

make the chemostat turnover rate and the conversion efficiencies equal to 1).

System (2.2) has, provided

$$\eta(x)S_{01} + \zeta(x)S_{02} > 1, \tag{2.3}$$

a unique nontrivial steady state which is globally asymptotically stable. To see this, note first of all that the population growth rate of consumers with trait  $x$  under *steady* environmental conditions  $I$  is given by

$$r(x, I) = -1 + \eta(x)S_1 + \zeta(x)S_2. \tag{2.4}$$

So a first steady-state condition reads

$$r(x, I) = 0. \tag{2.5}$$

In addition there are feedback conditions to guarantee that  $I$  is constant, viz.,

$$\begin{cases} S_{01} - S_1 - \eta(x)S_1X = 0, \\ S_{02} - S_2 - \zeta(x)S_2X = 0. \end{cases} \tag{2.6}$$

If we solve (2.6) for  $S_1$  and  $S_2$  in terms of  $X$  and substitute the result into (2.5), we obtain one equation

$$-1 + \frac{\eta(x)S_{01}}{1 + \eta(x)X} + \frac{\zeta(x)S_{02}}{1 + \zeta(x)X} = 0 \tag{2.7}$$

in one unknown,  $X$ . The left-hand side of (2.7) is a monotone decreasing function of  $X$  with limit  $-1$  for  $X \rightarrow \infty$ . So there is a positive solution if and only if the value of the left-hand side is positive for  $X = 0$ , which amounts exactly to condition (2.3) (note that this inequality guarantees that the consumer population starts growing exponentially when introduced in the *virgin* environment  $I = (S_{0i}^{(0)})$ ). To deduce the global stability, first observe that, for  $t \rightarrow \infty$

$$S_1 + S_2 + X \rightarrow S_{01} + S_{02} \tag{2.8}$$

(just add all equations of (2.2) to obtain a linear equation for  $S_1 + S_2 + X$ ). A standard phase plane analysis of the two-dimensional system obtained by putting  $X$  equal to  $S_{01} + S_{02} - S_1 - S_2$  in the equations for  $S_1$  and  $S_2$  now yields the desired conclusion, see [Smith and Waltman \(1984\)](#) for more details.

We conclude that, under condition (2.3), the population dynamics of a monomorphic consumer leads to a unique steady-state attractor.

The analogue of (2.2) for the competition of *two* consumer populations, one with trait  $x$  and the other with trait  $y$ , is the system

$$\begin{cases} \frac{dS_1}{dt} = S_{01} - S_1 - \eta(x)S_1X_1 - \eta(y)S_1X_2, \\ \frac{dS_2}{dt} = S_{02} - S_2 - \zeta(x)S_2X_1 - \zeta(y)S_2X_2, \\ \frac{dX_1}{dt} = -X_1 + \eta(x)S_1X_1 + \zeta(x)S_2X_1, \\ \frac{dX_2}{dt} = -X_2 + \eta(y)S_1X_2 + \zeta(y)S_2X_2. \end{cases} \tag{2.9}$$

In steady state both  $r(x, I)$  and  $r(y, I)$  are zero. These are two linear equations in the two unknowns  $S_1$  and  $S_2$ . The solution reads

$$\begin{pmatrix} S_1 \\ S_2 \end{pmatrix} = \frac{1}{\eta(x)\xi(y) - \eta(y)\xi(x)} \begin{pmatrix} \xi(y) - \xi(x) \\ \eta(x) - \eta(y) \end{pmatrix}. \tag{2.10}$$

The two feedback relations can next be used to deduce that the steady-state densities of the two consumer populations are

$$\begin{pmatrix} X_1 \\ X_2 \end{pmatrix} = \begin{pmatrix} \frac{\xi(y)S_{01}}{\xi(y) - \xi(x)} - \frac{\eta(y)S_{02}}{\eta(x) - \eta(y)} - \frac{\eta(y) - \xi(y)}{\eta(x)\xi(y) - \eta(y)\xi(x)} \\ -\frac{\xi(x)S_{01}}{\xi(y) - \xi(x)} + \frac{\eta(x)S_{02}}{\eta(x) - \eta(y)} + \frac{\xi(x) - \eta(x)}{\eta(x)\xi(y) - \eta(y)\xi(x)} \end{pmatrix}. \tag{2.11}$$

Note, however, that in order to be meaningful the expressions for  $X_i$  should be positive and, it then follows automatically, by the two feedback equations, that  $0 < S_i < S_{0i}$ . The translation of these conditions into conditions on the pair  $(x, y)$  is of course cumbersome.

The steady state is a global attractor whenever it satisfies the sign conditions  $X_i > 0$ , Wolkowitz, (here it plays a role that saturation effects are ignored).

According to the Competitive Exclusion Principle, three or more consumer populations cannot coexist in steady state on two resources. And indeed, if  $r(x, I)$ ,  $r(y, I)$  and  $r(z, I)$  are all put equal to zero we have three linear equations in just two unknowns,  $S_1$  and  $S_2$ , so generically there is no solution.

### 3. The selection–mutation equation and its Hamilton–Jacobi limit

If reproduction is not completely faithful, a consumer with trait  $y$  may generate offspring with trait  $x$ . Let  $K(x, y)$  be the corresponding probability density. One then expects to find, after a while, consumers of all possible traits. Let  $n(t, \cdot)$  denote the density of consumers at time  $t$ . The system

$$\begin{cases} \frac{dS_1}{dt}(t) = S_{01} - S_1(t) - S_1(t) \int_0^1 \eta(x)n(t, x) dx, \\ \frac{dS_2}{dt}(t) = S_{02} - S_2(t) - S_2(t) \int_0^1 \xi(x)n(t, x) dx, \\ \frac{\partial n}{\partial t}(t, x) = -n(t, x) + \int_0^1 K(x, y) \\ \quad \times \{S_1(t)\eta(y) + S_2(t)\xi(y)\}n(t, y) dy, \end{cases} \tag{3.1}$$

describes the interaction, via the resources, of the various types of consumers, as well as the effect of mutation. It is therefore called a selection–mutation (system of) equation(s).

Here we focus, for simplicity, on the situation that the offspring of an individual with trait  $x$  has a trait distribution as described by the density  $K(x, \cdot)$ . In particular we do not incorporate a Dirac mass at  $x$ , so, in a sense, the mutation probability equals one. Many variants are possible and our analysis below extends to them; in particular a proportion of reproduction might

arise without mutation as in most population genetics models (Bürger, 2000, p. 163), an additional death rate  $d(x)$  could be added, mutations could be modeled by a diffusion rather than an integral operator.

Let now  $K$  depend on a small parameter  $\varepsilon$ , the idea being that mutations are necessarily small, which we incorporate by assuming that  $K_\varepsilon(x, y)$  is negligibly small for  $x$  outside an  $\varepsilon$ -neighborhood of  $y$ , see also Calcina and Cuadrado (2004). Rescale time by putting  $\tau = \varepsilon t$  (this scaling achieves that, when we let  $\varepsilon$  vanish, the time scale is adapted to observing the effect of mutations). Abusing notation by writing  $\tau$  again as  $t$  we can now rewrite the last equation of (3.1) as

$$\frac{\varepsilon}{n(t, x)} \frac{\partial n}{\partial t}(t, x) = -1 + \int_0^1 K_\varepsilon(x, y) \{S_1(t)\eta(y) + S_2(t)\xi(y)\} \frac{n(t, y)}{n(t, x)} dy. \tag{3.2}$$

In terms of  $\varphi$  defined by

$$\varphi(t, x) = \varepsilon \ln n(t, x), \tag{3.3}$$

the left-hand side equals  $\frac{\partial \varphi}{\partial t}(t, x)$  while the second term at the right-hand side can be written as

$$\int_0^1 K_\varepsilon(x, y) \{S_1(t)\eta(y) + S_2(t)\xi(y)\} e^{\frac{\varphi(t, y) - \varphi(t, x)}{\varepsilon}} dy. \tag{3.4}$$

Now assume that  $K_\varepsilon(x, y)$  is sufficiently small for  $y$  outside an  $\varepsilon$  neighborhood of  $x$ . We then make the change of integration variable  $y = x + \varepsilon z$  and approximate

$$\frac{\varphi(t, y) - \varphi(t, x)}{\varepsilon} \quad \text{by} \quad \frac{\partial \varphi}{\partial x}(t, x)z.$$

Furthermore, we assume that the likelihood of a new trait as a result of a mutation only depends on the distance to the original trait. So we replace the kernel  $K_\varepsilon$  by a convolution kernel  $\tilde{K}$  and approximate

$$K_\varepsilon(x, y) dy \quad \text{by} \quad \tilde{K}(z) dz,$$

where  $\tilde{K}$  is a nonnegative and even function defined on  $(-\infty, +\infty)$  which has integral 1 (here we lose the possibility to study subtleties of mutations in small neighborhoods of the boundary points  $x = 0$  and  $x = 1$  but this is not our point here). By formally taking the limit  $\varepsilon \rightarrow 0$  in (3.2) we obtain

$$\begin{aligned} \frac{\partial \varphi}{\partial t}(t, x) \\ = r(x, I) + (S_1(t)\eta(x) + S_2(t)\xi(x))H\left(\frac{\partial \varphi}{\partial x}(t, x)\right), \end{aligned} \tag{3.5}$$

where  $r$  is as defined in (2.4) and  $H$  is defined by

$$H(p) = \int_{-\infty}^{\infty} \tilde{K}(z)e^{-pz} dz - 1. \tag{3.6}$$

Note that  $H(0) = 0$  and that for an even function  $\tilde{K}$  we have  $H'(0) = 0$  and  $H''(0) > 0$ , so  $H$  is convex. We call  $H$

the *Hamiltonian* corresponding to  $\tilde{K}$ . Also note that we abuse notation once more by not distinguishing  $\varphi$  defined by (3.3) from its limit for  $\varepsilon \rightarrow 0$ .

The above formalism and limit are classically related to large deviations (Evans and Souganidis, 1989; Fleming and Soner, 1993; Freidlin, 1992; Perthame and Souganidis, 2004), a method that is also used in population genetics (Champagnat et al., 2001), and has been widely used for diffusion models such as the Kimura–Lande approximation.

Rewriting (3.3) as

$$n(t, x) = e^{\frac{\varphi(t, x)}{\varepsilon}}, \tag{3.7}$$

it becomes clear that we should have

$$\varphi(t, x) \leq 0 \tag{3.8}$$

in the limit for  $\varepsilon \rightarrow 0$  (see Section 6 for a derivation of the bounds that substantiate the “should”). The points where  $\varphi$  equals 0 are of particular interest since, again in the limit  $\varepsilon \rightarrow 0$ ,  $n$  is concentrated in these points (in the limit  $n$  is no longer a density, but a measure).

Suppose  $\bar{x} = \bar{x}(t)$  is such that

$$\varphi(t, \bar{x}(t)) = 0. \tag{3.9}$$

Then, because of (3.8), necessarily at a maximum point in  $x$  one has

$$\frac{\partial \varphi}{\partial x}(t, \bar{x}(t)) = 0. \tag{3.10}$$

Since also

$$0 = \frac{d}{dt} \varphi(t, \bar{x}(t)) = \frac{\partial \varphi}{\partial t}(t, \bar{x}(t)) + \frac{\partial \varphi}{\partial x}(t, \bar{x}(t)) \frac{d\bar{x}}{dt}(t) \tag{3.11}$$

we must have that

$$\frac{\partial \varphi}{\partial t}(t, \bar{x}(t)) = 0. \tag{3.12}$$

Substituting (3.12) and (3.10) into (3.5) and using  $H(0) = 0$  we find that

$$r(\bar{x}(t), I) = 0. \tag{3.13}$$

The Competitive Exclusion Principle as formulated at the end of the preceding section now implies at once that there can be at most two points  $\bar{x}_1(t)$  and  $\bar{x}_2(t)$  for which (3.9) holds.

This observation allows us to rewrite the limiting version of the first two equations of (3.1) in the form

$$\begin{aligned} S_1(t) &= \frac{S_{01}}{1 + c_1 \eta(\bar{x}_1(t)) + c_2 \eta(\bar{x}_2(t))}, \\ S_2(t) &= \frac{S_{02}}{1 + c_1 \zeta(\bar{x}_1(t)) + c_2 \zeta(\bar{x}_2(t))}, \end{aligned} \tag{3.14}$$

where  $c_1$  and  $c_2$  are the sizes of the subpopulations with, respectively, trait  $\bar{x}_1(t)$  and trait  $\bar{x}_2(t)$ . The limiting problem thus takes the Hamilton–Jacobi form (3.5)–(3.8) which amounts to (3.5)–(3.9)–(3.14). If the population is dimorphic, the two constraints induced by (3.9) at two points  $\bar{x}_1(t)$  and  $\bar{x}_2(t)$  allow to recover the “Lagrange multipliers”  $S_i(t)$ , and then the population densities  $c_1$ ,  $c_2$  are recovered from (3.14). If the population is monomorphic, then there is only one free constant  $c := c_1 + c_2$  and Eq. (3.5) has to be complemented by a relation between  $S_1(t)$  and  $S_2(t)$ , namely

$$S_1(t) = \frac{S_{01}}{1 + c \eta(\bar{x}(t))}, \quad S_2(t) = \frac{S_{02}}{1 + c \zeta(\bar{x}(t))}. \tag{3.15}$$

The switch from one case to the other (and thus the search for additional criteria for uniqueness of the solution) is a problem we leave open for the moment. See Section 7 for an algorithmic solution. In Fig. 1 we present an example computed with these methods for up-take functions obtained with the analysis in Section 4.

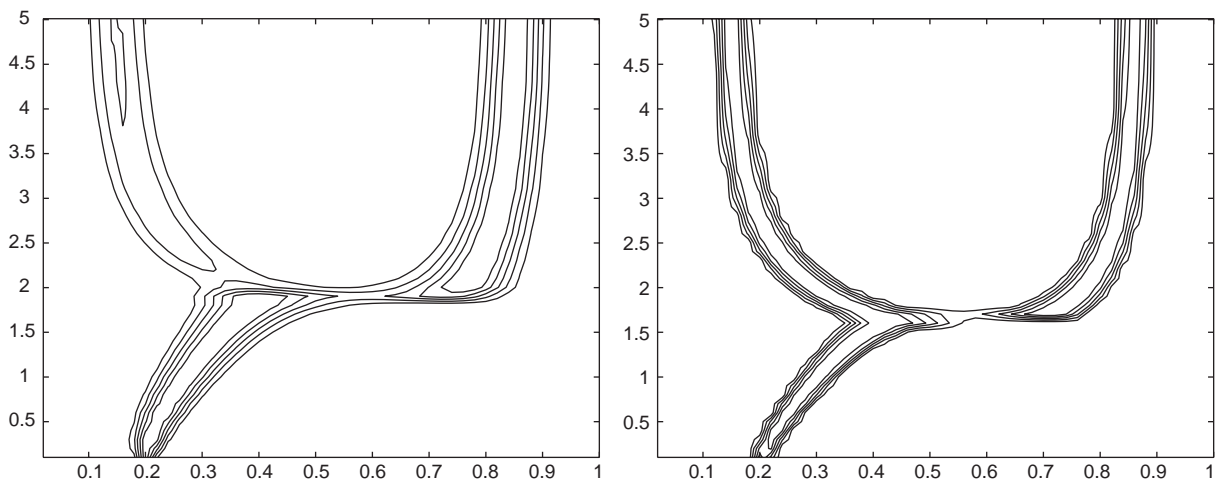


Fig. 1. Branching in system (3.1) departing from a monomorphic situation with trait  $x = 0.2$ . The  $x$ -axis represents the trait and the  $y$ -axis is time. Left: direct simulation through (7.1). Right: simulation of the H.-J. equation (3.5). The figures represent the contour lines of  $n$  (left), and  $\varphi$  (right). The numerical method is described in Section 7.

In conclusion of this section we remark that ansatz (3.7) works equally well when mutation described by a diffusion term (rather than an integral operator), as in some parts of Bürger (2000) and Ferriere et al. (2004), and lead to the hamiltonian  $H(\nabla\varphi) = c|\nabla\varphi|^2$ .

**4. Trait substitutions, singular points and branching**

In this section we adopt the Adaptive Dynamics point of view by assuming that mutations are extremely rare at the time scale of ecological interaction, see Diekmann (2004) for a gentle introduction. We study under which circumstances a monomorphic situation, described by (2.2), can switch to dimorphic (described by (2.9)) ignoring the transient dynamics directly following a mutation (this is what actually happens in the limit  $\varepsilon \rightarrow 0$ ).

*4.1. Invasibility*

Imagine a resident consumer population which is monomorphic, i.e. described by (2.2). It sets the environmental condition at a steady level. If the resident has trait  $x$ , we denote the corresponding vector of substrate concentrations by  $I_x$ .

Now suppose that, due to a mutation, a consumer with trait  $y$  enters the scene. Will this invader initiate an exponentially growing clan of  $y$  individuals? If we ignore the issue of demographic stochasticity, the answer is provided by the sign of the *invasion exponent*

$$s_x(y) := r(y, I_x), \tag{4.1}$$

in the sense that it is “yes” if  $s_x(y) > 0$  and “no” if  $s_x(y) < 0$ . If we focus on small mutations the relevant quantity is the *selection gradient*

$$\left. \frac{\partial s}{\partial y} \right|_{y=x} = \frac{\partial r}{\partial x}(x, I_x). \tag{4.2}$$

If the selection gradient is positive, mutations that increase the trait value are successful.

For the present system it seems feasible to prove rigorously that a successful invader will out-compete the resident, and thus become the new resident, if there is no *mutual invasibility*, i.e. if  $s_y(x) < 0$ . Here we simply assume this, while referring to Dercole (2002) and Geritz (2005) for a general justification of such an assumption in the case of small mutations.

So in the absence of mutual invasibility a successful mutant causes a *trait substitution*, i.e., the resident is, after a period of ecological interaction which is short at the time scale of mutation, monomorphic again, but with a different trait.

*4.2. Singular points*

A trait  $\bar{x}$  at which the selection gradient vanishes is called a *singular point*. The classification of singular points is the corner stone of Adaptive Dynamics theory (Metz et al., 1996; Geritz et al., 1997; Diekmann, 2004) as much information about the dynamics can be derived once all singular points and their character are known.

If we supplement the steady-state condition (2.5) by the singularity condition

$$0 = \frac{\partial s}{\partial y} = \frac{\partial r}{\partial x}(x, I) = \eta'(x)S_1 + \xi'(x)S_2 \tag{4.3}$$

we obtain a system of two linear equations in the unknown  $S_1$  and  $S_2$ . The solution is given by

$$\begin{pmatrix} S_1 \\ S_2 \end{pmatrix} = \frac{1}{\eta(x)\xi'(x) - \eta'(x)\xi(x)} \begin{pmatrix} \xi'(x) \\ -\eta'(x) \end{pmatrix}. \tag{4.4}$$

Substituting these expressions in the feedback conditions (2.6) and eliminating the unknown  $X$  we obtain the equation

$$\begin{aligned} &\xi(x)\eta'(x)S_{01} + \eta(x)\xi'(x)S_{02} \\ &= \frac{\xi'(x)\eta'(x)(\xi(x) - \eta(x))}{\eta(x)\xi'(x) - \xi(x)\eta'(x)} \end{aligned} \tag{4.5}$$

which the trait  $x$  should satisfy in order to be a singular point. Conversely, any solution of (4.5), such that the  $S_i$  defined by (4.4) satisfy  $0 < S_i < S_{0i}$ , yields a singular point.

The classification of singular points involves second-order derivatives of the invasion exponent  $s_x(y)$  and these we compute next

$$\begin{aligned} c_{22} &:= \left. \frac{\partial^2 s}{\partial y^2} \right|_{y=x} = \frac{\partial^2 r}{\partial x^2}(x, I_x) = \eta''(x)S_1 + \xi''(x)S_2 \\ &= \frac{\eta''(x)\xi'(x) - \xi''(x)\eta'(x)}{\eta(x)\xi'(x) - \xi(x)\eta'(x)}, \end{aligned} \tag{4.6}$$

$$\begin{aligned} c_{12} &:= \left. \frac{\partial^2 s}{\partial x \partial y} \right|_{y=x} = \eta'(x) \frac{dS_1}{dx} + \xi'(x) \frac{dS_2}{dx}, \\ &= \left( \left( \frac{\xi(x)}{\xi'(x)} \right)^2 S_{01} + \left( \frac{\eta(x)}{\eta'(x)} \right)^2 S_{02} \right)^{-1} \\ &\quad \times \left( \frac{\xi'(x) - \eta'(x)}{\eta(x)\xi'(x) - \xi(x)\eta'(x)} - S_{01} - S_{02} \right). \end{aligned} \tag{4.7}$$

(The computation of  $\frac{dS_i}{dx}$  starts from (2.5) and the form of (2.6) resulting from elimination of  $X$ , which are two equations in the unknowns  $S_1$  and  $S_2$ , parametrized by the trait  $x$ . One then applies the Implicit Function Theorem.) There is no need to compute  $c_{11} := \left. \frac{\partial^2 s}{\partial x^2} \right|_{y=x}$  since the identity  $s_x(x) \equiv 0$  implies that  $c_{11} + 2c_{12} + c_{22} = 0$ .

Our aim is to find a singular point which satisfies

$$\begin{cases} c_{12} < 0, \\ c_{22} < -c_{12}, \\ c_{22} > 0, \end{cases} \quad (4.8)$$

since these are the conditions for a *branching point* (the first guarantees that one has mutual invasibility near the singular point, the second that the singular point is *convergence stable*, i.e., an attractor for the monomorphic adaptive dynamics, and the third that branching is guaranteed since  $(x, x)$  is a repeller for the dimorphic adaptive dynamics, see Metz et al. (1996), Geritz et al. (1997) and Diekmann (2004)). Incidentally, note that the last two conditions guarantee that the first is satisfied.

### 4.3. Symmetric trade-off

In order to make further progress, it helps to specify  $\eta$  and  $\xi$  in more detail. Implicitly we assumed already that  $(\eta(0), \xi(0)) = (0, 1)$ ,  $(\eta(1), \xi(1)) = (1, 0)$  and that  $\eta$  is increasing while  $\xi$  is decreasing. Now we require that

$$\begin{cases} \eta(x) = x - \delta\phi(x), \\ \xi(x) = 1 - x - \delta\phi(x), \end{cases} \quad (4.9)$$

where  $\phi$  is a  $C^2$  function which vanishes in  $x = 0$  and  $x = 1$  and  $\phi$  and  $\delta$  are such that

$$\delta \sup_{0 \leq x \leq 1} |\phi'(x)| < 1 \quad (4.10)$$

to make sure that  $\eta$  and  $\xi$  are monotone. Specialists are more efficient than generalists, in a sense, when  $\phi$  is positive. When  $\phi$  is negative it is the other way around. We introduce the positive parameter  $\delta$  to measure the strength of such a trade-off effect (but we refrain from normalizing  $\phi$  explicitly, e.g. by fixing its value for  $x = \frac{1}{2}$ ).

To simplify the analysis we next introduce symmetry by assuming that

$$S_{01} = S_{02} = S_0 \quad (4.11)$$

and

$$\phi(x) = \phi(1 - x). \quad (4.12)$$

If  $(S_1, S_2, X)$  is a steady state corresponding to trait  $x$  then, under these conditions, the steady state corresponding to  $1 - x$  is  $(S_2, S_1, X)$ . And if we call  $(x, y)$ , with  $0 \leq x, y \leq 1$ , a *point of neutrality* when  $s_x(y) = 0$  then, whenever  $(x, y)$  is neutral, so is  $(1 - x, 1 - y)$ . Or, in other words, the curve of neutral points is invariant under reflection in the midpoint  $(\frac{1}{2}, \frac{1}{2})$  of the square  $(x, y) : 0 \leq x, y \leq 1$ . Note that singular points correspond, generically, to intersections of a neutrality curve with the diagonal. The symmetry thus suggests that  $x = \frac{1}{2}$  may very well be a singular point. Let us check whether this is indeed the case.

Note first of all that (4.12) implies that  $\phi'(\frac{1}{2}) = 0$ . Hence  $\eta'(\frac{1}{2}) = 1 - \xi'(\frac{1}{2})$ . Since  $\eta(\frac{1}{2}) = \xi(\frac{1}{2})$  we deduce from (4.4) that for  $x = \frac{1}{2}$  the steady-state values of  $S_1$  and  $S_2$  are equal and the value is  $(1 - 2\delta\phi(\frac{1}{2}))^{-1}$ . In combination with  $\eta'(\frac{1}{2}) + \xi'(\frac{1}{2}) = 0$  this implies that the selection gradient vanishes for  $x = \frac{1}{2}$  (see (4.3)), so  $x = \frac{1}{2}$  is indeed a singular point.

Evaluating expressions (4.6) and (4.7) for  $x = \frac{1}{2}$  we find

$$c_{22} = \frac{-2\delta\phi''(\frac{1}{2})}{1 - 2\delta\phi(\frac{1}{2})} \quad (4.13)$$

and

$$c_{12} = \left(\frac{1}{2} - \delta\phi\left(\frac{1}{2}\right)\right)^{-2} \left(\frac{1}{S_0(1 - 2\delta\phi(\frac{1}{2}))} - 1\right). \quad (4.14)$$

The last inequality of (4.8) only requires

$$\phi''\left(\frac{1}{2}\right) < 0. \quad (4.15)$$

The middle one amounts to

$$S_0 > \left(1 - 2\delta\phi\left(\frac{1}{2}\right)\right)^{-1} \times \left(1 + \frac{1}{2}\delta\left(1 - 2\delta\phi\left(\frac{1}{2}\right)\right)\phi''\left(\frac{1}{2}\right)\right)^{-1} \quad (4.16)$$

and when the middle and the last hold, so does the first.

For the special case

$$\phi(x) = x(1 - x), \quad (4.17)$$

the only condition thus is

$$S_0 > \left(1 - \frac{1}{2}\delta\right)^{-1} \left(1 - \delta\left(1 - \frac{1}{2}\delta\right)\right)^{-1}. \quad (4.18)$$

For

$$\phi(x) = x(1 - x)[x(1 - x) - \alpha] \quad (4.19)$$

we find the conditions

$$\alpha < \frac{1}{2} \quad (4.20)$$

and

$$S_0 > \left(1 - \frac{1}{8}\delta(1 - 4\alpha)\right)^{-1} \times \left(1 + \delta\left(\alpha - \frac{1}{2}\right)\left(1 - \frac{1}{8}\delta(1 - 4\alpha)\right)\right)^{-1}. \quad (4.21)$$

### 4.4. Dimorphisms

Recall that dimorphic steady states are explicitly described by expressions (2.10) and (2.11). The invasion exponent is now given by

$$s_{x,y}(z) = r(z, I_{x,y}) = -1 + \eta(z)S_{1,x,y} + \xi(z)S_{2,x,y} \quad (4.22)$$

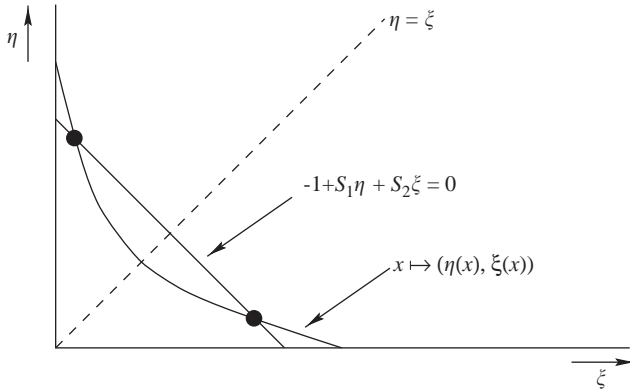


Fig. 2. Elements for the analysis of dimorphic situations.

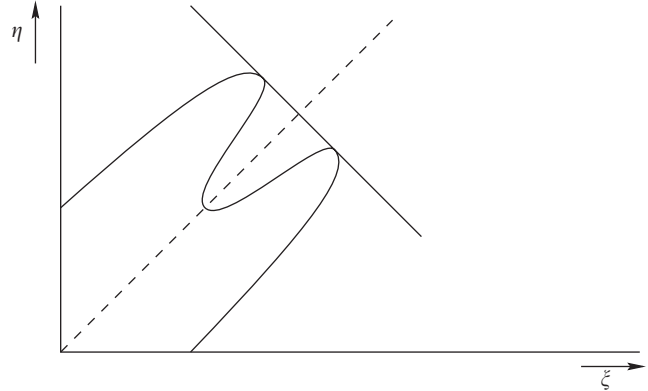


Fig. 3. The  $(\xi, \eta)$  curve used for constructing branching points.

with  $S_{i,x,y}(z)$  given by (2.10). As we learned from Rueffler et al. (2004), there is a convenient way to analyze (4.22) graphically.

After Fig. 2, first plot the curve  $x \mapsto (\eta(x), \xi(x))$ . If, as we assumed,  $\eta(x) = \xi(1 - x)$  then this curve is symmetric with respect to reflection in the diagonal. Accordingly the intersection with the diagonal occurs for  $x = \frac{1}{2}$  and corresponds to the “extreme generalist” singular point. Condition (4.15) guarantees local concavity of the curve near this point.

Next draw in the same picture the straight line

$$-1 + S_1\eta + S_2\xi = 0 \tag{4.23}$$

for some values of  $S_1$  and  $S_2$ . If this line intersects the curve in two points, we can express  $S_1$  and  $S_2$  in terms of the coordinates of these two points. Thus we rederive (2.10), with  $x$  and  $y$  the traits that yield the points.

The invasibility condition

$$s_{x,y}(z) > 0 \tag{4.24}$$

now means that the point on the curve corresponding to trait  $z$  should be above the line. Thus we see at once that when the curve is globally concave, like in the case (4.17)  $\phi(x) = x(1 - x)$ , depicted in Fig. 2 the two traits grow wider and wider apart and converge to the boundary of trait space (i.e., the ultimate dimorphism consists of the two extreme specialists,  $x = 0$  and  $y = 1$ ).

When  $\phi$  is given by (4.19), a suitable choice of the parameters  $\alpha$  and  $\delta$  leads to the curve depicted in Fig. 3. The graphical criterion now yields that the dimorphism corresponding to the two “tops”, i.e., the two traits at which the tangent line to the curve has slope  $-1$ , is uninhabitable (or, in other words, unbeatable).

Note that when  $y = 1 - x$  expression (2.10) simplifies to

$$\begin{pmatrix} S_1 \\ S_2 \end{pmatrix} = \frac{1}{1 - 2\delta\phi(x)} \begin{pmatrix} 1 \\ 1 \end{pmatrix}. \tag{4.25}$$

If  $S_1 = S_2$ , the line (4.23) has slope  $-1$ . Moreover, the environmental condition is then completely described by a scalar quantity, the common value of  $S_1$  and  $S_2$ .

So if we constrain the dimorphisms to satisfy the symmetry condition  $y = 1 - x$ , the “pessimization principle” (cf. Mylius and Diekmann, 1995) applies and evolution will minimize the common value of  $S_1$  and  $S_2$  which, according to (4.25), amounts to minimizing  $\phi$ . Finally note that the condition  $\phi'(\bar{x}) = 0$  is equivalent to the condition that the tangent to  $x \mapsto (\eta(x), \xi(x))$  has slope  $-1$  in  $x = \bar{x}$ .

#### 4.5. The boundary of trait space

To complement the information obtained by a singular point analysis, we pay special attention to boundary mono- and dimorphisms, as these too may serve as attractors for the adaptive dynamics.

A monomorphic population with trait  $x = 0$  sets the environmental condition at  $S_1 = S_{01}$ ,  $S_2 = 1$ . The selection gradient

$$\begin{aligned} \frac{\partial r}{\partial x}(0, I_0) &= \eta'(0)S_{01} + \xi'(0) \\ &= (1 - \delta\phi'(0))S_{01} - 1 - \delta\phi'(0) \end{aligned} \tag{4.26}$$

determines both whether nearby traits can invade and whether  $x = 0$  is an attractor. The condition

$$S_{01} > \frac{1 + \delta\phi'(0)}{1 - \delta\phi'(0)} \tag{4.27}$$

guarantees that  $x = 0$  is a repeller with respect to the adaptive dynamics. Similarly one finds that  $x = 1$  is unstable if

$$S_{02} > \frac{1 - \delta\phi'(0)}{1 + \delta\phi'(0)}. \tag{4.28}$$

A dimorphic population with traits  $x = 0$  and  $y = 1$  sets both  $S_1$  and  $S_2$  at the value 1, so the invasion exponent (4.22) equals  $-2\delta\phi(z)$ . Accordingly the dimorphism  $(0, 1)$



is adaptively stable if  $\phi'(0) > 0$  and  $\phi'(1) < 0$  but unstable if either of these inequalities is reversed.

#### 4.6. The canonical equation

“Canonical equation” usually refers to a differential equation for the position of the dominant trait(s) in trait space. In case of a one-dimensional trait, the time derivative of any position is proportional to the selection gradient. The proportionality factor incorporates such features as the mutation probability per birth event, the variance of the distribution of mutant traits, the probability that a potentially successful mutant does not go extinct due to demographic stochasticity and the equilibrium resident population size. We refer to Diekmann and Law (1996), Champagnat et al. (2001) and Dercole (2002) for further details including a derivation from a birth–death process with mutation. We now turn to study whether such a canonical equation can be derived in our setting (note that in this setting the chance effects involved in mutations are incorporated while demographic stochasticity is not).

### 5. An alternative for the canonical equation

At the end of Section 3 we derived, starting from the Hamilton–Jacobi equation (3.5) and the constraint (3.8), property (3.13) expressing that in a point  $\bar{x}(t)$  in which  $\varphi$  assumes its maximum value zero, necessarily the consumer growth rate equals zero. Here we take these considerations a step further: we derive an ODE for  $\bar{x}$  which involves the local shape of  $\varphi$  in  $\bar{x}$ , as captured by the second-order derivative  $\frac{\partial^2 \varphi}{\partial x^2}(t, \bar{x}(t))$ . An interesting (yet expected) feature here is that the system *cannot be closed*, because an ODE for the second derivative of  $\varphi$  uses its third derivative, etc. This reflects that the trait distribution is not determined by just a few moments. Yet, as we will show, some information can be derived.

We differentiate (3.10) with respect to  $t$  and we obtain

$$\frac{\partial^2 \varphi}{\partial t \partial x} + \frac{\partial^2 \varphi}{\partial x^2} \frac{d\bar{x}}{dt} = 0 \tag{5.1}$$

(here and in the following we omit the argument  $(t, \bar{x}(t))$ ). Differentiating (3.5) with respect to  $x$  we find, in general

$$\begin{aligned} \frac{\partial^2 \varphi}{\partial t \partial x}(t, x) &= \frac{\partial r}{\partial x}(I, x) + (S_1(t)\eta'(x) + S_2(t)\zeta'(x))H \\ &\quad \times \left( \frac{\partial \phi}{\partial x}(t, x) \right) + (S_1(t)\eta(x) + S_2(t)\zeta(x))H' \\ &\quad \times \left( \frac{\partial \phi}{\partial x}(t, x) \right) \frac{\partial^2 \phi}{\partial x^2}(t, x) \end{aligned} \tag{5.2}$$

but if we specialize to  $x = \bar{x}(t)$  then, since  $H(0) = 0$  and  $H'(0) = 0$ , this boils down to

$$\frac{\partial^2 \varphi}{\partial t \partial x} = \frac{\partial r}{\partial x}(I, \bar{x}). \tag{5.3}$$

Combining (5.1) and (5.3) we obtain an *alternative for the canonical equation*, namely

$$\frac{d\bar{x}}{dt} = \left( -\frac{\partial^2 \varphi}{\partial x^2} \right)^{-1} \frac{\partial r}{\partial x}(I, \bar{x}). \tag{5.4}$$

Notice that  $-\frac{\partial^2 \varphi}{\partial x^2}$  is a nonnegative (unknown) coefficient because  $\bar{x}$  corresponds to a maximum of  $\varphi(t, \cdot)$ . Therefore one can read the direction in which  $\bar{x}(t)$  moves off from (5.4) and in fact from the selection gradient  $\frac{\partial r}{\partial x}$ .

If  $\varphi$  has a single maximum (or, in other words, the consumer population is quasi-monomorphic), (5.4) is a single ODE and

$$I = \left( \frac{\frac{S_{01}}{1 + \eta(\bar{x})X}}{\frac{S_{02}}{1 + \zeta(\bar{x})X}} \right), \tag{5.5}$$

where  $X = X(\bar{x})$  is the unique solution of (cf. (2.7))

$$\frac{\eta(\bar{x})S_{01}}{1 + \eta(\bar{x})X} + \frac{\zeta(\bar{x})S_{02}}{1 + \zeta(\bar{x})X} = 1. \tag{5.6}$$

This provides an algorithm for computing  $I = I(\bar{x})$ .

If  $\varphi$  has two maxima we provide  $\bar{x}$  with an index taking the values 1 and 2. The coupling between the two versions of (5.4) is provided by  $I$  which is now defined by (cf. (2.10))

$$I = \frac{1}{\eta(\bar{x}_1)\zeta(\bar{x}_2) - \eta(\bar{x}_2)\zeta(\bar{x}_1)} \left( \frac{\zeta(\bar{x}_2) - \zeta(\bar{x}_1)}{\eta(\bar{x}_1) - \eta(\bar{x}_2)} \right). \tag{5.7}$$

To go further we may differentiate (5.2) once more with respect to  $x$  and subsequently put  $x = \bar{x}(t)$ . We obtain similarly, using also (3.13), the differential equation

$$\frac{d}{dt} \left( \frac{\partial^2 \varphi}{\partial x^2}(t, x) \right) = \frac{\partial^2 r}{\partial x^2}(I(t), x) + H''(0) \left( \frac{\partial^2 \varphi}{\partial x^2}(t, x) \right)^2. \tag{5.8}$$

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

$$\frac{d}{dt} \left( \frac{\partial^2 \varphi}{\partial x^2} \right) = \frac{\partial^2 r}{\partial x^2}(I, \bar{x}) + H''(0) \left( \frac{\partial^2 \varphi}{\partial x^2} \right)^2 + \frac{\partial^3 \varphi}{\partial x^3} \frac{d\bar{x}}{dt}. \tag{5.9}$$

Continuing this process to recover  $\frac{\partial^3 \varphi}{\partial x^3}$ , 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 generated by (3.5) under constraint (3.8).

Let us now focus on the ODE (5.4) describing a quasi-monomorphic population. The steady state should satisfy

$$\frac{\partial r}{\partial x}(I(\bar{x}), \bar{x}) = 0 \tag{5.10}$$

or, in AD jargon,  $\bar{x}$  should be a singular point. Define, as usual, (see (4.6) and (4.7))

$$c_{22} = \frac{\partial^2 r}{\partial x^2}(I(\bar{x}), \bar{x}), \tag{5.11}$$

$$c_{12} = \frac{\partial^2 r}{\partial x \partial I}(I(\bar{x}), \bar{x}) \frac{dI}{dx}(\bar{x}) \tag{5.12}$$

and note that (since  $\frac{\partial^2 \varphi}{\partial x^2}$  “enters” the differential equation for  $\bar{x}$  only via a signed factor) whether or not  $\bar{x}$  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

$$c_{22} + c_{12} < 0 \tag{5.13}$$

or, in the jargon of AD, when the singular point is convergence stable.

The steady-state equation corresponding to (3.5) reads

$$H\left(\frac{\partial \varphi}{\partial x}(x)\right) = \frac{-r(I, x)}{S_1 \eta(x) + S_2 \xi(x)}. \tag{5.14}$$

Since  $H \geq 0$ , there can be a solution only if the condition  $r \leq 0$  holds for the relevant arguments. Now let  $\bar{x}$  be a singular point. Put  $I = I(\bar{x})$  in (5.14). Then, in order for (5.14) to be solvable, we need that the condition

$$c_{22} < 0 \tag{5.15}$$

holds. Or, in other words, with a singular point one can associate a steady state only when it is ESS (this conclusion can also be derived from (5.9)).

**6. Rigorous derivation of the H.-J. limit**

This section is devoted to the mathematical derivation of the Hamilton–Jacobi equation in a simplified case where mutations arise with a fixed rate, but we compensate by considering also a death rate  $d$ . Namely, we consider the following variant, for  $x \in \mathbb{R}$ ,

$$\begin{cases} \frac{d}{dt} S_{1,\varepsilon}(t) = \frac{1}{\varepsilon} [S_1^0 - S_{1,\varepsilon} [1 + \int_{\mathbb{R}} \eta(x) n_\varepsilon(t, x) dx]], \\ \frac{d}{dt} S_{2,\varepsilon}(t) = \frac{1}{\varepsilon} [S_2^0 - S_{2,\varepsilon} [1 + \int_{\mathbb{R}} \xi(x) n_\varepsilon(t, x) dx]], \\ \frac{d}{dt} n_\varepsilon(t, x) = \frac{1}{\varepsilon} [-dn_\varepsilon(t, x) + S_{1,\varepsilon}(t) \eta(x) n_\varepsilon(t, x) \\ + S_{2,\varepsilon}(t) \xi(x) n_\varepsilon(t, x) + \int_{\mathbb{R}} K_\varepsilon(x - x') \\ \times (n_\varepsilon(t, x') - n_\varepsilon(t, x)) dx'], \end{cases} \tag{6.1}$$

with nonnegative initial data  $S_{1,\varepsilon}(t = 0), S_{2,\varepsilon}(t = 0), n_\varepsilon^0(x)$ . We again perform the change of unknowns

$$n_\varepsilon(t, x) = e^{\varphi_\varepsilon(t,x)/\varepsilon}, \quad n_\varepsilon^0(x) = e^{\varphi_\varepsilon^0(x)/\varepsilon}, \tag{6.2}$$

and carry out the same analysis as in Section 3. We also set

$$H(p) = \int_{\mathbb{R}} K(z) e^{-p \cdot z} dz - 1. \tag{6.3}$$

Then, we arrive formally, in the limit when  $\varepsilon$  vanishes, at

$$\begin{cases} S_1(t) = \frac{S_1^0}{1 + I_1(t)}, \quad I_1(t) = \int_{\mathbb{R}} \eta(x) n(t, x) dx, \\ S_2(t) = \frac{S_2^0}{1 + I_2(t)}, \quad I_2(t) = \int_{\mathbb{R}} \xi(x) n(t, x) dx, \\ \frac{\partial}{\partial t} \varphi(t, x) = -d + S_1(t) \eta(x) + S_2(t) \xi(x) + H(\nabla \varphi(t, x)), \\ \max_{x \in \mathbb{R}} \varphi(t, x) = 0, \quad \forall t \geq 0, \\ n(t, \cdot) \text{ is supported by the maximum points of } \varphi. \end{cases} \tag{6.4}$$

At this point, we need to make precise assumptions

$$x \mapsto \eta(x), \xi(x) \text{ are positive, Lipschitz continuous and bounded,} \tag{6.5}$$

$$K(x) \geq 0, \quad \int_{\mathbb{R}} K(x) dx = 1, \quad K \text{ is even,} \tag{6.6}$$

$$d > 0, \quad S_1^0 > 0, \quad S_2^0 > 0, \tag{6.7}$$

$$x \mapsto \varphi_\varepsilon^0(x) \text{ is uniformly Lipschitz continuous,} \tag{6.8}$$

$$\begin{aligned} \int_{\mathbb{R}} n_\varepsilon^0(x) dx = M^0 > 0, \quad S_{i,\varepsilon}(t = 0) \\ \text{are bounded and bounded away from} \\ 0 \text{ for } i = 1, 2. \end{aligned} \tag{6.9}$$

We prove a statement that is in fact weaker than the validity of Eq. (6.4), namely

**Theorem 6.1.** *Assume (6.5)–(6.9), then the (nonnegative) solution to system (6.1) satisfies*

- (i) *the functions  $S_{1,\varepsilon}(t), S_{2,\varepsilon}(t), \int_{\mathbb{R}} n_\varepsilon(t, x) dx$  are uniformly bounded,*
- (ii) *the function  $\varphi_\varepsilon(t, x)$  is uniformly Lipschitz continuous on  $[0, T] \times \mathbb{R}$ , for all  $T > 0$ ,*
- (iii) *the functions  $\varphi_\varepsilon$  and  $\Sigma_{i,\varepsilon}(t) = \int_0^t S_{i,\varepsilon}(s) ds$  (for  $i = 1, 2$ ) converge locally uniformly, after extracting a subsequence, to Lipschitz continuous functions  $\varphi, \Sigma_i(t)$ , and the H.-J. equation is fulfilled in the sense that  $\psi(t, x) = \varphi(t, x) - \Sigma_1(t) \eta(x) - \Sigma_2(t) \xi(x)$  satisfies in the viscosity sense*

$$\begin{cases} \frac{\partial}{\partial t} \psi(t, x) = -d + H(\nabla \psi + \Sigma_1(t) \nabla \eta(x) + \Sigma_2(t) \nabla \xi(x)), \\ \max_{x \in \mathbb{R}} \varphi(t, x) \leq 0 \quad \forall t \geq 0. \end{cases} \tag{6.10}$$

The motivation for writing the equation in terms of  $\psi$  rather than in terms of  $\varphi$  is that the coefficients  $\Sigma_i$  in (6.10) are now continuous, which is better fitted to the concept of viscosity solutions than the merely bounded coefficients  $S_i$ . We have also simplified as much as

possible the setting and some of the assumptions are not optimal (in particular the uniform Lipschitz continuity assumptions).

The result can be extended as follows:

**Theorem 6.2.** *If additionally  $\varphi_\varepsilon^0(x) \rightarrow -\infty$  as  $|x| \rightarrow \infty$  (uniformly) and*

$$S_1^0 \min_{y \in \mathbb{R}} \eta(y) + S_2^0 \min_{y \in \mathbb{R}} \zeta(y) > d, \tag{6.11}$$

then  $\int_{\mathbb{R}} n_\varepsilon(t, x) dx$  is uniformly bounded away from 0 and

$$\max_{x \in \mathbb{R}} \varphi(t, x) = 0 \quad \forall t \geq 0. \tag{6.12}$$

The use of Hamilton–Jacobi equations is by now standard in the description of the propagation of fronts in parabolic equations describing an invasion process (in ecology, phase transitions, etc.), see for example Evans and Souganidis (1989) and Barles et al. (1990) or for integral equations for jump processes, see Perthame and Souganidis (2004). The possibility to describe the evolution of point concentrations seems less studied. Some examples have been derived directly from stochastic processes (through representation formulas) in Freidlin (1992) but the general formalism, including the constraint (6.12) combined with Lagrange multipliers  $S$ , seems completely new.

**Proof of Theorem 6.1.** We begin with the a priori bounds (i). We integrate the equation for  $n_\varepsilon$  with respect to  $x$  and add-up the three equations of (6.1). We arrive at

$$\begin{aligned} \frac{d}{dt} \left[ S_{1,\varepsilon}(t) + S_{2,\varepsilon}(t) + \int_{\mathbb{R}} n_\varepsilon(t, x) dx \right] \\ = S_1^0 + S_2^0 - S_{1,\varepsilon}(t) - S_{2,\varepsilon}(t) - d \int_{\mathbb{R}} n_\varepsilon(t, x) dx. \end{aligned}$$

Therefore, by the maximum principle we deduce, using assumptions (6.7), (6.9),

$$0 < \underline{M} \leq S_{1,\varepsilon}(t) + S_{2,\varepsilon}(t) + \int_{\mathbb{R}} n_\varepsilon(t, x) dx \leq \overline{M} < \infty,$$

with

$$\begin{aligned} \underline{M} &= \min \left[ S_{1,\varepsilon}(t=0) + S_{2,\varepsilon}(t=0) \right. \\ &\quad \left. + \int_{\mathbb{R}} n_\varepsilon^0(x) dx, \frac{S_1^0 + S_2^0}{\max(1, d)} \right], \\ \overline{M} &= \max \left[ S_{1,\varepsilon}(t=0) + S_{2,\varepsilon}(t=0) \right. \\ &\quad \left. + \int_{\mathbb{R}} n_\varepsilon^0(x) dx, \frac{S_1^0 + S_2^0}{\min(1, d)} \right]. \end{aligned}$$

Because the quantities are nonnegative, this proves the upper bounds on all the quantities.

Next, we prove (ii). We begin by estimating space derivatives. We set  $p(t, x) = \frac{\partial}{\partial x} \varphi_\varepsilon(t, x)$ , and

compute

$$\begin{aligned} \frac{\partial}{\partial t} \varphi_\varepsilon(t, x) &= -d - 1 + S_{1,\varepsilon}(t)\eta(x) \\ &\quad + S_{2,\varepsilon}(t)\zeta(x) + \int_{\mathbb{R}} K(z) e^{(\varphi_\varepsilon(t, x - \varepsilon z) - \varphi_\varepsilon(t, x))/\varepsilon}, \end{aligned} \tag{6.13}$$

$$\begin{aligned} \frac{\partial}{\partial t} p(t, x) &= S_{1,\varepsilon}(t)\eta'(x) + S_{2,\varepsilon}(t)\zeta'(x) \\ &\quad + \int_{\mathbb{R}} K(z) e^{(\varphi_\varepsilon(t, x - \varepsilon z) - \varphi_\varepsilon(t, x))/\varepsilon} \\ &\quad \times (p(t, x - \varepsilon z) - p(t, x)). \end{aligned}$$

This equation admits  $P(t, x) = K_0 + tK_1$  as a supersolution with  $K_0 = \max_{y \in \mathbb{R}, \varepsilon} |\nabla \varphi_\varepsilon^0(y)|$ ,  $K_1 = \max_{t, x} [S_{1,\varepsilon}(t)|\eta'(x)| + S_{2,\varepsilon}(t)|\zeta'(x)|]$  (using assumptions (6.5), (6.8)). Therefore the maximum principle gives

$$|p(t, x)| \leq K_0 + tK_1.$$

It remains to estimate time derivatives. To do that, we just notice that all the terms on the right-hand side of (6.13) are bounded (by assumption (6.5) and the space Lipschitz continuity) and thus  $\varphi_\varepsilon$  is Lipschitz continuous (locally in time).

We can now derive point (iii). Using Ascoli’s lemma and points (i) and (ii), we may extract subsequences which converge as indicated in the statement. Then, the usual arguments for viscosity solutions (see Barles, 2002; Crandall and Lions, 1992; Bardi and Capuzzo Dolcetta, 1997; Fleming and Soner, 1993) yield the viscosity solution criteria. Next, we derive that  $\varphi$  is nonpositive. To do so, we use step (i) and especially that  $\int_{\mathbb{R}} n_\varepsilon(t, x) dx \leq \overline{M}$  and argue by contradiction. If we had  $\max_{x \in \mathbb{R}} \varphi(t, x) > 0$  for some time, then also  $\varphi_\varepsilon(t, x) > 0$  uniformly in  $\varepsilon$  for  $t, x$  in some open set (by uniform continuity). But this is impossible since  $\int e^{\varphi_\varepsilon(t, x)/\varepsilon} dx \leq \overline{M}$ .  $\square$

**Proof of Theorem 6.2.** We set  $M(t) = \int_{\mathbb{R}} n_\varepsilon(t, x) dx$ ,  $S(t) = \min_{y \in \mathbb{R}} \eta(y)S_{1,\varepsilon}(t) + \min_{y \in \mathbb{R}} \zeta(y)S_{2,\varepsilon}(t)$ ,  $S^0 = \min_{y \in \mathbb{R}} \eta(y)S_1^0 + \min_{y \in \mathbb{R}} \zeta(y)S_2^0$  and we write the (rough) inequalities

$$\begin{cases} \frac{d}{dt} M(t) \geq \frac{1}{\varepsilon} [-(d+1) + S(t)]M(t), \\ \frac{d}{dt} S(t) \geq \frac{1}{\varepsilon} [S^0 - S(t)(1 + \beta M(t))], \end{cases}$$

with  $\beta = \max(\max_{y \in \mathbb{R}} \eta(y), \max_{y \in \mathbb{R}} \zeta(y))$ . Direct manipulations show that this system maintains  $M(t)$  away from 0.

Then, we argue as before to prove that we cannot have  $\max_{x \in \mathbb{R}} \varphi(t, x) < 0$  for some  $t \geq 0$ . Indeed, by uniform continuity, this would imply  $\max_{x \in \mathbb{R}} \varphi_\varepsilon(t, x) < -\alpha$  for

some  $\alpha > 0$  and thus

$$\int_{\mathbb{R}} n_{\varepsilon}(t, x) dx = \int_{\mathbb{R}} e^{\varphi_{\varepsilon}(t, x)/\varepsilon} dx \rightarrow 0, \quad \text{as } \varepsilon \rightarrow 0,$$

a contradiction.

### 7. Numerical method

The numerical tests presented above compare a direct simulation with a H.-J. solution. We present the algorithms in the following three subsections.

Our purpose here is not to develop original or sophisticated methods for solving the problem we have encountered. We simply wish that the interested reader can reproduce the results. Therefore we always opt for simplicity. Notations for this section are:  $\Delta t$  is the time step and  $t^k = k \Delta t$ . Then the exponent represents the time step, the index  $i = 1, 2$  represents the two nutrients (and we sometimes use  $\eta_1 = \eta, \eta_2 = \zeta$ ), the index  $j \in \{1, \dots, N\}$  represents the grid variable associated with a finite difference scheme for the equation for  $n(t, x)$  ( $x_j = j \Delta x, \Delta x = 1/N$ ). Finally, for the mutation kernel  $\tilde{K}$ , we use the convolution model (see Section 3) and call  $2M + 1$  the number of points for discretizing it (and thus  $\varepsilon = M/N$ ).

#### 7.1. Direct simulation

We first present the algorithmic basis of the direct simulation of system (3.1). Here we have opted for a semi-implicit finite difference scheme to ensure stability while keeping simplicity,

$$\begin{cases} S_i^{(k+1)} = S_i^0 - \Delta t S_i^{(k+1)} [1 + \langle n^k \eta_i \rangle], \\ n_j^{(k+1)} = n_j^{(k)} - \Delta t n_j^{(k+1)} + \Delta t \\ \quad \times ([S_1^{(k+1)} \eta + S_2^{(k+1)} \zeta] n^{(k)} \star \tilde{K})_j, \end{cases} \quad (7.1)$$

where all variables are extended by 0 outside of the interval  $\{1, \dots, M\}$ ,

$$\langle n^k \eta \rangle = \frac{1}{N} \sum_{j=1}^N n_j^{(k)} \eta_j,$$

$$(\eta n^{(k)} \star \tilde{K})_j = \frac{1}{2M + 1} \sum_{m=-M}^M \eta_{j-m} n_{j-m}^{(k)} \tilde{K}_m.$$

Notice that this scheme preserves the a priori bounds of Section 6 because it preserves positivity and the fundamental equality

$$Q^{(k+1)}(1 + \Delta t) = Q^{(k)} + \Delta t (S_1^0 + S_2^0),$$

$$Q^{(k)} := S_1^{(k)} + S_2^{(k)} + \frac{1}{N} \sum_{j=1}^N n_j^{(k)}.$$

In practice we have always chosen  $\tilde{K}_m := 1$  (an even and piecewise constant function of mass 1).

#### 7.2. H.-J.: single nutrient

Here, we explain the numerical resolution of the constraint in the H.-J. system (3.5) in the case of a single nutrient, i.e., when  $S_2^0 = 0, S_2(t) \equiv 0$ . In this case (corresponding to  $S_2 \equiv 0$ ), the H.-J. equation is given by

$$\begin{cases} \frac{d}{dt} \varphi(t, x) = -1 + S(t) \eta(x) [1 + H(\nabla \varphi(t, x))], \\ \max_{x \in \mathbb{R}} \varphi(t, x) = 0 \quad \forall t \geq 0. \end{cases} \quad (7.2)$$

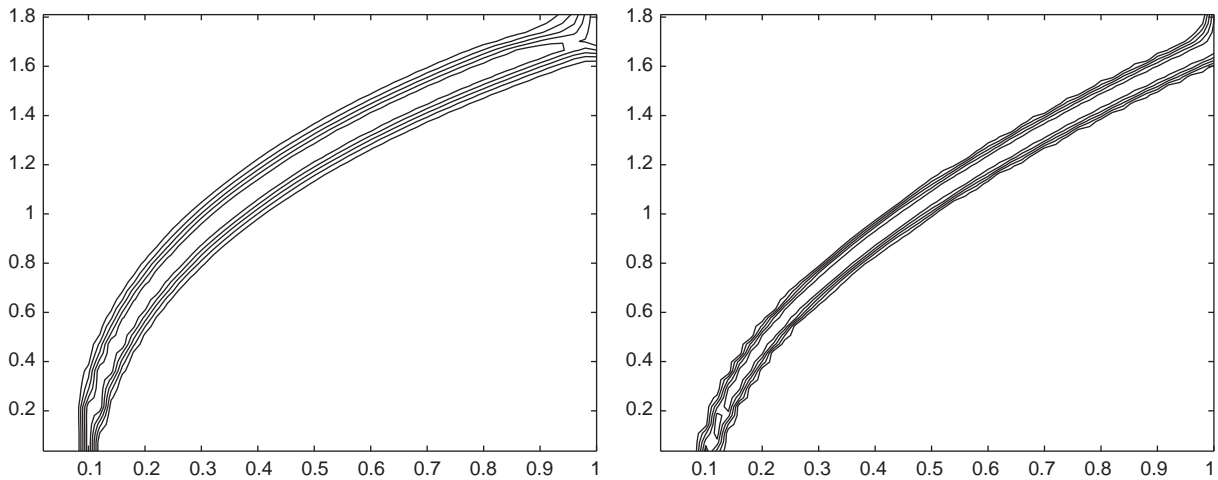


Fig. 4. Evolution of the dominant trait (x-axis) with time (y-axis) (case with a single resource;  $\eta(x) = .5 - x$ ). Left: direct simulation through (7.1). Right: simulation of the H.-J. equation (7.2). The figures represent the contour lines of  $n$  (left) and  $\varphi$  (right).

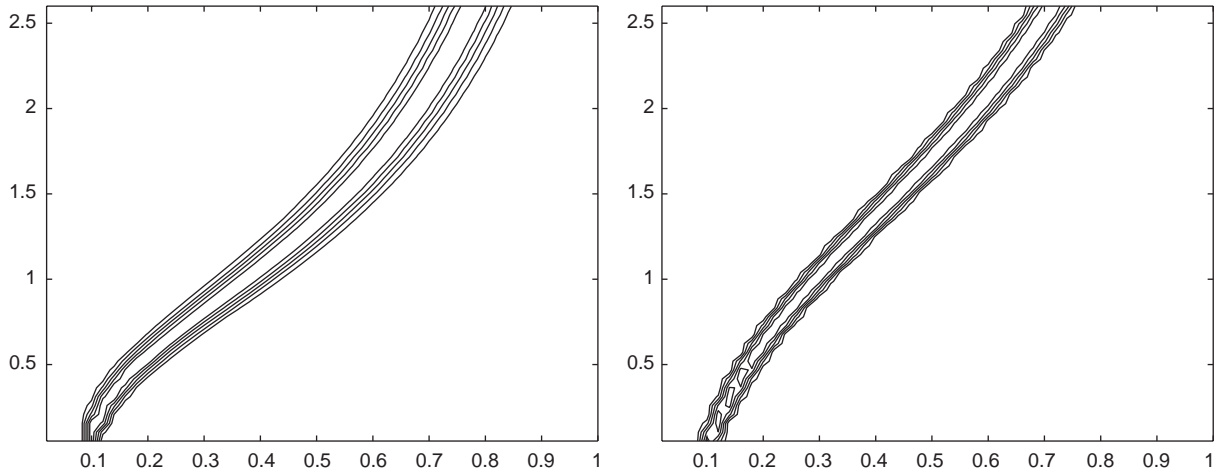


Fig. 5. Same as Fig. 4 with  $\eta(x) = .5 - x(2 - x)$ .

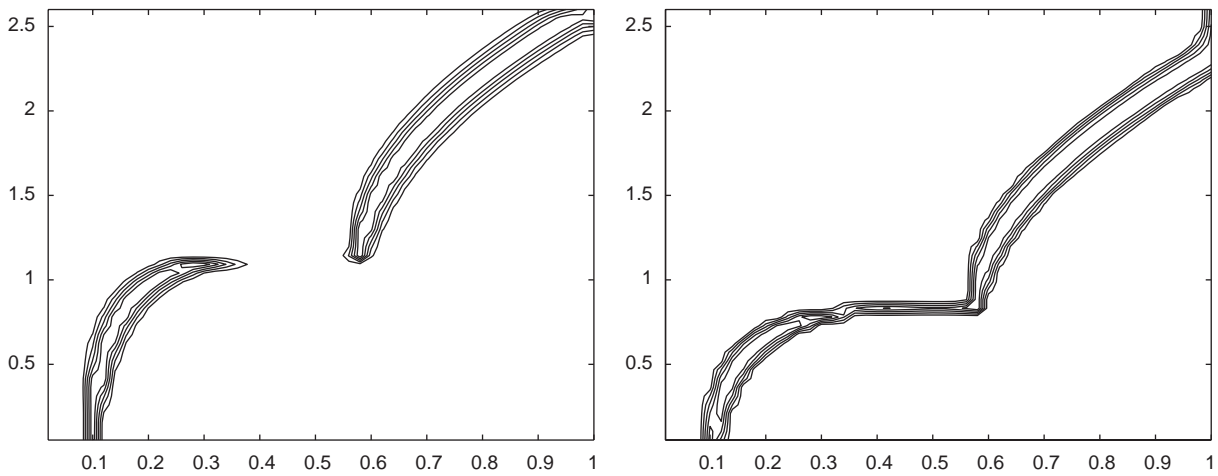


Fig. 6. Same as Fig. 4 with  $\eta(x) = \min(.45 + x^2, .55 + .4x)$ .

A discretized version is as follows

$$\begin{cases} \varphi_j^{(k+1)} = \varphi_j^{(k)} + \Delta t \left[ -1 + S^{(k)} \eta_j \right. \\ \quad \left. \times \left[ 1 + \mathcal{H} \left( \frac{\varphi_{j+1}^{(k)} - \varphi_j^{(k)}}{\Delta x}; \frac{\varphi_j^{(k)} - \varphi_{j-1}^{(k)}}{\Delta x} \right) \right] \right], \\ \max_{1 \leq j \leq N} \varphi_j^{(k)} = 0 \quad \forall k. \end{cases} \tag{7.3}$$

The subtlety here is that the solution of the H.-J. equation requires an upwind solver for the Hamiltonian  $H$ , denoted by  $\mathcal{H}$ , (see Augoula and Abgrall (2000) and the references therein for recent and classical references on the subject).

The new additional difficulty here is to satisfy the constraint, which can be done as follows. For all  $1 \leq m \leq N$ , we can first compute a value  $\Sigma_m^k$  of the (Lagrange) variable  $S^k$  by imposing that the updated

value  $\varphi_m^{k+1}$  vanishes,

$$0 = \varphi_m^{(k)} + \Delta t \left[ -1 + \Sigma_m^{(k)} \eta_m \right. \\ \quad \left. \times \left[ 1 + \mathcal{H} \left( \frac{\varphi_{m+1}^{(k)} - \varphi_m^{(k)}}{\Delta x}; \frac{\varphi_m^{(k)} - \varphi_{m-1}^{(k)}}{\Delta x} \right) \right] \right].$$

Then the choice

$$S^{(k)} = \min_{1 \leq m \leq N} \Sigma_m^{(k)},$$

gives the solution to (7.3). Indeed, for the particular index  $m_0$  where the min is achieved, we clearly have  $\varphi_{m_0}^{(k+1)} = 0$ . For the other indices, the inequality  $\Sigma_m^{(k)} \geq S^{(k)}$  leads to  $\varphi_m^{(k+1)} \leq 0$ .

The numerical experiments presented in Figs. 4–6 present several comparisons between a direct simulation using algorithm (7.1) and the discretized H.-J. solution (7.3). Direct simulations are performed with  $N = 1500$  points for the direct simulation and 200 points in the H.-J. setting. We have taken the value of  $M = 5$  which

corresponds to  $\varepsilon \approx .3 \times 10^{-2}$  for the computations in 4, 6. In Fig. 6 the direct simulation is computed with  $N = 3000$  points,  $\varepsilon \approx .15 \times 10^{-2}$ . These comparisons show the ability of the two models to compute, not only continuous evolution, but also a jump in the dominant trait.

7.3. H.-J.: two nutrients

In the case of two nutrients, we have to face a specific difficulty which is to choose between the dimorphic case (where the two Lagrange multipliers  $S_1, S_2$  are to be computed) and the monomorphic case with the additional constraint (3.15) (recall the discussion at the end of Section 3). We begin again with a discrete version

$$\begin{cases} \varphi_j^{(k+1)} = \varphi_j^{(k)} + \Delta t \left[ -1 + [S_1^{(k)}\eta_j + S_2^{(k)}\xi_j] \right. \\ \quad \left. \times \left[ 1 + \mathcal{H} \left( \frac{\varphi_{j+1}^{(k)} - \varphi_j^{(k)}}{\Delta x}; \frac{\varphi_j^{(k)} - \varphi_{j-1}^{(k)}}{\Delta x} \right) \right] \right], \\ \max_{1 \leq j \leq N} \varphi_j^{(k)} = 0 \quad \forall k. \end{cases} \tag{7.4}$$

At the moment we do not have a clear criterion to decide which case applies and we use preferentially the dimorphic case whenever the values  $S_1$  and  $S_2$ , which are computed by the algorithm described below, satisfy  $0 < S_1 < S_1^0$  and  $0 < S_2 < S_2^0$ . If not, we introduce a single coefficient  $c$  which relates the Lagrange multipliers  $S_1$  and  $S_2$  to each other and allows us to apply the algorithm of Section 7.2 replacing  $\Sigma_m(t)\eta_m$  by

$$\frac{S_1^0}{1 + c\eta_m} \eta_m + \frac{S_2^0}{1 + c\xi_m} \xi_m,$$

and choosing  $c_m$  such that the corresponding discrete H.-J. equation vanishes at the index  $m$ , after which we see that  $c^{(k)} = \max_{1 \leq m \leq N} c_m$  gives a solution just as before.

It remains to describe the dimorphic algorithm. We consider now two indices  $l \neq m$  and compute  $S_1(l, m), S_2(l, m)$  such that for both  $j = l$  and  $j = m$  we have

$$0 = \varphi_j^{(k)} + \Delta t \left[ -1 + [S_1(l, m)\eta_j + S_2(l, m)\xi_j] \right. \\ \left. \times \left[ 1 + \mathcal{H} \left( \frac{\varphi_{j+1}^{(k)} - \varphi_j^{(k)}}{\Delta x}; \frac{\varphi_j^{(k)} - \varphi_{j-1}^{(k)}}{\Delta x} \right) \right] \right].$$

If one of these values also gives for all  $1 \leq j \leq N$ ,

$$\varphi_j^{(k)} + \Delta t \left[ -1 + [S_1(l, m)\eta_j + S_2(l, m)\xi_j] \right. \\ \left. \times \left[ 1 + \mathcal{H} \left( \frac{\varphi_{j+1}^{(k)} - \varphi_j^{(k)}}{\Delta x}; \frac{\varphi_j^{(k)} - \varphi_{j-1}^{(k)}}{\Delta x} \right) \right] \right] \leq 0,$$

and

$$0 \leq S_1(l, m) \leq S_1^0, \quad 0 \leq S_2(l, m) \leq S_2^0,$$

then we consider that this is a solution to problem (7.4) and we update  $S_1^{(k)} = S_1(l, m), S_2^{(k)} = S_2(l, m)$ . If such a choice is not possible, we go to the monomorphic choice (which is always possible).

The numerical result for a branching case is presented in Fig. 1, again with  $N = 1500, M = 5$  for the direct simulation and  $\eta = x - 1.8x(1 - x)[x(1 - x) - 6/25], \xi = 1 - x - 1.8x(1 - x)[x(1 - x) - 6/25]$ .

8. Conclusion

A quantitative trait in a population may change as a response to the combined effect of mutation and selection, where selection acts by way of an ecological feedback loop. Our aim has been twofold. First, we wanted to introduce a very simple example of “branching”, the change from monomorphism to dimorphism, in order to demonstrate the phenomenon as well as its analysis in the framework of Adaptive Dynamics. Even though the example allows a clear ecological interpretation, we did not strive to derive new biological insights, since an attempt in that direction would inevitably lead to making the example more complex (see Rueffler et al. (submitted) for a more ambitious attempt in this direction). Secondly, we wanted to introduce a new approach for analyzing the eco-evolutionary dynamics, viz. the Hamilton–Jacobi formalism, and demonstrate the power of the corresponding numerical implementations in establishing the ensuing dynamics. The hope is, of course, that this approach allows to study far more complicated models.

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