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Bet-hedging in stochastically switching environments

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HIGHLIGHTS

- Bet-hedging in stochastically switching environments is analyzed via adaptive dynamics.
- Expansions of Lyapunov exponents for linear 2-dim. systems and different time scales are derived.
- Fast time-scale: homogeneous phenotype, adapted to the average environment is optimal.
- Middle range time scale: bet-hedging is optimal.
- Slow time scale: phenotype adapted to one environment only is optimal.

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ABSTRACT

We investigate the evolution of bet-hedging in a population that experiences a stochastically switching environment by means of adaptive dynamics. The aim is to extend known results to the situation at hand, and to deepen the understanding of the range of validity of these results. We find three different types of evolutionarily stable strategies (ESSs) depending on the frequency at which the environment changes: for a rapid change, a monomorphic phenotype adapted to the mean environment; for an intermediate range, a bimorphic bet-hedging phenotype; for slowly changing environments, a monomorphic phenotype adapted to the current environment. While the last result is only obtained by means of heuristic arguments and simulations, the first two results are based on the analysis of Lyapunov exponents for stochastically switching systems.

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1. Introduction

In recent years, it has become more and more evident that isogenic bacterial populations show different phenotypes. This phenomenon is also known as phenotypic heterogeneity and is often connected to bistability in regulatory pathways. A textbook example is persister cells in *Escherichia coli*: a certain fraction of the population largely deactivates their metabolism and rest. These cells do not divide and so stop contributing to the population growth, but they survive antibiotic attacks while active cells are

killed. At the time the antibiotics are removed from the environment, some persisters can wake up again and form the nucleus of a re-appearing population (Balaban et al., 2004). Another example is the lactose metabolism of *E. coli*: if a gratuitous inducer (an inducer that is not metabolized but is able to bind to the repressor of the lac operon) is present, a part of the bacteria does and a part does not express *lac* (Smits et al., 2006). Obviously, the rationale of this effect is related to the changing lactose densities in the environment. A third example is *Vibrio harveyi* that communicates by a quorum-sensing system. It has been shown that only a fraction of the cells respond to the signaling molecules in this communication, though the population is clonal and all cells maintain the ability to produce and to sense the signals. The deeper reason for this observation is still unclear (Anetzberger et al., 2009). More examples can be found in the review paper of Smits et al. (2006).

These observations trigger two different questions. (i) What are the molecular mechanisms of the regulatory networks utilized to create heterogeneity? (ii) What is the purpose of this strategy in the light of evolution?

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The answer to the first question, which is not the focus of the present work, has been a major research topic in recent years: bacteria often make use of bistable pathways in combination with stochasticity due to small molecule numbers (Balaban et al., 2004; Elowitz et al., 2002; Ribeiro, 2008; Satory et al., 2011; Müller et al., 2008) in order to create heterogeneity. The regulatory systems are designed to switch stochastically between different states; the rate at which a cell jumps between the states as well as the fraction of the population that is in a certain state can be adapted to the environmental statistics very precisely over a wide range.

The present work primarily deals with the second question raised above: why, under which conditions, are observed bimorphic phenotypes evolutionarily stable? Bimorphism should provide a selective growth advantage over monomorphism, otherwise we do not expect this strategy to be evolutionarily stable. This point is of major interest as the two-type strategy may be considered as the beginning of a differentiation between different types of cells. It could be interpreted as a first step toward a system of specialized cells acting as a unit, perhaps even as an early form from which multicellular organisms evolved. Fluctuations of environmental conditions seem to be one of the main reasons for bimorphic strategies (Gaal et al., 2012) and bet-hedging in the sense of risk minimization (de Jong et al., 2011), though not the only scenario that promotes heterogeneity (Ackermann et al., 2008). We take up the basic ideas of Gaal et al. (2012) and consider an environment that assumes two different states (cold and hot, rainy and dry, etc.). We assume that no monomorphic phenotype can be optimal to cope with both environments in that different properties are required for adaptation. We furthermore assume that it is not possible or too expensive to maintain the properties of both phenotypes within one cell and that an active switching in response to the environment does not lead to desirable results, e.g. because the production of sensory molecules necessary to recognize the current environment is too expensive, or because active switching is too slow. Therefore, e.g. at the time of cell division, daughter cells decide about the type they become, or cells actively switch phenotype later in their life, but in the latter case not in response to the current environment but at a constant rate.

The role of adaptation in response to fluctuating environments has been discussed for a long time in theoretical population genetics; the first papers have been concerned with obtaining some idea of which mutation rates in slowly changing environments would be optimal in the sense that they keep the balance between adaptedness and adaptability in an optimal way (Kimura, 1967; Leigh, 1970). A number of papers (see e.g. Cohen, 1966; Ellner and Hairston, 1994; Sasaki and Ellner, 1995; Svardal et al., 2011 and references therein) focussed on a classical model for seed that either germinate soon or hibernate (or assume other inactive, long-living phenotypes) for time-discrete models with variable environments. In these papers it is proven that genotypic variations are stable that evolutionary branching points in the sense of Metz et al. (1995) and Geritz et al. (1998) do occur. These papers focussed on the consideration of genotypes; given a genotype, an individual selects its phenotype from a given distribution. The phenotype is neither changed during life nor depends on the mother's phenotype. In these models, strategies interpreted as bet-hedging appeared to be optimal in varying environment: if some offspring hibernates for years, there will be germinating offspring in favorable years, even if they are relatively seldom and randomly distributed. The seeds of a plant “test” each year, and the successful seed is able to produce a lot of offspring, compensating for the less lucky seeds that fail to reproduce.

Only recently, bacteria became model organisms to investigate not a genotypic but a certain phenotypic heterogeneity known as bet-hedging (Acar et al., 2007). This model and its successors differ from those mentioned above in that these new models allow

individuals to change their phenotype during live, resp. to allow the daughter cell's phenotype to depend on that of their mothers. Based on numerical simulations, a link between the rate at which the environment switches and the rate at which a bimorphic phenotype of bacteria changes its subtype has been conjectured already in that paper (Acar et al., 2007). This conjecture has been confirmed in a time-discrete setup considering models with a finite number of individuals (King and Masel, 2007; Fudenberg and Imhof, 2012). The implications of periodic environments have been analyzed by Pang and Tzeng (2008) and Gaal et al. (2012). In the present work, we extend these considerations to a stochastically fluctuating environment. Stochastic environments have been considered in Salathe et al. (2009) and Thattai and van Oudenaarden (2004), mainly by means of Monte Carlo simulations. Kussell and Leibler (2005) proposed a heuristic approximation of the Lyapunov exponent based on a separation of time scales, while Jablonka et al. (1995) focus on upper and lower estimates for the Lyapunov exponent. Here, we were able to extend the results of Gaal et al.: for rapidly switching environments, a monomorphic type, adapted to the averaged conditions, is optimal; if the environment switches on an intermediate time-scale, a bimorphic bet-hedger strategy is optimal; the rates at which the types are changed are – up to higher order terms – one over the average time the corresponding environment is present. However, if the time scale of the environmental change becomes even slower, then a monomorphic type adapted to the current environment will outcompete the bet-hedger. This is, for very rapidly and very slowly changing environments, we find one monomorphic type; the difference is that this type is adapted to the average environment in the first case, and to the current environment in the second type.

The paper is structured as follows: In Section 2.1, we develop a model for large populations in stochastically changing environments: the population dynamics itself can be formulated in a deterministic manner, and the environment switches stochastically between two different states. The results of the model analysis are summarized in Section 2.2. The proofs of the results, which are rather technical, can be found in the appendix. Section 2.3 is devoted to a heuristic discussion of a completely stochastic model, where also the populations themselves follow a stochastic birth–death process. These considerations illuminate the range of validity of the results derived in the first two subsections, and give some hint from which effects are to be expected in completely stochastic models. In contrast to the deterministic setup, in the case of a slowly changing environment, the completely stochastic model predicts that cells exhibiting a monomorphic phenotype, adapted to one environment only, will perform best. However, it is out of scope for the present work to perform a strict analysis of this completely stochastic case. In Section 3 we discuss the results obtained so far and their relevance for biological systems.

The appendix is split into two parts: in Appendix A the Lyapunov exponent of a stochastically switching system, that jumps between two linear, two-dimensional ordinary differential equations (ODEs), is determined. In particular, the asymptotics of the Lyapunov exponent for switching on a rapid respectively very slow time scale is discussed. These formulas are applied to our model in Appendix B in order to prove the theorems stated in Section 2.2.

2. Bet-hedging in a stochastic environment

2.1. Model

We develop a model for a population with two phenotypes in a stochastically switching environment. Adaptive dynamics will be

the method used to analyze this model. For an introduction to adaptive dynamics see, e.g. Geritz et al. (1998). We first give thought to the most simple setup: one homogeneous population that grows according to a logistic model in a constant environment

$$s'_0 = bs_0 - (\bar{\mu} + s_0)s_0.$$

The rate b denotes the birth/cell division rate. The mortality rate consists of one intrinsic part $\bar{\mu}$ that is independent of the population size s_0 , and one part that is caused by competition – only the latter depends on the population size. In the present work, we assume the mortality rate to be linearly increasing with population size. This assumption is merely due to technical reasons; more complex dependencies will not lead to different results, as long as different phenotypes do not compete in a different manner.

Now we take into account that the population consists of distinct phenotypes. Different phenotypes will have different behavior. The net growth rate for a small population size $\beta = b - \bar{\mu}$ is thought to depend on a parameter r that characterizes the phenotype. The parameter r can be adapted to the environmental conditions by genetic or epigenetic changes. Later, we will find that this process of adaptation leads to a value of r that maximizes the net growth rate $\beta = \beta(r)$.

It is instructive to give an explicit example. Let us assume that the two different environmental states correspond to the availability of a certain nutrient. For the first environment, denoted by α_1 , the concentration of this nutrient is high, while for the second environment, α_2 , the nutrient availability is low. To process this nutrient, enzymes are required. The number (or concentration) of these enzymes is given by r . If the bacteria have none of these enzymes ($r=0$) they cannot utilize the nutrient at hand; it is better to invest some energy and produce some enzymes. Let us furthermore assume that these enzymes are degraded at a certain rate. This is, there are certain maintenance costs. If bacteria try to maintain a high level of enzymes ($r \gg 1$), the maintenance energy will be larger than the energy they obtain by processing the nutrient. For given nutrient level α , there will be an optimal enzyme concentration $r^* = r^*(\alpha)$, at which the net energy harvest is maximal. The bacteria transform this energy into the net reproduction rate, such that we expect the reproduction rate β to depend not only on r but also on the environment α ; for α given, we expect $\beta(r, \alpha)$ to be a unimodal function in r . A numerical example we will use in Section 2.3 reads

$$\beta = \beta(r, \alpha) = b(r) - \bar{\mu}(r) = 1 + re^{-r/\alpha},$$

but the theorems we develop do not require this special form.

We now assume that α jumps between two values α_1 and α_2 according to a homogeneous Markov process. That is, $\alpha = \alpha_t$ is a stochastic process, and also $s_0(t)$ becomes a stochastic process via $s'_0 = \beta(r, \alpha_t)s_0 - s_0^2$. Successively, small mutations adapt the phenotype r of the resident until it cannot be invaded any more by a mutant with a different phenotype. We will also consider a population using a more refined strategy: the phenotype is split into two phenotypic states, one with parameter r_1 and the other with parameter r_2 . The individuals using this bimorphic two-component strategy will either give birth to both components or change – at a small rate – their subtype. The model equations read

$$\begin{aligned} s'_1 &= s_1(\beta(r_1, \alpha_t) - \varepsilon_1 - s) + \varepsilon_2 s_2 \\ s'_2 &= s_2(\beta(r_2, \alpha_t) - \varepsilon_2 - s) + \varepsilon_1 s_1 \end{aligned}$$

where

$$s = s_1 + s_2.$$

Note that there are two possible interpretations of the terms $\varepsilon_i s_j$: either cells change their lifestyle and switch at rate ε_i to the opposite type or newly produced cells assume the other type.

Then, β is the overall reproduction rate, s.t. $\beta(r_i, \alpha_t) s_i$ is the total incidence of newborns where a part $\varepsilon_i s_i$ assumes the other type.

We denote the rates ε_i as transition rates. The bimorphic phenotype is described by four parameters $(r_1, r_2, \varepsilon_1, \varepsilon_2)$. The optimal choice of these parameters will be worked out below. We couple this system with the monomorphic strategy,

$$\begin{aligned} s'_0 &= (\beta(r, \alpha_t) - s)s_0 \\ s'_1 &= s_1(\beta(r_1, \alpha_t) - \varepsilon_1 - s) + \varepsilon_2 s_2 \\ s'_2 &= s_2(\beta(r_2, \alpha_t) - \varepsilon_2 - s) + \varepsilon_1 s_1 \end{aligned}$$

where, again, $s = s_0 + s_1 + s_2$ denotes the total population size. We rescale the solution in order to compensate for the effect of the bounded carrying capacity,

$$u_0(t) = s_0(t) e^{\int_0^t s(\tau) d\tau}, \quad u_1(t) = s_1(t) e^{\int_0^t s(\tau) d\tau}, \quad u_2(t) = s_2(t) e^{\int_0^t s(\tau) d\tau}.$$

As the original equations have been coupled only due to competition which we scaled away, we find that the equations for the rescaled solutions decouple,

$$\frac{d}{dt} u_0 = \beta(r, \alpha_t) u_0$$

$$\frac{d}{dt} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = M_{\alpha_t}(r_1, r_2) \begin{pmatrix} u_1 \\ u_2 \end{pmatrix},$$

$$\text{where } M_{\alpha_t}(r_1, r_2) := \begin{pmatrix} \beta(r_1, \alpha_t) - \varepsilon_1 & \varepsilon_2 \\ \varepsilon_1 & \beta(r_2, \alpha_t) - \varepsilon_2 \end{pmatrix}.$$

We have two decoupled systems in u_0 and in u_1, u_2 . Asymptotically and on an average, both systems will grow/shrink exponentially fast (Theorem A.1). In the present setup, the phenotype with the larger average growth rate (that is, the larger Lyapunov exponent) outcompetes the other phenotype. Find in Metz (2008) a deeper explanation for the connection between evolution and Lyapunov exponent in case of fluctuating environments.

It is possible to reformulate this result in “classical” terms of adaptive dynamics (see e.g. Geritz et al., 1998; Metz, 2008). Let us first innocently ignore the fluctuating environment. Let us furthermore assume that only type s_0 is present; in this case, s_0 will grow until $s_0 = \beta(r, \alpha_t)$. If s_1, s_2 enter as rare mutants, we find $d(s_1, s_2)^T / dt = M_{\alpha_t}(s_1, s_2)^T - \beta(r, \alpha_t)(s_1, s_2)^T$. Therefore, the fitness $s_x(y)$ of the mutant y in the presence of the resident x is given by

$$s_x(y) = \rho(M_{\alpha_t}) - \beta(r, \alpha_t).$$

Similarly, the s_1, s_2 population without s_0 grows until its total population equals the spectral radius of M_{α_t} . The fitness of a rare s_0 -mutant reads

$$s_x(y) = \beta(r, \alpha_t) - \rho(M_{\alpha_t}).$$

If we now recall, that we have a fluctuating environment, we understand that we have to replace $\beta(r, \alpha_t)$ by the Lyapunov exponent of the monomorphic, and $\rho(M_{\alpha_t})$ by the Lyapunov exponent for the bimorphic type. If we investigate an invading, rare, bimorphic mutant in the presence of a bimorphic resident, or a monomorphic mutant in the presence of the monomorphic resident, in all combinations we find always

$$s_x(y) = \text{Lyapunov exponent for } y - \text{Lyapunov exponent for } x$$

where y denotes the mutant, and x the resident. Because of the model-structure, the difference of the exponential growth rates determines the fitness. An evolutionarily stable strategy (ESS) is defined as a local maximum of $s_x(y)$, which implies that any local maximum of the exponential growth rates form an ESS.

2.2. Optimal phenotype

We now specify the Markov process α_t . We assume that the resident times in state α_1 and α_2 are exponentially distributed with mean Tq_1 and Tq_2 resp., where $q_1 + q_2 = 1$, and $q_i > 0$. This means, T specifies the time scale at which the process jumps, while q_1 , and q_2 give the information in which a fraction of the time the process is in state α_1 resp. α_2 resp. We assume from now on that $\beta(r, \alpha)$ is unimodal in r for α fixed. We find two completely different situations for rapidly changing environments (T small) and slowly changing environments (T large). Let us start with a rapidly changing environment.

Theorem 2.1. For small T , the ESS consists of a homogeneous strategy. This strategy r^* maximizes the Lyapunov exponent

$$\lambda_0 = \hat{\beta}(r) = \rho(E(M_{\alpha_t}(r, r))) = \rho(q_1 M_{\alpha_1}(r, r) + q_2 M_{\alpha_2}(r, r)) = q_1 \beta(\alpha_1, r) + q_2 \beta(\alpha_2, r)$$

where $\rho(M)$ denotes the spectral radius of a matrix M . There is $T_0 > 0$, s.t. for all $T \in (0, T_0)$ this homogeneous population cannot be invaded by a bimorphic mutant strategy.

The proof of this theorem is rather technical and deferred to the appendix, see [Theorem B.5](#).

Remark 2.2. Even if $\beta(\alpha_1, r)$ and $\beta(\alpha_2, r)$ are unimodal functions, the linear combination $q_1 \beta(\alpha_1, r) + q_2 \beta(\alpha_2, r)$ may very well exhibit two (and, for non-generic examples, also many) local maxima. Therefore, even for seemingly well behaving examples, a periodically or stochastically changing environment may lead to multiple ESSs (note that an ESS is locally defined, i.e. an ESS is only stable against the immigration of mutants with a resembling phenotype, i.e. the parameters of the mutant are thought to be arbitrarily close to that of the resident; there may be mutants with distinctively dissimilar parameters that are able to invade). We may find, e.g. one colony of bacteria consisting of only one monomorphic genotype, and another colony only of another monomorphic genotype, and both genotypes are ESS. Generically we do not find two different genotypes within one colony, as members of two different ESSs will have different maximal Lyapunov exponents, i.e. one of the two genotypes will generically outcompete the other.

Also the proof of the following theorem, describing the situation for a slowly changing environment, can be found in the appendix, in [Proposition B.6](#) and [Corollary B.7](#).

Theorem 2.3. For T large, the zero order approximation of the Lyapunov exponent reads

$$\lambda_0 = E(\rho(M_{\alpha_t})) = q_1 \rho(M_{\alpha_1}) + q_2 \rho(M_{\alpha_2}).$$

There are bimorphic strategies that are able to invade all monomorphic strategies. A first order analysis reveals that an ESS, characterized by parameters r_1, r_2, ϵ_1 and ϵ_2 , is given by

$$r_1 = r_1^* + \mathcal{O}(1/T), \quad r_2 = r_2^* + \mathcal{O}(1/T),$$

$$\epsilon_1 = \frac{1}{q_1 T} + \mathcal{O}(1/T^2), \quad \epsilon_2 = \frac{1}{q_2 T} + \mathcal{O}(1/T^2),$$

where r_l^* maximizes the function $\beta(r, \alpha_l)$, $l=1,2$. That is, there is $T_1 > 0$ s.t. for all $T > T_1$ no monomorphic or bimorphic strategy is able to invade the bimorphic strategy with the parameters given, if the parameters of the invader are close enough to these values.

Remark 2.4. The proof of this theorem, in particular Eq. (B.3), has one more interesting consequence: let ρ_{ij} denotes the asymptotic, relative abundance of subtype i in environment α_j ; i.e. if we condition on environment α_j (artificially fix α_j for all times), then

ρ_{ij} denotes the asymptotic frequency of type i . We find

$$\rho_{2,1} = \frac{\epsilon_1}{\beta(r_1, \alpha_1) - \beta(r_2, \alpha_1)} + \mathcal{O}(1/T),$$

$$\rho_{1,2} = \frac{\epsilon_2}{\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2)} + \mathcal{O}(1/T).$$

The connection between the relative abundance and transition-rates $\epsilon_i \approx 1/(q_i T)$ allows growth rates $\beta(r_i, \alpha_j)$ and relative abundance ρ_{ij} to be connected with the average length of the time interval during which one environment prevails,

$$Tq_1 \approx (\rho_{2,1}(\beta(r_1, \alpha_1) - \beta(r_2, \alpha_1)))^{-1}, \quad Tq_2 \approx (\rho_{1,2}(\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2)))^{-1}.$$

2.3. Effect of finite population size

The result for very large T strongly depends on the assumption that population densities are appropriate to describe the population, i.e. that the population size is large. Single individuals are not visible in this analysis. In principle, a rare mutant needs an infinitely long time until it grows to recognizable size. For finite populations, this is no longer true – a rare mutant is able to take over within a finite time. If T is large, the competing mutant may only experience a single environment till takeover; in this case, the best phenotype is, of course, the one that is optimized for this environment. A trivial example is, e.g. recurrent glacial epochs: the time scale is so long that it does not pay to develop a bet-hedging strategy. Instead, species adapt to the environment genetically (Fig. 1).

Consequently, there is a threshold T_1 ; if the environment changes more rapidly ($T < T_1$), a monomorphic phenotype, optimized for the average environment, will develop. Above this threshold ($T > T_1$), we predict the appearance of a bimorphic phenotype. Furthermore, we expect a second threshold T_2 : if the fluctuation of the environment is slower ($T > T_2$), we again expect a monomorphic phenotype that is specialized to the current environment. Heuristically, the value T_2 can be determined if we know the equilibrium size of a successful resident population N , and the optimal growth rates for the two environments. We only present a heuristic calculation – the precise arguments require the introduction of a stochastic birth–death processes for the population dynamics, which is by far out of the scope of the present work. Nevertheless, we obtain some insight by these simplified computations.

The worst situation for a resident bet-hedger, and the best for a monomorphic mutant is given if the environment changes after a long time from α_2 to α_1 , say, and a monomorphic phenotype optimized to α_1 invades. If we define this instant as zero, $t=0$, the initial conditions for the mutant $s_0(0)$ (one individual), and the bet-hedger $s_1(0), s_2(0)$ (N individuals), read

$$s_0(0) = 1, \quad s_1(0) = \frac{N\epsilon_1}{\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2)},$$

$$s_2(0) = N \left(1 - \frac{\epsilon_1}{\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2)} \right).$$

Using the decoupled equations, we find that $u_0(t) = 1 \cdot e^{\beta(r_1, \alpha_1)t}$. Subpopulation $u_2(t)$ decreases exponentially fast and can be neglected. Subpopulation $u_1(t)$ is approximately given by

$$u_1(t) = \frac{N\epsilon_1}{\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2)} e^{(\beta(r_1, \alpha_1) - \epsilon_1)t}.$$

The appropriate subtype of the bet-hedger starts with a larger initial value, but increases slightly slower. The fraction of bet-hedgers in the complete population reads roughly

$$\frac{s_1}{s_0 + s_1 + s_2} = \frac{u_1}{u_0 + u_1 + u_2} \approx \frac{e^{-\epsilon_1 t}}{e^{-\epsilon_1 t} + (\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2)) / (\epsilon_1 N)}$$

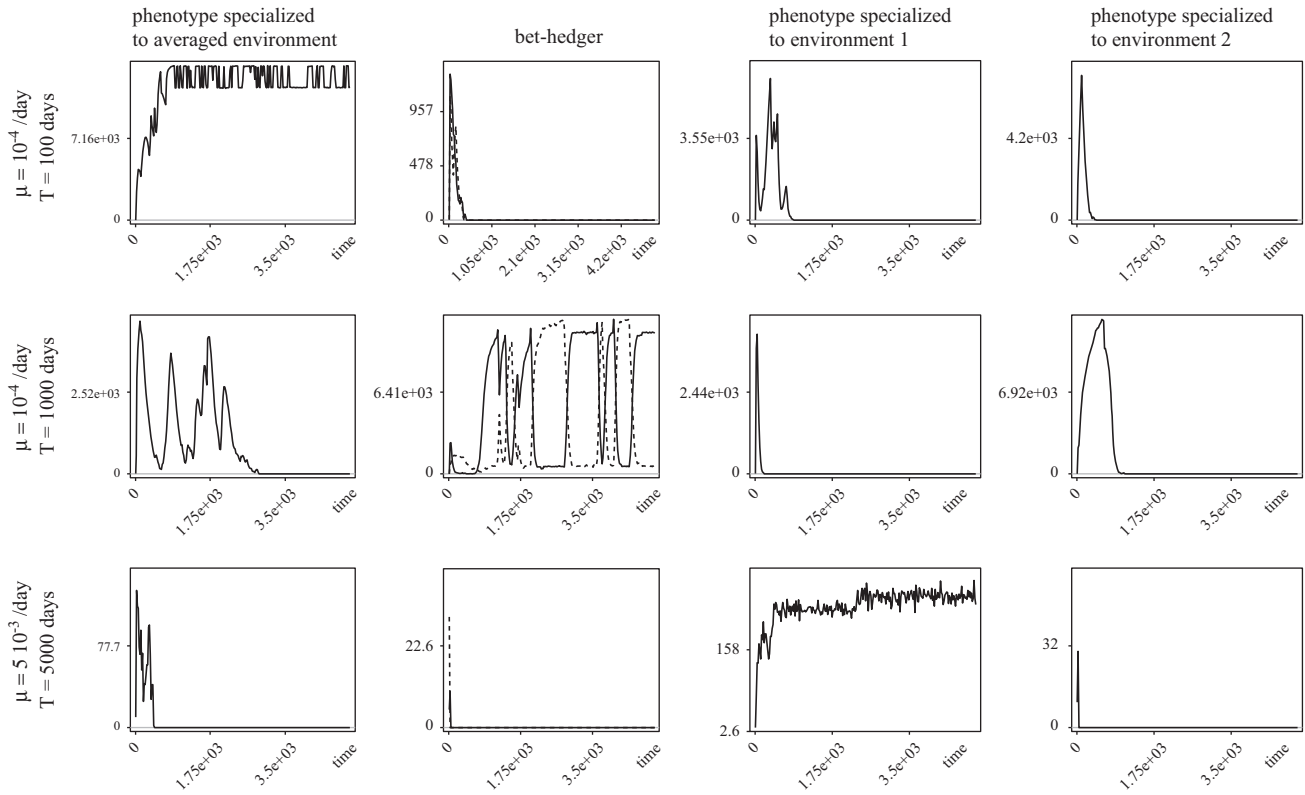


Fig. 1. Simulation of the stochastic model with four competing phenotypes (columns): specialized to the average environment, bet-hedger (one phenotypic type indicated by a solid, and the other by a dotted line), and the phenotypes specialized to environment one/two. The effect of different time scales for the environmental switching process is shown (rows); note that the population size is smaller for the last simulation. Details can be found in [Appendix C](#), in particular the meaning of parameter μ .

$$\approx \frac{\varepsilon_1 N}{(\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2))} e^{-\varepsilon_1 t}.$$

We know that $\varepsilon_1 = 1/(q_1 T)$ (up to higher order terms), and therefore

$$\frac{s_1}{s_0 + s_1 + s_2} \approx \frac{N}{q_1 T (\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2))} e^{-t/(q_1 T)}.$$

If this fraction drops below $1/N$, the resident dies out: here again, the assumption comes in that we have a finite population size, and one individual is the smallest possible population size – although we use differential equations. We find $s_1/(s_0 + s_1 + s_2) < 1/N$ is approximately equivalent with time t larger than time t_0 given by

$$t > t_0 = -q_1 T \log \left(\frac{N^2}{q_1 T (\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2))} \right).$$

The time τ_1 until the environment switches again is exponentially distributed with parameter $1/(q_1 T)$. The probability for $t > t_0$ at the time of the next switch reads

$$P(t_0 < \tau_1) = 1 - e^{-t_0/(q_1 T)} = 1 - \frac{N^2}{q_1 T (\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2))}.$$

This expression tends to one for $T \rightarrow \infty$. If T becomes large enough, the bet-hedger will be eventually outcompeted by a genotype that is solely adapted to the current environment. In this case, adaption to environments does not use the bet-hedging mechanism but the classical evolution/mutation mechanism that yields one monomorphic genotype that is optimally adapted to the current environment.

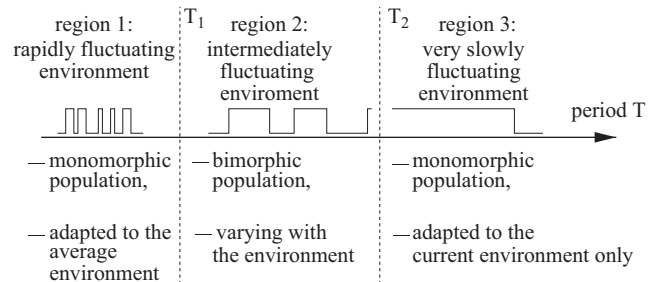


Fig. 2. Sketch of the situations for different fluctuation frequencies. T_1 and T_2 denote the periods that separate the three regimes.

3. Discussion

We discussed a model for bet-hedging in stochastically switching environments by means of adaptive dynamics. The main result is the observation that three different time scales for the switching of the environment lead to three different types of ESSs (see [Fig. 2](#)). In the rapidly switching regime, the best suited phenotype is adapted to the averaged environment. This finding is intuitive as in many cases it is too expensive to shift the complete population in a responsive way from one phenotype to another, following the environment fluctuating with a high frequency; instead, each individual cell experiences the average over the rapidly fluctuating influences. That is, the environment influences the growth rate via an (appropriately taken) mean. The advantage of bet-hedging is the fact that there is always a (small) number of individuals prepared to grow to large numbers if the environment changes. We are able to obtain some estimate, how large this fraction will be (of course after the environmental switch is long enough ago

s.t. the shift of phenotypes has had enough time to happen): this fraction can be computed as a function of the timing (average time one environment is present), and the difference of the growth-rate in the two phenotypical types. The advantage, to be able to grow the adapted type of the bimorphic population to the predominant type, can only be used if the current environment lasts long enough that this initially small subpopulation is able to grow to large numbers. In a rapidly changing environment this is not the case any more. If one thinks this argument is over, this observation yields the definition of a rapidly changing environment: consider a small, specialized population present in a frequency given by the non-dominant phenotype of an optimized bet-hedger. The reference time scale is the time required for this small population to grow to large numbers. If this time is larger than the time scale at which the environment changes, bet-hedging does not pay any more. Each phenotype encounters both environments. As a phenotype is not able to adapt its properties (this is our basic assumption), it has to cope with both environments in a reasonable way. The analysis of our model indicates that the growth rate in this case is given by an appropriate average over both environments. An averaged environment is equivalent to a constant environment; obviously, at least in the present setup, a monomorphic population performs best in a constant environment. However, even if for constant environment a unique ESS exists, in the rapidly fluctuating environment there may be two (or, for rather artificial examples, arbitrarily many) different ESSs. We may find isolated populations as colonies of bacteria in one of the ESSs, i.e. different local populations (clonal colonies) may consist of different genotypes. However, as residents of different ESSs will have different Lyapunov exponents, in a direct competition, there will be one winner. That is, although we expect to find local populations (colonies) that consist of different residents, we do not expect to find different genotypes within one local population (one colony).

If the environmental switching becomes slower, a bimorphic, bet-hedging phenotype turns into an ESS. Two different phenotypes appear, each adapted to one environment. They support each other by ensuring a minimal size of the other phenotypic state. This happens either by changing the type at a low rate or after cell division some daughter cells assume the other state than their mother cells had (Ratcliff and Denison, 2010).

According to Theorem 2.3, the optima for the phenotypic parameters r_i and the transition rates ε_i are asymptotically determined by two separated optimization problems. It is possible to connect two different tasks to the parameters $\beta(\cdot, \cdot)$ resp. ε_i : the parameters $\beta(\cdot, \cdot)$ represent the reproduction rate. This part is most likely tuned by the metabolism. It adapts to one of the two environments; the timing of the environments is, at this point, not of importance. The second part of the parameters are the transition rates ε_i . These rates are, in contrast to the reproduction rates, only influenced by the timing of the environment. The kind of environment (or, equivalently, the size of the reproduction rate allowed by the environment) does not influence the transition rates. This is, there are two different aspects of the environments: their properties and their timing. These two separated parts are addressed by separated rates: the reproduction rates and the transition rates. A cell may adapt to a different timing in only adjusting the transition rates. The core metabolism and cell cycle that determine the reproduction rate needs not to be redesigned.

If the frequency becomes even lower, a bet-hedging strategy does not pay any more. In the time window after a switch of the environment, a specialized phenotype, adapted to the current environment, is able to take over. Thinking of glacial ages, the results for this third region are very intuitive. However, they are only based on heuristic arguments and deserve a strict mathematical investigation. It may very well be that other aspects are of

similar importance. For instance, if the time scale becomes large, the transition rates become small. If the population is finite, this leads to the fact that there is not continuously a certain percentage of the “wrong” type present, but that only from time to time the “wrong” type appears. Is this the case, the bet-hedging strategy is basically inapplicable.

Svardal et al. (2011) note that only the invariant measure of the environmental states matters to determine if genetic polymorphism evolves, but not possible autocorrelations. I.e., only the fraction of time that an environment spends in a certain state is of importance, but not the timing (fast or slow fluctuations). This is different in the present case: the timing of the environmental changes is crucial to determine if bet-hedging forms an ESS. The fundamental difference between the two papers is the fact that Svardal et al. consider faithfully reproducing genotypes, where the phenotype distribution is fully determined by the genotype. Given the genotype, no further dynamics in phenotypes take place. This assumption is reasonable for many situations, in particular for seed banks. In this case, one can prove that the timing of the environment does not influence the optimal genotype distribution. In the present case, however, the performance of the population distinctively depends not only on the genotype but also on the ratio of the phenotypes. This ratio changes in time, even if the genotype is fixed – when the environment switches, the population needs time until it has re-structured and the dominating phenotype changes to the one which is better adapted to the environment: this change is mainly due to reproduction, and not to switching of individuals. Therefore, not only the invariant measure but also the timing of the stochastic process governing the environment matters in our case of bet-hedging.

Of course, the present study suffers from the fundamental shortcomings of all comparable approaches: the phenotypes to compare are only some from an unlimited number of possible phenotypes. We neglected e.g. that bet-hedging does not exclude the concurrent existence of additional responsive elements in the decision pathway in one or both switch direction(s), affecting the ε_1 and/or ε_2 in response to an environmental change. Another effect to investigate is the fact that bacteria actively change the environment, either deliberately to “engineer” the environment (the usage of exoenzymes is an example), or as a side-product of their metabolism (think of alcohol in wine). The theoretical approaches considered so far only scratched the surface of an interesting, but complex process; non-constant environments will play a central role in most of the more realistic scenarios, and hence also the possibility for phenotypic multi-state strategies.

Interestingly enough, there are experimental validations for the predictions developed theoretically in recent years. Beaumont et al. (2009), and Rainey et al. (2011) report an experiment, where a *Pseudomonas fluorescens* that originally did not show bet-hedging phenotypes have been put in an environment periodically switching between static (colonies grow on gel) and shaken batch cultures (glass microcosms). Only few cells have been taken from static to the shaken environment, representing a kind of bottleneck. Some of the replicas indeed developed a bet-hedging phenotype. This experiment is at least a hint that the theory developed in other papers and also here indeed describes relevant mechanisms present in nature. However, it is more difficult to show these effects *in vivo*, as e.g. Wiklund et al. tried Wiklund and Friberg (2011) in a study about the hibernation behavior of a butterfly (*Pararge aegeria*) or Simons (2009) who considered timing of germination in *Lobelia inflata* (Indian tobacco). Both species live in a periodic environment (seasons). The butterflies exhibit two clearly distinct hibernation strategies that can be interpreted as bet-hedging. In a five year experiment, Simons observed a dependency of the fitness of seeds under fluctuating environmental conditions in the field on the diversification of

germination time, measured by standard deviation of the mean time of germination, which fits to theoretical bet-hedging predictions. However, in this case it is difficult to tell if this finding can be accounted to a bet-hedging strategy as defined e.g. by de Jong et al. (2011), or may at least partly be interfered by e.g. aspects of genotype variation.

Appendix A. Switching system

A.1. Problem formulation

Assumptions. Let $M_l \in \mathbb{R}^{2 \times 2}$, $l=1,2$, denote M -matrices with positive off-diagonal elements (irreducibility of $\exp(M_l)$), and α_t a $\{1,2\}$ -valued Markov process: the waiting times between jumps from state one to two (from two to one) of α_t are exponentially distributed; let us assume that the parameters of these distributions are $1/(Tq_l)$, where $l \in \{1,2\}$, and $q_1 + q_2 = 1$. Consider the differential equation

$$x' = M_{\alpha_t} x, \quad x(0) = x_0 \tag{A.1}$$

where x_0 is non-negative and non-zero. The long term behavior will be exponential growth, this is, there is a Lyapunov exponent $\lambda \in \mathbb{R}$ s.t.

$$e^{-\lambda t} x(t) = \mathcal{O}(1) \quad a.s.$$

For a nice introduction to Lyapunov coefficients see e.g. Arnold and Wihstutz (1986), Arnold and Kloeden (1989). To keep the proof simple, we assume generic conditions: The Perron eigenvalues as well as the Perron eigenvectors of M_1 and M_2 are different.

Theorem A.1. For $T \rightarrow 0$, we find for the maximal Lyapunov exponent λ_0 that

$$\lambda_0 = \rho(E(M_\alpha)) = \rho(q_1 M_1 + q_2 M_2)$$

while for $T \rightarrow \infty$, we have

$$\lambda_0 = E(\rho(M_\alpha)) = q_1 \rho(M_1) + q_2 \rho(M_2)$$

where $\rho(\cdot)$ denotes the spectral radius of a matrix. The first order approximation in this case reads

$$\begin{aligned} \lambda_0 = E(\rho(M_\alpha)) &= q_1 \rho(M_1) + q_2 \rho(M_2) \\ &+ \frac{1}{T} \ln \left[\delta_1^{-1} \delta_2^{-1} \{ -\lambda_{-,1} \delta_2 + [-\lambda_{-,2} \mathbf{e}^T M_1 + \mathbf{e}^T M_2 M_1] \} \begin{pmatrix} \psi_2 \\ 1 - \psi_2 \end{pmatrix} \right] \\ &+ \mathcal{O}(T^{-2}) \end{aligned}$$

where $\lambda_{\pm,l}$ are the larger (“+”) and the smaller (“−”) eigenvalues for M_l , $\delta_l = \lambda_{+,l} - \lambda_{-,l}$, $\mathbf{e} = (1, 1)^T$, and $(\psi_2, 1 - \psi_2)^T$ is the Perron right eigenvector for M_2 with normalized l_1 -norm.

The proof of this theorem requires several considerations. We start with a time-discrete Markov chain, related to this problem.

A.2. Idea

Remark A.2. If the diagonal elements of M_l are non-positive, add cI to both matrices (same $c > 0$), s.t. M_l become strictly positive. Then, $x(t)$ is multiplied by e^{ct} ; this exponential growth can be easily corrected. This is, we only need to prove our theorem for strictly positive matrices M_l .

Construction of an embedded Markov chain: Before we consider the ODE directly, we define an embedded time-discrete system: Let $y_0 = x(0)$, and $\{t_i\}_{i \in \mathbb{N}}$ denote the switching times. This is, $\tau_{2i} = t_{2i} - t_{2i-1}$ are exponentially distributed with expectation $q_1 T$, say, and $\tau_{2i+1} = t_{2i+1} - t_{2i}$ are exponentially distributed with

expectation $q_2 T$. Let $y_{i+1} = e^{M_2 \tau_{2i}} e^{M_1 \tau_{2i+1}} y_i$. Then, $y_i = x(t_{2i})$. This Markov process inherits most of the information about the original time-continuous process, especially w.r.t. convergence properties: let \mathbf{e}_l denote the l 'th unit vector, and $\mathbf{e} = (1, 1)^T$. Define

$$\phi_i = \mathbf{e}_1^T y_i / \mathbf{e}^T y_i.$$

The matrices M_1 and M_2 as well as y_0 are positive, thus $\phi_i \in [0, 1]$. y_i is determined by ϕ_i and $\mathbf{e}^T y_i$, as $y_i = (\mathbf{e}^T y_i)(\phi_i, 1 - \phi_i)^T$. Thus, $y_{i+1} = B y_i = (\mathbf{e}^T y_i) B(\phi_i, 1 - \phi_i)^T$ for some linear random operator $B = e^{M_2 \tau_2} e^{M_1 \tau_1}$, and

$$\phi_{i+1} = \frac{\mathbf{e}_1^T e^{M_2 \tau_{2i}} e^{M_1 \tau_{2i+1}} y_i}{\mathbf{e}^T e^{M_2 \tau_{2i}} e^{M_1 \tau_{2i+1}} y_i} = \frac{\mathbf{e}_1^T e^{M_2 \tau_{2i}} e^{M_1 \tau_{2i+1}} (\phi_i, 1 - \phi_i)^T}{\mathbf{e}^T e^{M_2 \tau_{2i}} e^{M_1 \tau_{2i+1}} (\phi_i, 1 - \phi_i)^T} =: F(\tau_{2i}, \tau_{2i+1}; \phi_i) \tag{A.2}$$

Note that this projection of vectors is also used in Kloeden and Kozyakin (2013a,b) to establish random attractors for tridiagonal Markov chains. Due to the linearity of the structure, we obtain a well-defined Markov process for the directions ϕ_i . The exponential growth factor for one step starting with direction ψ , and given τ_1, τ_2 reads as $r(\psi, \tau_1, \tau_2) = \mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} (\psi, 1 - \psi)^T$. Let $(\phi_n, \tau_1^{(n)}, \tau_2^{(n)})$ denote the Markov chain consisting of the three components: direction of the vector at the beginning of step n , and resident times in state one resp. state two during time step n . The growth rate is given as

$$\begin{aligned} \lambda_0 &= \lim_{n \rightarrow \infty} \frac{\ln[\prod_{i=1}^n (\mathbf{e}^T e^{M_2 \tau_2^{(i)}} e^{M_1 \tau_1^{(i)}} (\phi_i, 1 - \phi_i)^T)]}{\sum_{i=1}^n (\tau_1^{(i)} + \tau_2^{(i)})} \\ &= \lim_{n \rightarrow \infty} \frac{\frac{1}{n} \sum_{i=1}^n \ln(\mathbf{e}^T e^{M_2 \tau_2^{(i)}} e^{M_1 \tau_1^{(i)}} (\phi_i, 1 - \phi_i)^T)}{\frac{1}{n} \sum_{i=1}^n (\tau_1^{(i)} + \tau_2^{(i)})}. \end{aligned}$$

Note that $\phi_i, \tau_1^{(i)}, \tau_2^{(i)}$ are independent random variables (ϕ_i depends on the $\tau_l^{(j)}$ only for $j < i$). We obtain the following proposition.

Corollary A.3. If the Markov chain for ϕ_n is ergodic, we find the Lyapunov exponent determined by

$$\lambda_0 = \frac{E \ln(\mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} (\psi, 1 - \psi)^T)}{E(\tau_1) + E(\tau_2)}$$

where the expectation is taken w.r.t. the invariant measure of (ψ, τ_1, τ_2) .

The aim of the following considerations is first of all to establish an exponentially rapid convergence to the invariant measure, i.e. the ergodicity of the Markov chain. In the next step we determine the limit of the invariant measure for T being small resp. large. Finally, we work out the asymptotics for the Lyapunov exponent itself.

A.3. Elementary properties of the random functions F_i

F can be considered as the composition of two random functions,

$$F(\tau_{2i}, \tau_{2i+1}; \phi_i) = F_1(\tau_{2i}; F_2(\tau_{2i+1}; \phi_i))$$

where

$$F_l(\tau; \psi) = \frac{\mathbf{e}_l^T e^{M_l \tau} (\psi, 1 - \psi)^T}{\mathbf{e}^T e^{M_l \tau} (\psi, 1 - \psi)^T}.$$

To simplify notations, we define that $[a, b]$ is always to read as $[\min\{a, b\}, \max\{a, b\}]$. That is, $[1, 0]$ is to read as the interval $[0, 1]$. Let y_l be the Perron-eigenvectors of M_l , and $\psi_l = \mathbf{e}_l^T y_l / \mathbf{e}^T y_l$. Without restriction, $\psi_1 < \psi_2$.

Proposition A.4. Let $\lambda_{\pm,l}$ be the eigenvalues of M_l , $\lambda_{+,l} > \lambda_{-,l}$. Define $\delta_l = \lambda_{+,l} - \lambda_{-,l}$, $\eta_l = \exp(-\delta_l \tau_l)$, and $\zeta_l = -\lambda_{+,l}/\lambda_{-,l}$. Then,

$$F_l(\tau; \psi) = \frac{(-\lambda_{-,l})(\zeta_l \eta_l + 1)\psi + (1-\eta_l)\mathbf{e}_1^T M_l(\psi, 1-\psi)^T}{(-\lambda_{-,l})(\zeta_l \eta_l + 1) + (1-\eta_l)\mathbf{e}^T M_l(\psi, 1-\psi)^T}$$

The probability density of the random variable $F_l(\tau; \psi)$, given a fixed (deterministic) $\psi \in [0, 1]$, reads

$$\varphi_{l;\psi}(x) = \vartheta_l (F_l^{-1}(x; \psi))^{\vartheta_l - 1} \left| \frac{d}{dx} F_l^{-1}(x; \psi) \right|$$

where $\vartheta_l = 1/(q_l T \delta_l)$.

Proof. We use the representation $e^{M_l \tau} = \alpha_l(\tau)I + \beta_l(\tau)M_l$ where

$$\alpha_l(\tau) = \frac{(\lambda_{+,l} e^{\lambda_{+,l} \tau} - \lambda_{-,l} e^{\lambda_{-,l} \tau})}{(\lambda_{+,l} - \lambda_{-,l})}, \quad \beta_l(\tau) = \frac{(e^{\lambda_{+,l} \tau} - e^{\lambda_{-,l} \tau})}{(\lambda_{+,l} - \lambda_{-,l})}$$

Note that Perron–Frobenius theory tells us that $\lambda_{+,l} > \lambda_{-,l}$ s.t. $\alpha_l(\tau)$, $\beta_l(\tau)$ are well-defined. Define $\delta_l = \lambda_{+,l} - \lambda_{-,l}$, $\eta_l = \exp(-\delta_l \tau_l)$, and $\zeta_l = -\lambda_{+,l}/\lambda_{-,l}$. Then,

$$\alpha_l(\tau_l) = e^{\lambda_{+,l} \tau_l} (-\lambda_{-,l})(\zeta_l \eta_l + 1) / \delta_l, \quad \beta_l(\tau_l) = e^{\lambda_{+,l} \tau_l} (1 - \eta_l) / \delta_l$$

and

$$F_l(\tau; \psi) = \frac{(-\lambda_{-,l})(\zeta_l \eta_l + 1)\psi + (1-\eta_l)\mathbf{e}_1^T M_l(\psi, 1-\psi)^T}{(-\lambda_{-,l})(\zeta_l \eta_l + 1) + (1-\eta_l)\mathbf{e}^T M_l(\psi, 1-\psi)^T}$$

This is, we can view the result of the random function not as a map that acts on ψ but as a map that acts on the random variable η_l , where ψ is a (by now: deterministic) parameter. This point of view allows to derive the probability density $\varphi_{l;\psi}(x)$ of the random variable $F_l(\eta_l, \psi)$. The inverse of $y = F_l(\eta_l, \psi)$, given ψ , reads

$$F_l^{-1}(y; \psi) = \frac{[(-\lambda_{-,l})\psi + \mathbf{e}_1^T M_l(\psi, 1-\psi)^T] - y[(-\lambda_{-,l}) + \mathbf{e}^T M_l(\psi, 1-\psi)^T]}{y[(-\lambda_{-,l})\zeta_l - \mathbf{e}^T M_l(\psi, 1-\psi)^T] - [\psi(-\lambda_{-,l})\zeta_l - \mathbf{e}_1^T M_l(\psi, 1-\psi)^T]}$$

Let X be exponentially distributed with expectation qT , $\eta = \exp(-\delta X)$. Then,

$$P(\eta < x) = P(X > -\ln(x)/\delta) = \int_{-\ln(x)/\delta}^{\infty} (qT)^{-1} e^{-t/(qT)} dt = x^{qT/\delta}$$

The density reads $\vartheta x^{\vartheta-1}$ where $\vartheta = 1/(qT\delta)$, which is a beta($\vartheta, 1$) distribution.

Therefore, the distribution of $F_l(\tau; \psi)$ is given by

$$\varphi_{l;\psi}(x) = \vartheta_l (F_l^{-1}(x; \psi))^{\vartheta_l - 1} \left| \frac{d}{dx} F_l^{-1}(x; \psi) \right|$$

and $\vartheta_l = 1/(q_l T \delta_l)$. \square

Remark A.5. (1) The function $\varphi_{l;\psi}$ is $C^\infty(\psi, \psi_l)$,

$\text{supp}(\varphi_{l;\psi}) \subseteq [\psi, \psi_l]$

where the function is strictly bounded away from zero in the interval $[\psi, \psi_l]$ for $\vartheta_l \leq 1$; in case of $\vartheta_l > 1$, the function possesses a zero of order $\vartheta_l - 1$ at ψ_l .

(2) On the support of $\varphi_\psi(x)$, the derivative $F_x(x; \psi)$ is bounded and bounded away from zero, uniformly in x and ψ .

Proposition A.6. If ψ_l is the projection of the Perron eigenvector of M_l , then there exists a $C > 0$ s.t. for $x \in [\psi, \psi_l]$ one has

$$1 - (\psi - x) / (\psi - \psi_l) \geq F_l^{-1}(x; \psi) \geq 1 - C(\psi - x) / (\psi - \psi_l).$$

Proof. The function $F_l(x; \psi)$ is convex in x ; additionally, we know $F_l(1; \psi) = \psi$ and $F_l(0; \psi) = \psi_l$, which yields

$$F_l(x; \psi) \geq x\psi + (1-x)\psi_l.$$

Furthermore,

$$\frac{d}{d\eta} \left(\frac{(-\lambda_{-,l})(\zeta_l \eta + 1)\psi + (1-\eta)\mathbf{e}_1^T M_l(\psi, 1-\psi)^T}{(-\lambda_{-,l})(\zeta_l \eta + 1) + (1-\eta)\mathbf{e}^T M_l(\psi, 1-\psi)^T} \right) \Big|_{\eta=1} = 1$$

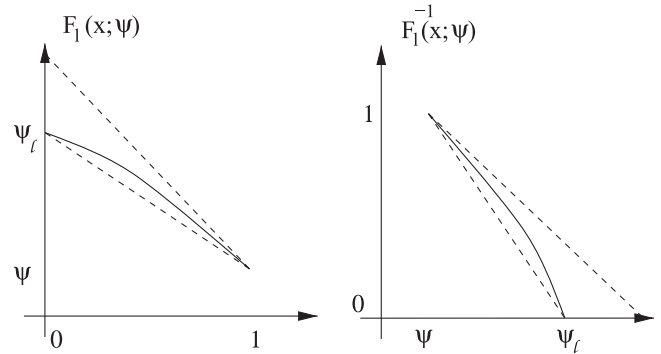


Fig. A1. Estimation of $F_l(x; \psi)$.

$$\begin{aligned} &= \frac{-(1-\psi)(-\lambda_{-,l})\zeta_l + \mathbf{e}_1^T M_l(\psi, 1-\psi)^T}{(-\lambda_{-,l})(\zeta_l + 1)} \\ &= \frac{-(1-\psi_l + \psi_l - \psi)\lambda_{+,l} + \mathbf{e}_1^T M_l(\psi_l + \psi - \psi_l, 1 - \psi_l + \psi_l - \psi)^T}{\lambda_{+,l} + |\lambda_{-,l}|} \\ &= \frac{(\psi - \psi_l)\lambda_{+,l} + \mathbf{e}_1^T M_l(1, -1)^T (\psi - \psi_l)}{\lambda_{+,l} + |\lambda_{-,l}|} = (\psi - \psi_l) / \hat{\alpha}_l \end{aligned}$$

and hence $F_l(x; \psi) \leq \psi + x(\psi - \psi_l) / \hat{\alpha}_l$ (see Fig. A1). This observation implies for the inverse function the inequality

$$(x - \psi_l) / (\psi - \psi_l) \geq F_l^{-1}(x; \psi) \geq 1 - C(\psi - x) / (\psi - \psi_l) \quad \text{for } x \in [\psi, \psi_l] \quad \square$$

Corollary A.7. The distribution $\varphi_{l;\psi}$ is $C^\infty[\psi, \psi_l]$, has the support $[\psi, \psi_l]$ and the local behavior $(x - \psi_l)^{\vartheta_l - 1}$ close to ψ_l (within its support). In case of $\vartheta_l \geq 1$, $\varphi_{l;\psi}|_{[\psi, \psi_l]}$ is uniformly (in ψ and x) bounded away from zero. In case of $\vartheta_l < 1$, the density is uniformly bounded away from zero (in x and ψ) on closed subsets of $[\psi, \psi_l]$.

A.4. Convergence results

We first show that $[\psi_1, \psi_2]$ is an absorbing set that attracts the chain exponentially fast. In a second step we will focus on the dynamics within this absorbing set.

Proposition A.8. The set $[\psi_1, \psi_2]$ is absorbing for the Markov chain, and attracts the Markov chain exponentially fast: let $(\phi_n)_{n \in \mathbb{N}}$ be the Markov chain, then there is $c > 0$ s.t. $P(\phi_n \notin [\psi_1, \psi_2]) \leq Ce^{-cn}$.

Proof. The set $[\psi_1, \psi_2]$ is absorbing as $\text{supp}(\varphi_{l;\psi}) \subseteq [\psi, \psi_l]$. Let $\psi \notin [\psi_1, \psi_2]$ and $\delta = |\psi_1 - \psi_2|/2$. The function $\psi \mapsto \int_{\psi_1 - \delta}^{\psi_1 + \delta} \varphi_{1;\psi}(x) dx$ is continuous and strictly positive; thus, the integral is uniformly bounded away from zero. Furthermore, $\int_{\psi_1}^{\psi_2} \varphi_{2;\psi}(x) dx > \varepsilon_2 > 0$ for $\psi' \in [\psi_1 - \delta, \psi_1 + \delta] \cap [0, 1]$. These two observations imply for the Markov chain $(\phi_i)_{i \in \mathbb{N}}$ that

$$P(\phi_{i+1} \in [\psi_1, \psi_2]) = \int_{\psi_1}^{\psi_2} \varphi_{\phi_i}(x) dx > \varepsilon > 0$$

where ε is independent on ϕ_i . As $[\psi_1, \psi_2]$ is invariant, we find

$$\begin{aligned} P(\phi_i \notin [\psi_1, \psi_2]) &= P(\phi_i \notin [\psi_1, \psi_2] | \phi_{i-1} \in [\psi_1, \psi_2]) P(\phi_{i-1} \in [\psi_1, \psi_2]) \\ &\quad + P(\phi_i \notin [\psi_1, \psi_2] | \phi_{i-1} \notin [\psi_1, \psi_2]) P(\phi_{i-1} \notin [\psi_1, \psi_2]) \\ &= (1 - P(\phi_i \in [\psi_1, \psi_2] | \phi_{i-1} \in [\psi_1, \psi_2])) P(\phi_{i-1} \in [\psi_1, \psi_2]) \\ &\leq (1 - \varepsilon) P(\phi_{i-1} \in [\psi_1, \psi_2]) \end{aligned}$$

With $c = -\ln(1 - \varepsilon)$ we obtain $P(\phi_i \notin [\psi_1, \psi_2]) \leq e^{-ci}$. \square

For convenience of the reader we recall a criterion for compactness of integral operators (stated in Dunford and Schwartz, 1958, Problem 54, Chapter VI) resp. the dominance of the Perron-eigenvalue (Marek, 1970, Theorems 2.2 and 2.3).

Proposition A.9. If a function $k : [a, b]^2 \rightarrow \mathbb{R}$ is measurable and satisfies

$$\text{ess sup}_{x \in (a,b)} \int_a^b |k(x,y)| dy \leq M, \quad \text{ess sup}_{y \in (a,b)} \int_a^b |k(x,y)| dx \leq M,$$

then the integral operator $T : L^1(a, b) \rightarrow L^1(a, b)$, $Tu(x) = \int_a^b k(x, y) u(y) dy$ is compact.

In order to quote the theorem about the dominance of the spectral radius, we start off with some notation and definitions: a pointed cone in a real Banach space X is a set $K \neq \emptyset$ s.t. $K + K \subseteq K$, $\lambda K \subseteq K$ for $\lambda \geq 0$, and $K \cap (-K) = \{0\}$. The dual cone K' consist of all linear functionals $x' : X \rightarrow \mathbb{R}$ for that $x'K \subseteq [0, \infty)$. An operator T in X is called strictly non-supporting if for each $x \in K$, $x \neq 0$, there is a number $n = n(x)$ s.t. for all $x' \in K'$, $x' \neq 0$, we have $\langle x', T^n x \rangle \geq 0$. We use $X = L^1(0, 1)$ and $K = \{f \in L^1(0, 1) | f \geq 0\}$. In this situation, the following result holds (Marek, 1970, Theorems 2.2 and 2.3).

Theorem A.10. If $A : L^1(0, 1) \rightarrow L^1(0, 1)$ is a compact, linear, positive, and strictly non-supporting operator, then

- (1) the spectral radius $\rho(A)$ is a simple eigenvalue of A with non-negative eigenfunction,
- (2) there is no other non-negative eigenfunction,
- (3) the absolute value of all other eigenvalues λ of A is strictly smaller than the spectral radius, $|\lambda| < \rho(A)$.

We apply these two results to our situation.

Proposition A.11. The operator $S_l : L^1(0, 1) \rightarrow L^1(0, 1)$ given by

$$S_l u(x) = \int_0^a \varphi_{l,\psi}(x) u(\psi) d\psi$$

is compact.

Proof. As $\varphi_{l,\psi}(x)$ is the density of a random variable, we have $\int_0^1 \varphi_{l,\psi}(x) dx = 1$. Now, $|\int_0^1 \varphi_{l,\psi}(x) d\psi| = |\int_x^{\psi_l} \varphi_{l,\psi}(x) d\psi|$ and, due to the estimates derived above and due to the fact that $|(d/dx) F_l^{-1}(x; \psi)|$ is bounded, we have

$$c \int_x^{\psi_l} \left(\frac{x-\psi_l}{\psi-\psi_l} \right)^{\theta_l-1} d\psi \geq |\int_x^{\psi_l} \varphi_{l,\psi}(x) d\psi| \geq 0$$

The integrand of the l.h. integral becomes singular in case of $x \rightarrow \psi_l$ and $\theta_l \in (0, 1)$ (the only case for that the integral may become infinite). Since

$$c \int_x^{\psi_l} \left| \frac{\psi_l-x}{\psi-\psi_l} \right|^{\theta_l-1} d\psi = \frac{c}{2-\theta_l} |\psi_l-x|^{\theta_l-1} |\psi-\psi_l|^{2-\theta_l} \Big|_x^{\psi_l} = \frac{c}{2-\theta_l} |\psi_l-x|$$

we conclude $\int_0^1 \varphi_{l,\psi}(x) d\psi \leq M$ for some constant M , and thus the integral operator S_l is compact. \square

Corollary A.12. The Perron operator $S : L^1(0, 1) \rightarrow L^1(0, 1)$ of the Markov chain, given by $S = S_2 \circ S_1$, is compact.

Proposition A.13. The integral operator S restricted to function on the absorbing region, $\tilde{T}S = S|_{L^1(\psi_1, \psi_2)}$, satisfies the conditions of Theorem A.10.

Proof. \tilde{S} is bounded, positive, and compact. It remains to show that \tilde{S} is strictly non-supporting. As $\tilde{S}u(x) = \int_{\psi_1}^{\psi_2} \varphi_{\psi}(x) u(\psi) d\psi$, and $\varphi_{\psi}(x)$ is zero only for $x \in \{\psi_1, \psi_2\}$ and $\theta_l \geq 1$, a non-zero, non-negative function u is mapped to a function $\tilde{T}u$ with a positive measure on every set in $[\psi_1, \psi_2]$ with positive measure. Therefore, \tilde{S} is strictly supporting. \square

Notation: The function $\varphi_{\psi} : [\psi_1, \psi_2] \rightarrow \mathbb{R}$ denotes the kernel of the integral operator \tilde{S} .

Corollary A.14. There is a unique non-negative eigenfunction $\pi(x)$ of \tilde{S} corresponding to the eigenvalue 1 with $\|\pi\|_{L^1} = 1$. If one extends π to $[0, 1]$ by $\pi(x) = 0$ for $x \notin [\psi_1, \psi_2]$ and $f \in K$ satisfies $\|f\|_{L^1(0,1)} = 1$, then there are constants $c, C > 0$ s.t.

$$\|S^n f - \pi\|_{L^1(0,1)} \leq C e^{-cn}.$$

A.5. Asymptotic expansion of the invariant measure

Proposition A.15. If T large, we find that

$$\varphi_{\psi}(x) \rightarrow \delta_{\psi_2}(x)$$

in probability for $T \rightarrow \infty$.

Proof. Let ϕ_i be a sample of $\pi(\cdot)$ and $\phi_{i+1} = F(\tau_1, \tau_2; \phi_i)$. Given any direction ψ , the vector $e^{M_2 \tau_2}(\psi, 1-\psi)$ approaches the Perron-eigendirection indicated by ψ_2 for $\tau_2 \rightarrow \infty$. We find

$$\lim_{T \rightarrow \infty} \int_{\psi_1}^{\psi_2-\varepsilon} \varphi_{l;\psi}(x) dx \rightarrow 0$$

uniformly for $\psi \in [\psi_1, \psi_2]$. As any realization of ϕ_{i+1} is in $[\psi_1, \psi_2]$ a.s., we find independent of the realization ϕ_i that

$$P(\phi_{i+1} \in [\psi_2 - \varepsilon, \psi_2 + \varepsilon]) = 1 - P(\phi_{i+1} < \psi_2 - \varepsilon) \rightarrow 1. \quad \square$$

Corollary A.16. The unique invariant distribution $\pi(x)$ tends weakly to $\delta_{\psi_2}(x)$ for $T \rightarrow \infty$.

Remark A.17. We started with a time-continuous switching system, and jumped to the embedded time-discrete Markov chain, represented by the integral operators S resp. \tilde{S} . In order to work out the invariant measure of \tilde{S} , we now return to the time-continuous process. Given that at (continuous) time t , we apply matrix M_l , $l=1$ or $l=2$, we have

$$\psi(t) = \left(\frac{e^{M_1 t}(\psi(0), 1-\psi(0))^T}{e^T e^{M_1 t}(\psi(0), 1-\psi(0))^T} \right)$$

and a direct computation shows that $\psi(t)$ satisfies an ODE

$$\frac{d}{dt} \psi(t) = e^T \frac{d}{dt} \left(\frac{e^{M_1 t}(\psi(0), 1-\psi(0))^T}{e^T e^{M_1 t}(\psi(0), 1-\psi(0))^T} \right) = (e^T - \psi e^T) M_l \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix} =: f_l(\psi).$$

This means that without switching, the probability distribution $u^{(l)}(t, \psi)$ to find the system in direction ψ with the matrix M_l being active, is just transported with velocity $f_l(\psi)$. We thus obtain $\partial_t u^{(l)}(t, \psi) + \partial_{\psi}(f_l(\psi) u^{(l)}(t, \psi)) = 0$. Switching introduces jumps between the states (apply matrix one/matrix two). As the time intervals between the jumps are distributed according to an exponential distribution with rate $\mu_l = 1/(q_l T)$, we find the correlated random walk system (Othmer and Stevens, 1997; Haderler, 1999; Müller et al., 2008)

$$\begin{aligned} \partial_t u^{(1)}(t, \psi) + \partial_{\psi}(f_1(\psi) u^{(1)}(t, \psi)) &= -\mu_1 u^{(1)} + \mu_2 u^{(2)} \\ \partial_t u^{(2)}(t, \psi) + \partial_{\psi}(f_2(\psi) u^{(2)}(t, \psi)) &= \mu_1 u^{(1)} - \mu_2 u^{(2)} \end{aligned} \tag{A.3}$$

Here, we use the projection of the linear ODE $x' = M_{\alpha_t} x$ to the simplex with l^1 -norm one, as described e.g. in Haderler (1992), and then formulate the correlated random walk for the density of $x(t)$. The invariant measure of the embedded time-discrete system describes the probability distribution of a stationary state jumping from state 2 to state 1.

The following considerations closely follow Müller et al. (2008).

Corollary A.18. The invariant measure $\pi(\psi)$ of operator \tilde{T} is given by $u^{(2)}$ -component of the stationary state of (A.3), normalized to one,

$$\pi(\psi) = \frac{u^{(2)}(\psi)}{\int_{\psi_1}^{\psi_2} u^{(2)}(\psi') d\psi'}$$

Before investigating this representation of $\pi(x)$, we state a proposition about $f_1(\psi)$.

Proposition A.19. If $A \in \mathbb{R}^{2 \times 2}$ is a non-negative, irreducible matrix, and

$$f : [0, 1] \rightarrow \mathbb{R}, \quad \psi \mapsto (\mathbf{e}_1^T - \psi \mathbf{e}^T) A \begin{pmatrix} \psi \\ 1 - \psi \end{pmatrix},$$

then $f(\psi) = 0$ has exactly one solution $\hat{\psi}$ in $[0, 1]$ and $(\hat{\psi}, 1 - \hat{\psi})^T$ is the Perron-eigenvector of A . Furthermore, $f'(\hat{\psi}) = -\rho(A) + (\mathbf{e}_1^T - \hat{\psi} \mathbf{e}^T) A (1, -1)^T < 0$.

Proof. If $\hat{\psi}$ is the first component of the Perron-eigenvector with l^1 -norm one, a direct computation shows that $f(\hat{\psi}) = 0$. This computation can be also used to show that a solution of $f(\psi) = 0$ corresponds to an eigenvector. As any value $\psi \in [0, 1]$ corresponds to a non-negative vector, the theorem of Perron–Frobenius yields the uniqueness result. The derivative of $f(\hat{\psi})$ can be directly computed. As $f(0) > 0$, it is $f'(\hat{\psi}) \leq 0$. As $f(\psi)$ is quadratic in ψ , the only chance for $f'(\hat{\psi}) = 0$ is that $\hat{\psi}$ is a double zero. This in turn implies that $f(1) = a_{1,1} - a_{1,1} - a_{2,1} > 0$, and hence $a_{2,1} < 0$ in contradiction to the assumption that A is non-negative and irreducible. \square

Proposition A.20. If ψ^* is given by the direction of the eigenvalue of $q_1 M_1 + q_2 M_2$, then the invariant measure π of \tilde{T} approximates weakly a point mass at ψ^* for $T \rightarrow 0$.

Proof. We first find that the flow $j = f_1(\psi)u^{(1)}(\psi) + f_2(\psi)u^{(2)}(\psi)$ is zero for the stationary solution of the system. This observation allows to eliminate $u^{(1)}(x)$ from the ODE describing $f_2(\psi)u^{(2)}(x)$; we obtain

$$\frac{d}{d\psi} [f_2(\psi)u^{(2)}] = -\frac{\mu_1}{f_1(\psi)} [f_2(\psi)u^{(2)}(\psi)] - \frac{\mu_1}{f_1(\psi)} [f_2(\psi)u^{(2)}(\psi)].$$

Let ψ^* be given by the Perron-eigendirection of $q_1 M_1 + q_2 M_2$. Then,

$$u^{(2)}(\psi) = \frac{C}{f_2(\psi)} \exp \left[- \int_{\psi^*}^{\psi} \left(\frac{1}{q_1 f_1(\psi')} + \frac{1}{q_2 f_2(\psi')} \right) d\psi' \right]^{1/T}$$

where we used that $\mu_1 = 1/(q_1 T)$; C is a positive constant determined by the condition that the total probability $\int u^{(1)} + u^{(2)} d\psi = 1$. The integrand in the equation for $u^{(2)}(\psi)$ becomes zero if

$$\tilde{f}(\psi') = q_1 f_1(\psi') + q_2 f_2(\psi') = (\mathbf{e}_1^T - \psi' \mathbf{e}^T) A \begin{pmatrix} \psi' \\ 1 - \psi' \end{pmatrix} = 0$$

where $A = q_1 M_1 + q_2 M_2$. Proposition A.19 implies that the integrand changes sign exactly for $\psi' = \psi^*$. As $\tilde{f}(0) = \mathbf{e}_1^T A \mathbf{e}_2 > 0$ the

integrand is positive for $\psi' < \psi^*$ and negative for $\psi' > \psi^*$. Therefore, the integral is strictly negative for $\psi \neq \psi^*$ and possesses a unique maximum at $\psi = \psi^*$. By considering

$$\pi(\psi) = \frac{u^{(2)}(\psi)}{\int_{\psi_1}^{\psi_2} u^{(2)}(\psi') d\psi'}$$

we normalize the L^1 -norm of $u^{(2)}$ to one. For $T \rightarrow 0$, this function approaches a delta-peak at $\psi = \psi^*$. \square

Proposition A.21. If ψ_2 is given by the direction of the eigenvalue of M_2 , then the invariant measure π of \tilde{T} approximates weakly a point mass at ψ_2 for $T \rightarrow \infty$. Given a function $H(\psi) \in C^1[\psi_1, \psi_2]$, we find

$$\int_{\psi_1}^{\psi_2} H(\psi) \pi(\psi) d\psi = H(\psi_2) + \mathcal{O}(T^{-1}).$$

Proof. We know that f_2 possesses a unique zero at ψ_2^* . If T becomes large, the exponential term in $u_2(\psi)$ cannot kill the pole of $1/f_2(\psi)$ at $\psi = \psi_2$. As, in lowest order, $f_2(\psi) = f'(\psi_2)(\psi - \psi_2)$, we find for $\psi_2 > \psi > \psi^*$ that

$$\frac{1}{T} \int_{\psi^*}^{\psi} \left(\frac{1}{q_1 f_1(\psi')} + \frac{1}{q_2 f_2(\psi')} \right) d\psi' = \frac{-1}{T q_2 f'_2(\psi_2)} \ln(\psi - \psi_2^*) + \text{l.o.t.}$$

where l.o.t. represents lower order terms. According to Proposition A.19, $f'_2(\psi_2) < 0$ and thus

$$u_2(\psi) = (\psi_2 - \psi)^{-1+1/(T q_2 |f'_2(\psi_2)|)} + \hat{u}_2(\psi)$$

here $\hat{u}_2(\psi)$ is uniformly bounded and uniformly bounded away from zero. This is, for $1/T \rightarrow 0$, the integral of $u_2(\psi)$ tends to infinity with order $T q_2 |f'_2(\psi_2)|$, and hence

$$\pi(\psi) = \frac{1}{T q_2 |f'_2(\psi_2)|} (\psi_2 - \psi)^{-1+1/(T q_2 |f'_2(\psi_2)|)} \hat{\pi}(\psi; T) \chi_{[\psi_1, \psi_2]}(\psi),$$

where again $\hat{\pi}(\psi; T)$ is bounded and bounded away from zero; this function also depends on T and guarantees that $\int \pi d\psi$ is always exactly one. Now,

$$\begin{aligned} \int_{\psi_1}^{\psi_2} H(\psi) \pi(\psi) d\psi &= H(\psi_2) + \int_{\psi_1}^{\psi_2} \frac{H'(\hat{\psi})(\psi - \psi_2)^{1/(T q_2 |f'_2(\psi_2)|)}}{T q_2 |f'_2(\psi_2)|} \hat{\pi}(\psi; T) d\psi \\ &= H(\psi_2) + \mathcal{O}(T^{-1}). \quad \square \end{aligned}$$

The last two propositions are visualized in Fig. A2 by means of Monte-Carlo simulations and analytical computations; we find the function $\pi(\cdot)$ to resemble a normal distribution with small variance if $T \ll 1$, while it develops a singularity for $T \gg 1$ at ψ_2 .

A.6. Exponential growth rate

As the Markov chain describing the evolution of the direction ψ is ergodic, the conclusion of Corollary A.3 for the Lyapunov exponent is justified. We now are able to figure out the asymptotics of λ for $T \rightarrow 0$ resp. $T \rightarrow \infty$.

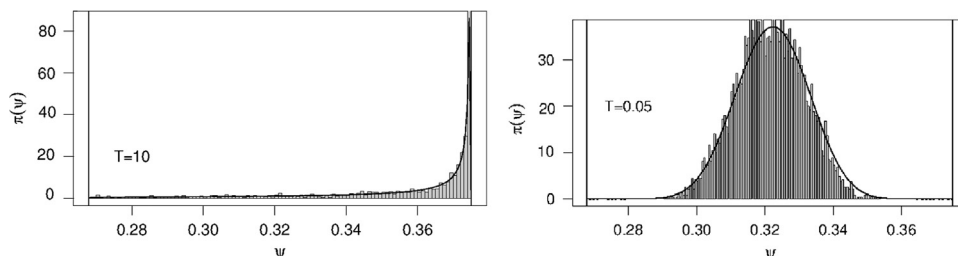


Fig. A2. Density $\pi(\psi)$ compared with Monte-Carlo simulation for large and small T . The left (right) vertical bar indicates ψ_1 (ψ_2).

Proof of Theorem A.1. First consider $T \rightarrow 0$. We know that $\pi(x)$ approaches a delta peak at ψ^* , the eigenvector of $q_1 M_1 + q_2 M_2 = E(M_\alpha)$. Let $\nu_l(\tau) = (q_l T)^{-1} e^{-\tau/(q_l T)}$. Then $E(\tau_l) = q_l T$ and

$$\begin{aligned} \lambda_0 &= \int_0^\infty \int_0^\infty \int_{\psi_1}^{\psi_2} \ln \left(\mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix} \right) \pi(\psi) \nu_1(\tau_1) \\ &\quad \nu_2(\tau_2) d\tau_1 d\tau_2 / (T(q_1 + q_2)) \\ &= \int_0^\infty \int_0^\infty \ln \left[\mathbf{e}^T (I + M_2 \tau_2 + M_1 \tau_1) \begin{pmatrix} \psi^* \\ 1-\psi^* \end{pmatrix} \right] \\ &\quad \nu_1(\tau_1) \nu_2(\tau_2) d\tau_1 d\tau_2 / (T(q_1 + q_2)) + \mathcal{O}(T) \\ &= \mathbf{e}^T \left(M_2 \frac{q_2}{q_1 + q_2} + M_1 \frac{q_1}{q_1 + q_2} \right) \begin{pmatrix} \psi^* \\ 1-\psi^* \end{pmatrix} + \mathcal{O}(T) \\ &= \rho(E(M_\alpha)) + \mathcal{O}(T). \end{aligned}$$

The limit $T \rightarrow \infty$ is slightly more involved. Before we start, we note that for $\mu, a, c > 0$ and $b > -a$

$$\int_0^\infty \ln(a + b e^{-c\tau}) \mu e^{-\mu\tau} d\tau = \ln(a) + \mathcal{O}(\mu).$$

We will use this fact in the following considerations. Together with Proposition A.21 we obtain

$$\begin{aligned} \lambda_0 &= \int_0^\infty \int_0^\infty \int_{\psi_1}^{\psi_2} \ln \left(\mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix} \right) \\ &\quad \pi(\psi) \nu_1(\tau_1) \nu_2(\tau_2) d\tau_1 d\tau_2 / (Tq_1 + Tq_2) \\ &= \int_0^\infty \int_0^\infty \int_{\psi_1}^{\psi_2} \ln [e^{\rho(M_1)\tau_1 + \rho(M_2)\tau_2} \delta_1^{-1} \delta_2^{-1} \mathbf{e}^T \\ &\quad ([\lambda_{+,2} e^{-\delta_2 \tau_2} - \lambda_{-,2} + (1 - e^{-\delta_2 \tau_2}) M_2] \\ &\quad [\lambda_{+,1} e^{-\delta_1 \tau_1} - \lambda_{-,1} + (1 - e^{-\delta_1 \tau_1}) M_1] \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix})] \\ &\quad \pi(\psi) \nu_1(\tau_1) \nu_2(\tau_2) d\tau_1 d\tau_2 / (Tq_1 + Tq_2) \\ &= q_1 \rho(M_1) + q_2 \rho(M_2) + \frac{1}{T} \ln \left[\delta_1^{-1} \delta_2^{-1} \mathbf{e}^T [-\lambda_{-,2} + M_2] \right. \\ &\quad \left. [-\lambda_{-,1} + M_1] \begin{pmatrix} \psi_2 \\ 1-\psi_2 \end{pmatrix} \right] + \mathcal{O}(T^{-2}) \\ &= E(\rho(M_\alpha)) + \frac{1}{T} \ln \left[\delta_1^{-1} \delta_2^{-1} \left\{ -\lambda_{-,1} \delta_2 + [-\lambda_{-,2} \mathbf{e}^T M_1 \right. \right. \\ &\quad \left. \left. + \mathbf{e}^T M_2 M_1] \begin{pmatrix} \psi_2 \\ 1-\psi_2 \end{pmatrix} \right\} \right] + \mathcal{O}(T^{-2}). \quad \square \end{aligned}$$

Remark A.22. It is straightforward to show that the function $E_\pi[\lambda_0]$ is monotone in T if α switches periodically. We conjecture that this property is also true in the present case.

Appendix B. Optimal strategies

In this subsection, we work out the parameter set $(r_1, r_2, \epsilon_1, \epsilon_2) \in \mathbb{R}_+^4$ that maximizes the Lyapunov coefficient for the switching system in the two different extremes, $T \rightarrow 0$ and $T \rightarrow \infty$. Before going into this direction, we state the following:

Proposition B.1. If $r_1 = r_2 = r$, then the Lyapunov coefficient is independent of T , ϵ_1 and ϵ_2 .

Proof. In this case, the matrices M_i are given by

$$M_i = \begin{pmatrix} \beta(r, \alpha_i) - \epsilon_i & \epsilon_2 \\ \epsilon_1 & \beta(r, \alpha_i) - \epsilon_2 \end{pmatrix}.$$

This is, $\lambda_{+,l} = \beta(r, \alpha_l)$ and $\lambda_{-,l} = \beta(r, \alpha_l) - \epsilon_1 - \epsilon_2$ where the left Perron eigenvector reads $(1, 1) = \mathbf{e}^T$. Thus,

$$\begin{aligned} \lambda_0 &= \int_0^\infty \int_0^\infty \int_{\psi_1}^{\psi_2} \ln \left(\mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix} \right) \\ &\quad \pi(\psi) \nu_1(\tau_1) \nu_2(\tau_2) d\psi d\tau_1 d\tau_2 / (T(q_1 + q_2)) \\ &= \int_0^\infty \int_0^\infty \int_{\psi_1}^{\psi_2} (\lambda_{+,2} \tau_2 + \lambda_{+,1} \tau_1) \pi(\psi) \nu_1(\tau_1) \\ &\quad \nu_2(\tau_2) d\tau_1 d\tau_2 / (T(q_1 + q_2)) \\ &= q_1 \lambda_{+,1} + q_2 \lambda_{+,2} = q_1 r \beta(r, \alpha_1) + q_2 r \beta(r, \alpha_2). \quad \square \end{aligned}$$

Note that in this particular case $r_1 = r_2$, $\rho(E(M_\alpha))$ and $E(\rho(M_\alpha))$ coincide.

B.1. Fast switching

In case of $T \ll 1$, the Lyapunov coefficient is well approximated by

$$\begin{aligned} \lambda &\approx \hat{\lambda}(r_1, r_2, \epsilon_1, \epsilon_2) \\ &:= \frac{1}{2} (\hat{\beta}(r_1) + \hat{\beta}(r_2) - \epsilon_1 - \epsilon_2 \pm \sqrt{(\hat{\beta}(r_1) - \epsilon_1 - \hat{\beta}(r_2) + \epsilon_2)^2 + 4\epsilon_1 \epsilon_2}) \end{aligned}$$

where

$$\hat{\beta}(r) = q_1 \beta_1(r) + q_2 \beta_2(r).$$

Theorem B.2. One has

$$\hat{\lambda}(r_1, r_2, \epsilon_1, \epsilon_2) \leq \max_{r \in \mathbb{R}_+} \hat{\beta}(r)$$

and equality holds true in each of the three cases

- (1) $r_1 = r_2 = r^*$, $\epsilon_1, \epsilon_2 \in \mathbb{R}_+$
- (2) $r_1 = r^*$, $r_2 \in \mathbb{R}_+$, $\epsilon_1 = 0$, $\epsilon_2 \in \mathbb{R}_+$
- (3) $r_2 = r^*$, $r_1 \in \mathbb{R}_+$, $\epsilon_1 \in \mathbb{R}_+$, $\epsilon_2 = 0$.

Proof. According to Appendix A, we have to compare $\hat{\beta}(r^*)$ and

$$\hat{\lambda} = \frac{1}{2} (\hat{\beta}(r_1) + \hat{\beta}(r_2) - \epsilon_1 - \epsilon_2 + \sqrt{(\hat{\beta}(r_1) - \epsilon_2 - \hat{\beta}(r_2) + \epsilon_1)^2 + 4\epsilon_1 \epsilon_2}).$$

Without restriction, let $\hat{\beta}(r_1) \geq \hat{\beta}(r_2)$:

$$\begin{aligned} &(\hat{\beta}(r_1) - \epsilon_2 - \hat{\beta}(r_2) + \epsilon_1)^2 + 4\epsilon_1 \epsilon_2 \\ &= (\hat{\beta}(r_1) - \hat{\beta}(r_2))^2 + 2(\hat{\beta}(r_1) - \hat{\beta}(r_2))(\epsilon_1 - \epsilon_2) + (\epsilon_1 - \epsilon_2)^2 + 4\epsilon_1 \epsilon_2 \\ &= (\hat{\beta}(r_1) - \hat{\beta}(r_2))^2 + 2(\hat{\beta}(r_1) - \hat{\beta}(r_2))(\epsilon_1 - \epsilon_2) + (\epsilon_1 + \epsilon_2)^2 \\ &\leq (\hat{\beta}(r_1) - \hat{\beta}(r_2))^2 + 2(\hat{\beta}(r_1) - \hat{\beta}(r_2))(\epsilon_1 + \epsilon_2) + (\epsilon_1 + \epsilon_2)^2 \\ &= ((\hat{\beta}(r_1) - \hat{\beta}(r_2)) + (\epsilon_1 + \epsilon_2))^2, \end{aligned}$$

and consequently

$$\hat{\lambda} \leq \frac{1}{2} (\hat{\beta}(r_1) + \hat{\beta}(r_2) + \hat{\beta}(r_1) - \hat{\beta}(r_2)) = \hat{\beta}(r_1) \leq \hat{\beta}(r^*)$$

Direct computations show that the cases (1)–(3) imply equality. \square

Proposition B.3. Let r^* be the parameter maximizing $\hat{\beta}(r)$ and consider the Lyapunov exponent λ_0 as a function of r_1, r_2, T . If $\nabla_r = (\partial_{r_1}, \partial_{r_2})^T$, then

$$\nabla_r \lambda_0(r_1, r_2, T)|_{r_1 = r_2 = r^*} = 0$$

for all $T \geq 0$; that is, r^* is a singular strategy in the sense of adaptive dynamics.

Proof. To begin with, we note that for $r_1 = r_2 = r$ it is $M_{\alpha_1} = M_{\alpha_2} + (\beta(r, \alpha_1) - \beta(r, \alpha_2))I$. Thus, the eigenvectors of M_{α_1} and M_{α_2} coincide and $\pi(\psi) = \delta_{\psi^*}(\psi)$ independent of T . Furthermore,

recall that

$$\partial_{r_1} e^{M_1 \tau_1} = e^{M_1 \tau_1} \int_0^{\tau_1} e^{-M_1 t'} (\partial_{r_1} M_1) e^{M_1 t'} dt'$$

This formula can be readily derived by investigation of the equation $x' = M_1 x$, $x(0) = x_0$ (take the derivative w.r.t. r_1 , and use the variation-of-constants formula). Now we start by taking the derivative of λ_0 w.r.t. r_1 :

$$\begin{aligned} & (T(q_1 + q_2) \partial_{r_1} \lambda_0(r_1, r_2, T))|_{r_1=r_2=r^*} \\ &= \int_0^\infty \int_0^\infty \int_{\psi_1}^{\psi_2} \frac{\partial_{r_1} \mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix}}{\mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix}} \pi \\ & (\psi) \nu_1(\tau_1) \nu_2(\tau_2) d\psi d\tau_1 d\tau_2 |_{r_1=r_2=r^*} \\ &+ \int_0^\infty \int_0^\infty \int_{\psi_1}^{\psi_2} \ln \left(\mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix} \right) (\partial_{r_1} \\ & \pi(\psi)) \nu_1(\tau_1) \nu_2(\tau_2) d\psi d\tau_1 d\tau_2 |_{r_1=r_2=r^*} =: I_1 + I_2. \end{aligned}$$

We consider the two integrals I_1 and I_2 separately; first we look at I_1 . Note that for $r_1 = r_2 = r^*$ the measure $\pi(\psi)$ is a point mass at $\psi = \psi^*$, where $(\psi^*, 1-\psi^*)$ is the right Perron eigenvector and \mathbf{e}^T the left Perron eigenvector of both M_{α_1} and M_{α_2} . Furthermore,

$$\partial_{r_1} M_1 = \partial_r \beta(r, \alpha_1)|_{r=r_1} \mathbf{e}_1 \mathbf{e}_1^T.$$

This is,

$$\begin{aligned} & \partial_{r_1} \mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} \begin{pmatrix} \psi \\ 1-\psi \end{pmatrix} |_{r_1=r_2=r^*} \\ &= \beta_r(r^*, \alpha_2) \mathbf{e}^T e^{M_2 \tau_2} \int_0^{\tau_2} e^{-M_2 t'} \mathbf{e}_1 \mathbf{e}_1^T e^{M_2 t'} dt' e^{M_1 \tau_1} \begin{pmatrix} \psi^* \\ 1-\psi^* \end{pmatrix} \\ &+ \beta_r(r^*, \alpha_1) \mathbf{e}^T e^{M_2 \tau_2} e^{M_1 \tau_1} \int_0^{\tau_1} e^{-M_1 t'} \mathbf{e}_1 \mathbf{e}_1^T e^{M_1 t'} dt' \begin{pmatrix} \psi^* \\ 1-\psi^* \end{pmatrix} \\ &= e^{\lambda_{+2} \tau_2 + \lambda_{+1} \tau_1} (\tau_1 \beta_r(r^*, \alpha_1) + \tau_2 \beta_r(r^*, \alpha_2)). \end{aligned}$$

With this result, we obtain $I_1 = T \partial_r \hat{\beta}(r)|_{r=r^*} = 0$.

Now we turn to I_2 . With an appropriate definition for $H(r_1, r_2, T)$, we rewrite this integral as

$$I_2 = \int_{\psi_1}^{\psi_2} H(r_1, r_2, T) (\partial_{r_1} \pi(\psi)) d\psi |_{r_1=r_2=r^*}.$$

For generic parameters (r_1, r_2, T) we obtain

$$\begin{aligned} \partial_r \pi(\psi) &= \partial_{r_1} \left(\frac{u_2(\psi)}{\int_{\psi_1}^{\psi_2} u_2(\psi') d\psi'} \right) \\ &= \frac{\partial_{r_1} u_2(\psi)}{\int_{\psi_1}^{\psi_2} u_2(\psi') d\psi'} - \frac{u_2(\psi)}{\int_{\psi_1}^{\psi_2} u_2(\psi') d\psi'} \int_{\psi_1}^{\psi_2} \frac{\partial_r u_2(\psi')}{\int_{\psi_1}^{\psi_2} u_2(\psi') d\psi'} d\psi' \\ &= \partial_r \ln(u_2(\psi)) \pi(\psi) - \int_{\psi_1}^{\psi_2} \partial_r \ln(u_2(\psi')) \pi(\psi') d\psi' \pi(\psi) \end{aligned}$$

which leads to

$$I_2 = \lim_{r_1 \rightarrow r^*} \int_{\psi_1}^{\psi_2} H(r_1, r_2, T, \psi) (\partial_r \ln(u_2(\psi))) - \int_{\psi_1}^{\psi_2} \partial_r \ln(u_2(\psi')) \pi(\psi') d\psi' \pi(\psi) d\psi |_{r_2=r^*}.$$

Note that for $r_1 \rightarrow r^*$ it is $\psi_1 \rightarrow \psi_2$ and $u_2(\cdot)$ becomes singular. We expand H w.r.t. ψ , find $I_2 = \lim_{r_1 \rightarrow r^*} (T_0 + T_1)$ with

$$\begin{aligned} T_0 &= H(r_1, r_2, T, \psi^*) \int_{\psi_1}^{\psi_2} (\partial_{r_1} \ln(u_2(\psi))) \\ &- \int_{\psi_1}^{\psi_2} \partial_{r_1} \ln(u_2(\psi')) \pi(\psi') d\psi' \pi(\psi) |_{r_2=r^*} \end{aligned}$$

$$T_1 = \int_{\psi_1}^{\psi_2} H'(r_1, r_2, T, \tilde{\psi}(\psi)) (\psi^* - \psi) (\partial_{r_1} \ln(u_2(\psi)))$$

$$- \int_{\psi_1}^{\psi_2} \partial_{r_1} \ln(u_2(\psi')) \pi(\psi') d\psi' \pi(\psi) d\psi |_{r_2=r^*}$$

and $\tilde{\psi}(\psi) \in (\psi_1, \psi_2)$ suited function given by the residual of the Taylor expansion. The term T_0 vanishes because of the structure of this integral. We also find that the second integral vanishes for $r_1 \rightarrow r^*$: if we consider the definition of u_2 , we find

$$\partial_{r_1} \ln(u_2) = - \frac{\partial_{r_1} f_2(\psi)}{f_2(\psi)} + \frac{1}{T} \int_{\psi^*}^{\psi} \frac{\partial_{r_1} f_1(\psi')}{q_1 f_1^2(\psi')} + \frac{\partial_{r_1} f_2(\psi')}{q_2 f_2^2(\psi')} d\psi'.$$

As $f_i(\psi)$ develop zeros of first order for $\psi \rightarrow \psi^*$ and $r \rightarrow r^*$, the term $(\psi - \psi^*)$ will force the integrand to be bounded; furthermore, $|\psi_1 - \psi_2| \rightarrow 0$ for $r_1, r_2 \rightarrow r^*$. Therefore, $T_2 \rightarrow 0$ for $r_1, r_2 \rightarrow r^*$. Note that $\partial_{r_2} \lambda_0$ can be derived in a similar way, or using the fact that we already know that $d/dr(\lambda_0(r, r, T)) = 0$. \square

Remark B.4. If we consider the case $\psi_1 = 0$, $r_1 = r^*$ and $r_2 \in \mathbb{R}_+$, the Lyapunov coefficient only depends on r_1 , also for $T > 0$. This is, for $\psi_1 = 0$ fixed and T small, there will be no Lyapunov coefficient larger than the maximal Lyapunov coefficient for $T = 0$.

Theorem B.5. There is a $T_1 > 0$ s.t. for all $T \in [0, T_1]$ the maximal Lyapunov coefficient of the stochastic switching system is equal to that for $T = 0$.

Proof. First of all, feasible parameter sets satisfy $\varepsilon_i \leq \min\{\beta(r_1, \alpha_1), \beta(r_1, \alpha_2)\}$. As the functions $\beta(r, \alpha_i)$ are bounded, the parameters ε_i are within a compact set. λ_0 depends smoothly on T . Given $\varepsilon_1, \varepsilon_2 > 0$, the Lyapunov coefficient assumes a proper maximum for $r_1 = r_2 = r^*$. This is, the location of any sequence of maxima for $T > 0$ necessarily approaches $(r_1, r_2) = (r^*, r^*)$. However, we know

$$\lambda_0(r_1, r_2, T) = E(\rho(M_\alpha)) + Tg(r_1, r_2, T),$$

where the function g represents the residual terms; from Proposition B.3 we know that $\nabla_r g = 0$. Therefore, if T is sufficiently, the second order terms of $E(\rho(M_\alpha))$ will dominate any second order terms of $Tg(r_1, r_2, T)$, and prevent the appearance of a second maximum in a neighborhood of (r^*, r^*) . In case of $\varepsilon = 0$ (similarly $\varepsilon_2 = 0$), the Lyapunov coefficient only depends on r_1 . It is straightforward to check that in this case $r_1 = r^*$ is optimal, while r_2 does not play a role. \square

B.2. Slow switching

If $T \gg 1$, the approximation of λ is given by

$$\lambda \approx q_1 \lambda_{+1}(r_1, r_2) + q_2 \lambda_{+2}(r_1, r_2)$$

where

$$\begin{aligned} \lambda_{\pm,1} &= \frac{1}{2}(\beta(r_1, \alpha_1) + \beta(r_2, \alpha_1) - \varepsilon_1 - \varepsilon_1 \\ &\pm \sqrt{(\beta(r_1, \alpha_1) - \varepsilon_2 - \beta(r_2, \alpha_1) + \varepsilon_1)^2 + 4\varepsilon_1 \varepsilon_2}), \end{aligned}$$

$$\begin{aligned} \lambda_{\pm,2} &= \frac{1}{2}(\beta(r_1, \alpha_2) + \beta(r_2, \alpha_2) - \varepsilon_1 - \varepsilon_2 \\ &\pm \sqrt{(\beta(r_1, \alpha_2) - \varepsilon_2 - \beta(r_2, \alpha_2) + \varepsilon_1)^2 + 4\varepsilon_1 \varepsilon_2}) \end{aligned}$$

Proposition B.6. For T sufficiently large, and $\varepsilon_1, \varepsilon_2$ sufficiently small (but positive), a bimorphic strategy is able to invade the optimal monomorphic strategy.

Proof. According to Theorem A.1, we have to compare $\bar{\beta}(r^*)$ and $q_1 \lambda_+(r_1, r_1) + q_2 \tilde{\lambda}_+(r_1, r_2)$.

Assume that r_1 is optimally adapted for α_1 , while r_2 is optimal for q_2 . As $\varepsilon_1, \varepsilon_2$ are small,

$$\begin{aligned} &(\beta(r_1, \cdot) - \varepsilon_2 - \beta(r_2, \cdot) + \varepsilon_1)^2 + 4\varepsilon_1\varepsilon_2 \\ &= (\beta(r_1, \cdot) - \beta(r_2, \cdot))^2 + 2(\beta(r_1, \cdot) - \beta(r_2, \cdot))(\varepsilon_1 - \varepsilon_2) + (\varepsilon_1 + \varepsilon_2)^2 \\ &= (\beta(r_1, \cdot) - \beta(r_2, \cdot))^2 + 2(\beta(r_1, \cdot) - \beta(r_2, \cdot))(\varepsilon_1 + \varepsilon_2) \\ &\quad + (\varepsilon_1 + \varepsilon_2)^2 + O(\varepsilon_2) \\ &= ((\beta(r_1, \cdot) - \beta(r_2, \cdot)) + (\varepsilon_1 + \varepsilon_2))^2 + O(\varepsilon_2). \end{aligned}$$

Now, for $\alpha = \alpha_1$, we have $\beta(r_1, \alpha_1) > \beta(r_2, \alpha_1)$, and for $\alpha = \alpha_1$ the inequality turns around. Hence,

$$\lambda_{+,1} = \beta(r_1, \alpha_1) + O(\varepsilon_1), \quad \lambda_{+,2} = \beta(r_2, \alpha_2) + O(\varepsilon_2)$$

and

$$q_1\lambda_+(r_1, r_2) + q_2\tilde{\lambda}_+(r_1, r_2) = q_1\beta(r_1, \alpha_1) + q_2\beta(r_2, \alpha_2) + O(\varepsilon_2).$$

As r_1, r_2 are optimal, we have $\beta(r_1, \alpha_1) > \beta(r^*, \alpha_1)$, and $\beta(r_2, \alpha_2) > \beta(r^*, \alpha_2)$. Hence,

$$\begin{aligned} q_1\lambda_{+,1}(r_1, r_2) + q_2\lambda_{+,2}(r_1, r_2) &> q_+\beta(r^*, \alpha_1) + q_-\beta(r^*, \alpha_2) \\ &+ O(\varepsilon_2) = \bar{\beta}(r^*) + O(\varepsilon_2). \end{aligned}$$

If ε_2 is sufficiently small, the monomorphic strategy r^* can be invaded by the bimorphic strategy. \square

In order to obtain some information about the size of the parameters r_1, r_2, ε_1 , and ε_2 for T large, note that we expect the rates ε_1 and ε_2 to be small; furthermore, the only sensible case is that r_1 is better for environment α_1 and r_2 for α_2 (or vice versa). This is, we focus on the case that $\varepsilon_1, \varepsilon_2$ are small and

$$\Delta\beta_1 := \beta(r_1, \alpha_1) - \beta(r_2, \alpha_1) > 0, \quad \Delta\beta_2 := \beta(r_1, \alpha_2) - \beta(r_2, \alpha_2) < 0.$$

Note that the inequalities are assumed to be strict – the following Taylor expansion breaks down in case of equality. A straightforward, but tedious computation yields under the given conditions (basically, we use the Feynman–Hellman formula, see [Thirring, 1979, Chapter 3.5](#))

$$\lambda_{+,1} = \beta(r_1, \alpha_1) - \varepsilon_1 + \frac{\varepsilon_1\varepsilon_2}{\Delta\beta_1} + \text{h.o.t.}, \tag{B.1}$$

$$\begin{aligned} \lambda_{-,1} &= \beta(r_2, \alpha_1) - \varepsilon_2 - \frac{\varepsilon_1\varepsilon_2}{\Delta\beta_1} + \text{h.o.t.}, \\ \lambda_{+,2} &= \beta(r_2, \alpha_2) - \varepsilon_2 - \frac{\varepsilon_1\varepsilon_2}{\Delta\beta_2} + \text{h.o.t.}, \end{aligned} \tag{B.2}$$

$$\begin{aligned} \lambda_{-,2} &= \beta(r_1, \alpha_2) - \varepsilon_1 + \frac{\varepsilon_1\varepsilon_2}{\Delta\beta_2} + \text{h.o.t.} \\ \begin{pmatrix} \psi_2 \\ 1 - \psi_2 \end{pmatrix} &= \begin{pmatrix} -\varepsilon_2/\Delta\beta_2 - \varepsilon_1\varepsilon_2/\Delta\beta_2^2 \\ 1 + \varepsilon_2/\Delta\beta_2 + \varepsilon_1\varepsilon_2/\Delta\beta_2^2 \end{pmatrix} + \text{h.o.t.} \end{aligned} \tag{B.3}$$

Therewith we find

$$\begin{aligned} -\lambda_{-,1}\delta_2 &= \Delta\beta_2\beta(r_2, \alpha_1) - \varepsilon_1\beta(r_2, \alpha_1) + \varepsilon_2(\beta(r_2, \alpha_1) - \Delta\beta_2) \\ &+ \varepsilon_1\varepsilon_2 \left(1 - \frac{\Delta\beta_2}{\Delta\beta_1} + \frac{2\beta(r_2, \alpha_1)}{\Delta\beta_2} \right) - \varepsilon_2^2 + \text{h.o.t.} \end{aligned}$$

$$\begin{aligned} -\lambda_{-,2}\mathbf{e}^T M_1(\psi_2, 1 - \psi_2)^T &= -\beta(r_1, \alpha_2)\beta(r_2, \alpha_1) + \varepsilon_1\beta(r_2, \alpha_1) \\ &+ \varepsilon_2\beta(r_1, \alpha_2)\frac{\Delta\beta_1}{\Delta\beta_2} \\ &+ \varepsilon_1\varepsilon_2 \frac{\beta(r_1, \alpha_1)\beta(r_2, \alpha_2) - \beta(r_1, \alpha_2)\beta(r_2, \alpha_1)}{\Delta\beta_2^2} + \text{h.o.t.} \end{aligned}$$

$$\begin{aligned} \mathbf{e}^T M_2 M_1(\psi_2, 1 - \psi_2)^T &= \beta(r_2, \alpha_2)\beta(r_2, \alpha_1) \\ &+ \varepsilon_2 \left(\Delta\beta_2 + \frac{\beta(r_2, \alpha_1)\beta(r_2, \alpha_2) - \beta(r_1, \alpha_1)\beta(r_1, \alpha_2)}{\Delta\beta_2} \right) \end{aligned}$$

$$+ \varepsilon_1\varepsilon_2 \left(1 + \frac{\beta(r_2, \alpha_1)\beta(r_2, \alpha_2) - \beta(r_1, \alpha_1)\beta(r_1, \alpha_2)}{\Delta\beta_2^2} \right) + \varepsilon_2^2 + \text{h.o.t.}$$

Altogether, we find (note that $\delta_2 = -\Delta\beta_2 + \text{h.o.t.}$, and $-\Delta\beta_2 = |\Delta\beta_2|$)

$$\begin{aligned} &\frac{1}{\delta_1\delta_2} \left[-\lambda_{-,1}\delta_2 - \lambda_{-,2}\mathbf{e}^T M_1(\psi_2, 1 - \psi_2)^T + \mathbf{e}^T M_2 M_1(\psi_2, 1 - \psi_2)^T \right] \\ &= \varepsilon_1\varepsilon_2 \left(\frac{1}{\Delta\beta_1} + \frac{1}{|\Delta\beta_2|} \right)^2 + \text{h.o.t.} \end{aligned}$$

If we use the lowest sensible order for the approximation of λ_0 , we obtain

$$\begin{aligned} \lambda_0 &\approx q_1\rho(M_1) + q_2\rho(M_2) + \frac{1}{T} \ln \left[\delta_1^{-1}\delta_2^{-1} \{-\lambda_{-,1}\delta_2 \right. \\ &\quad \left. + [-\lambda_{-,2}\mathbf{e}^T M_1 + \mathbf{e}^T M_2 M_1]\} \begin{pmatrix} \psi_2 \\ 1 - \psi_2 \end{pmatrix} \right] \\ &\approx q_1(\beta(r_1, \alpha_1) - \varepsilon_1) + q_2(\beta(r_2, \alpha_2) - \varepsilon_2) \\ &\quad + \frac{1}{T} (\ln(\varepsilon_1) + \ln(\varepsilon_2) + 2 \ln \left(\frac{1}{\Delta\beta_1} + \frac{1}{|\Delta\beta_2|} \right)). \end{aligned}$$

Maximizing the latter expression, we find that r_1 maximizes $\beta(r, \alpha_1)$, r_2 maximizes $\beta(r, \alpha_2)$, and

$$\varepsilon_1 = \frac{1}{q_1 T}, \quad \varepsilon_2 = \frac{1}{q_2 T}.$$

Corollary B.7. For T sufficiently large, we find optimal parameters r_1, r_2, ε_1 and ε_2 as

$$\begin{aligned} r_1 &= r_1^* + \mathcal{O}(1/T), \quad r_2 = r_2^* + \mathcal{O}(1/T), \quad \varepsilon_1 = \frac{1}{q_1 T} \\ &+ \mathcal{O}(1/T^2), \quad \varepsilon_2 = \frac{1}{q_2 T} + \mathcal{O}(1/T^2) \end{aligned}$$

where r_i^* maximize the functions $\beta(r, \alpha_i)$.

Appendix C. Stochastic simulation

For the stochastic simulation used to create [Fig. 1](#), we set up a stochastic branching process, with four types for the population. The variable α denotes the environmental variable, and μ the strength of competition (see [Table C1](#)). The transitions are described in [Table C2](#), while the parameter used is given in [Table C3](#). Note that in [Fig. 1](#) T as well as μ is modified (values are given in [Fig. 1](#)).

Let $\alpha_1 = 0.5$, and $\alpha_2 = 1$. The parameter r^* is chosen in such a way that it maximizes

$$E(\beta(r, \alpha_t)) = q_1\beta(r, \alpha_1) + q_2\beta(r, \alpha_2).$$

The parameters r_1 and r_1^* maximize $\beta(r, \alpha_1)$, while r_2 and r_2^* maximize $\beta(r, \alpha_2)$.

Table C1
State variables of the model.

Name	Range	Initial value	Interpretation
X	\mathbb{N}_0	10	Specialized to averaged environment
X_1	\mathbb{N}_0	5	Bet-hedger, subtype one
X_2	\mathbb{N}_0	5	Bet-hedger, subtype two
Z_1	\mathbb{N}_0	10	Specialized to environment one
Z_2	\mathbb{N}_0	10	Specialized to environment two
α	{1, 2}	1	Environmental variable

Table C2
Stochastic transitions.

Variable	Offset	Rate
α	$\rightarrow \alpha + 1$	$1/(q_1 \cdot T)$
α	$\rightarrow \alpha - 1$	$1/(q_2 \cdot T)$
X	$\rightarrow X + 1$	$X \cdot \beta(r^*, \alpha)$
X	$\rightarrow X - 1$	$(X + X_1 + X_2 + Z_1 + Z_2) \cdot X \cdot \mu$
X_1	$\rightarrow X_1 + 1$	$X_1 \cdot \beta(r_1, \alpha)$
X_1	$\rightarrow X_1 - 1$	$(X + X_1 + X_2 + Z_1 + Z_2) \cdot X_1 \cdot \mu$
X_2	$\rightarrow X_2 + 1$	$X_2 \cdot \beta(r_2, \alpha)$
X_2	$\rightarrow X_2 - 1$	$(X + X_1 + X_2 + Z_1 + Z_2) \cdot X_2 \cdot \mu$
(X_1, X_2)	$\rightarrow (X_1 - 1, X_2 + 1)$	$\epsilon_1 \cdot X_1$
(X_1, X_2)	$\rightarrow (X_1 + 1, X_2 - 1)$	$\epsilon_2 \cdot X_2$
Z_1	$\rightarrow Z_1 + 1$	$Z_1 \cdot \beta(r_1^*, \alpha)$
Z_1	$\rightarrow Z_1 - 1$	$(X + X_1 + X_2 + Z_1 + Z_2) \cdot Z_1 \cdot \mu$
Z_2	$\rightarrow Z_2 + 1$	$Z_2 \cdot \beta(r_2^*, \alpha)$
Z_2	$\rightarrow Z_2 - 1$	$(X + X_1 + X_2 + Z_1 + Z_2) \cdot Z_2 \cdot \mu$

Table C3
Parameters used.

Name	Definition or value
$\beta(r, \alpha)$	$1 + r \exp(-2r/(1 + \alpha))$
r^*	0.758
r_1	0.5
r_2	1
r_1^*	0.5
r_2^*	1
ϵ_1	$1/(T \cdot q_1)$
ϵ_2	$1/(T \cdot q_2)$
μ	0.0001/day
T	100 · day
q_1	0.5
q_2	0.5

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