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PERSISTENCE IN THE MORAN MODEL WITH RANDOM SWITCHING

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ABSTRACT. The paper is devoted to the study of the asymptotic behaviour of Moran process in random environment, say random selection. In finite population, the Moran process may be degenerate in finite time, thus we will study its limiting process in large population which is a Piecewise Deterministic Markov Process, when the random selection is a Markov jump process. We will then study its long time behaviour via the stochastic persistence theory of Benaïm [9]. It will enable us to show that persistence can occur, i.e. asymptotic coexistence of all species, when there are enough switching possibilities. This is true even if one species has never a predominant selection.

Key words : random selection, PDMP, Stochastic Persistence, Moran Process

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INTRODUCTION

Population dynamics is a complex phenomenon in which environment plays a determining role. In particular, environmental fluctuations may be a determining factor to conserve biodiversity. Some works on this subject, such as [28], [27], have already highlighted its influence on a population evolution and its primary role in the stability of ecosystems. From a theoretical point of view, it has also been proved that environmental fluctuations may permit coexistence in models where a constant environment does not ([1], [18], [12], [15] and [11]).

Among all these mathematical models able to include environmental variations, one of the most known in ecology but also in population genetics is the Moran model [30] with selection and immigration. It is a birth and death process: in a given population, an individual is chosen to die uniformly in the population and then a child chooses his parent proportionally to the abundance in the previous population. Environment influences birth (and eventually death), each species has a fitness that gives individuals of the same species more or less probabilities of being chosen as parents compared to the neutral case. The fitness changes randomly through time, and are modeled by a Markov chain.

Immigration represents interactions between the community studied and the external environment, its main role is to introduce new species or reintroduce a species and so to conserve biodiversity. One can also consider mutation, but in fact it has the same impact on the process, as we are in a fixed population size. Without immigration (or mutation) and for a fixed population size, it well known that a species invade definitively the community in a finite time [34]. But what happen for large population? Our objective is to prove that, in the large population limit (i.e the population size goes to infinity), environmental fluctuations can be sufficient to conserve biodiversity in the Moran model. It will be done through the notion of stochastic persistence developed by Benaïm and Schreiber in [36] and in [9].

Let us present the structure of the paper and the main results we obtain. In a first section, we present the Moran Model with random selection and we obtain a quantitative approximation of this discrete process (rescaled in time with respect to the size of the population) in the limit in large population towards a particular Piecewise Deterministic Markov Process (PDMP), which is the content of Section 1 and particularly Theorem 2. We thus have to study this PDMP in which only the selection parameter is random and is a pure jump Markov process. For two species the PDMP is the following (we only need to follow the dynamic of one species):

$$\begin{cases} \frac{dX_t}{dt} = s_t \frac{X_t(1 - X_t)}{1 + s_t X_t} \\ \mathbb{P}_{x,s}(s_{t+h} = s_k | s_t = s_j) = q_{j,k}h + o(h) \quad \text{if } j \neq k \end{cases} \quad (1)$$

where s_t is our selection jump Markov process taking values in some finite space.

In order to understand the long time behavior of this process, it is first particularly informative to understand this dynamic when the selection is constant, which is done in Section 2.

Then we will consider the long time behavior when the selection is a jump Markov process. To this end we introduce in Section 3 the notion of conservation of biodiversity, taken from Schreiber [35], see also [36]. We use the the definition of stochastic persistence [9] which (roughly) asserts that the process spend (a.s.) an infinite time away from the absorbing boundaries.

Section 4 is dedicated to the case where there are two species and a switch between two different environments. It is sufficient as more possible values of the environment may be captured by this setting, as the important feature is to switch from one favorable environment to a defavorable one. Proposition 1 gives explicit condition to get stochastic persistence or extinction of one of the species. For example, in Example 1, when the jump rates are constant and equal, stochastic persistence is ensured as soon as the two values of the selection process satisfies $-s_1 < s_2 < -s_1/(1 + s_2)$, that we illustrate numerically.

The general case is treated (partially) in Section 5, where are exhibited conditions under which a species may go to extinction or one species invade the other ones. However criterion for stochastic persistence given by [9] are quite difficult to handle in more than 2 species as it requires the explicit knowledge of all the ergodic measures. Therefore we consider and detail the case of 3 species in Section 6. When there are only two different environments, unfortunately there is no stochastic persistence. However some interesting phenomenon takes place such as a specie never favored nor defavored may nevertheless invade the community. Turning to three different environments we exhibit numerical conditions under which stochastic persistence occurs.

An appendix gathers the proof of Theorem 2 and some useful lemma.

1. MORAN MODEL WITH SELECTION AND IMMIGRATION AND ITS LARGE POPULATION LIMIT

1.1. Presentation of the model.

The Moran process was introduced in population genetics in 1958 [30] to describe the probabilistic dynamics in a constant size population in which many alleles compete for dominance. Similarly, it models the stochastic dynamics of a population in which several species coexist. In this section we describe in details the discrete model, i.e. the Moran process. A particularity of this model is that an event occurs at each time step. More precisely each event corresponds to the death of an individual and the birth of another who replaces it.

We consider a population, whose size is constant over time equal to J , composed of $S + 1$ species. The proportion of the i species at the n^{th} event is denoted X_n^i , $i \in \mathbb{S} = \{1, \dots, S + 1\}$, $n \in \mathbb{N}$.

As usual once we know $(X_n^i)_{i=1, \dots, S}$, we deduce the proportion for the last species, $X_n^{S+1} = 1 - \sum_{i=1}^S X_n^i$. We denote by $X_n = (X_n^i)_{i=1, \dots, S}$ the species vector or abundance vector. The dynamics of evolution follows the following pattern at the step n :

- (1) The individual designated to die is chosen uniformly among the community.

- (2) It is replaced by an individual that chooses its parent randomly in the community. The parent is then of the species i with probability

$$\frac{X_n^i(1 + s_n^i)}{1 + \sum_{k=1}^{S+1} X_n^k s_n^k}.$$

The $(s_n^i)_{i \in \mathbb{S}}$ are the selection parameters (or fitness) which evolve through time. They can be seen as an advantage (or a disadvantage) giving more weight to the i^{th} species. In a neutral case, where all the species have the same fitness, the above probability is equal to X_n^i , meaning that no species is advantaged.

We denote by s_n , the environment at step n , i.e the vector having for i^{th} coordinate s_n^i . In the following, $(s_n)_{n>0}$ will be a Markov chain taking values in a finite space E with cardinality K . Furthermore, we assume that for all $n \geq 0$, $s_n^{S+1} = 0$. Indeed, we can obtain it from any configuration by changing all the coefficients by $s_n^i = \frac{\tilde{s}_n^i - \tilde{s}_n^{S+1}}{1 + \tilde{s}_n^{S+1}}$. This assumption forces, if we take initially positive fitness, that the coefficients belong to the set $] - 1; \infty[$.

We assume throughout this work that $(s_n)_{n \geq 0}$ is autonomous, meaning that its evolution does not depend on $(X_n)_{n \geq 0}$. We further define U_n as the vector composed of X_n and s_n .

This model therefore describes a Markovian dynamic in which a species invades definitively the community almost surely in a finite time. This is due to the absence of immigration. Some works, such as [16] and [15], give an estimation of the absorbing time in non random environment. However, the invasion time is increasing with the population size J . Our main goal is to understand the behaviour of the process when the population is large. Do environmental switch improve or reduce biodiversity?

The species vector $(X_n)_{n \geq 0}$ is a Markovian random process. Let us describe the transition probabilities. Let x be the vector having for coordinate i , x^i . Denote $\Delta = \frac{1}{J}$, so for the i species:

$$P_{x^i+} = \mathbb{P}(X_{n+1}^i = x^i + \Delta | U_n = (x, s_n)) = (1 - x^i) \frac{x^i(1 + s_n^i)}{1 + \sum_{k=1}^{S+1} x^k s_n^k},$$

$$P_{x^i-} = \mathbb{P}(X_{n+1}^i = x^i - \Delta | U_n = (x, s_n)) = x^i \left(1 - \frac{x^i(1 + s_n^i)}{1 + \sum_{k=1}^{S+1} x^k s_n^k} \right),$$

$$P_{x^i+x^j-} = \mathbb{P}(\{X_{n+1}^i = x^i + \Delta\} \cap \{X_{n+1}^j = x^j - \Delta\} | U_n = (x, s_n)) = x^j \left(\frac{x^i(1 + s_n^i)}{1 + \sum_{k=1}^{S+1} x^k s_n^k} \right).$$

When the population size J is big, understanding the temporal evolution of the population is not easy from a mathematical and computing point of view. Thus we will approach the dynamics of this model by a continuous-time random differential equation when the population is large.

1.2. In large population. Let us start with the following proposition that characterises the order (relative to J) of the expectation, variance, and covariance of the abundance variation of a species during an event:

Proposition 1.

Let $\Delta_t = \frac{1}{J}$ and $n = tJ$. When J goes to infinity, we have :

- (1) $E[X_{n+1}^i - X_n^i | U_n = (x, s_n)] = \frac{1}{J} x^i \left(s_n^i - \sum_{k=1}^S x^k s_n^k \right) \left(1 + \sum_{k=1}^S x^k s_n^k \right)^{-1}$,
- (2) $Var[X_{n+1} - X_n | X_n = (x, s_n)] = O\left(\frac{1}{J^2}\right)$,
- (3) $Cov[X_{n+1}^i, X_{n+1}^l | U_n = (x, s_n)] = O\left(\frac{1}{J^2}\right)$.

This proposition shows that the expectation is of the order of $\frac{1}{J}$ whereas the variance is of order $\frac{1}{J^2}$. Considering a scale in $\frac{1}{J}$, the variation of variance over a time step becomes negligible in large population limit. Thus, we should obtain a limit process where only s could be random. With this choice, we keep a selection independent of the size of the population and the limit process is usually called the "strong selection approximation", see [20] and [29]. It is opposed to another possible choice, the "weak selection approximation", which consists in considering the selection inversely proportional to the size of the population. The paper [24] deals with this other possibility.

To emphasise the dependence on J , we use in this section the notation $U_n^J = (X_n^J, s_n^J)$. We give an approximation result under the following assumption.

Assumption 1. There exists a finite set E such that, for all J , the process $(s_n^J)_{n \geq 0}$ is an autonomous Markov chain defined on E . Moreover, if we denote by $P_{s,s'}^J$ the transition probability of $(s_n^J)_{n \geq 0}$, then for all $s \neq s'$, there exist $\alpha_s > 0$ and $Q_{s,s'} \geq 0$ such that

$$\lim_{J \rightarrow \infty} J P_{s,s'}^J = \alpha_s Q_{s,s'}.$$

We consider the rescaled piecewise linear extension $\tilde{s}_t^J = s_{[tJ]}^J$ of $(s_n^J)_{n \geq 0}$. Let denote by $P_{\tilde{s}^J}(s, s', t)$ the transition probabilities of \tilde{s}^J , then for all $s \neq s'$,

$$\lim_{J \rightarrow \infty} P_{\tilde{s}^J} \left(s, s', \frac{1}{J} \right) \times J = \alpha_s Q(s, s').$$

We also consider the interpolated continuous-time process $(\tilde{X}_t^J)_{t \geq 0}$ of $(X_n^J)_{n \geq 0}$ defined by

$$\tilde{X}_t^J = X_{[tJ]}^J + J \left(t - \frac{[tJ]}{J} \right) \left(X_{[tJ]+1}^J - X_{[tJ]}^J \right),$$

and we set $(\tilde{U}_t^J)_{t \geq 0} = (\tilde{X}_t^J, \tilde{s}_t^J)_{t \geq 0}$. Theorem 2 below means, under Assumption 1, when J tends to infinity the sequence of processes $(\tilde{U}_t^J)_{t \geq 0}$ converges towards $(U_t)_{t \geq 0} = (X_t, s_t)_{t \geq 0}$, where $(X_t)_{t > 0}$ is solution of

$$\begin{pmatrix} dX_t^1 \\ \vdots \\ dX_t^S \end{pmatrix} = \begin{pmatrix} X_t^1 \frac{s_t^1 - \sum_{k \in \mathcal{S}} X_t^k s_t^k}{1 + \sum_{k \in \mathcal{S}} X_t^k s_t^k} \\ \vdots \\ X_t^S \frac{s_t^S - \sum_{k \in \mathcal{S}} X_t^k s_t^k}{1 + \sum_{k \in \mathcal{S}} X_t^k s_t^k} \end{pmatrix} dt \quad (2)$$

and $(s_t)_{t \geq 0}$ is a continuous times Markov chain with αQ for generator.

The process $(U_t)_{t \geq 0}$ is a *Piecewise Deterministic Markov Processes* (PDMP). It evolves according to the deterministic dynamics of the equation (2) for some s fixed during a random time with exponential distribution. Then its behavior changes and adopts another dynamic when the parameter s switches. This kind of process was introduced by Davis [17]. The PDMPs' have become ubiquitous in stochastic modelling of various phenomena. They are applied to neuroscience [31], [32], [33], genetics [14], ecology [7], internet traffic [10], [21], [22], [5]. See also [2], [6] and [13] and the references therein for more details and applications.

For $(U_t)_{t \geq 0}$ and more generally for Markov processes, we use the following standard notations. If μ is a probability measure, we let \mathbb{P}_μ denote the law of $(U_t)_{t \geq 0}$ knowing that U_0 has distribution μ , and \mathbb{E}_μ denote the associated expectation. In the special case where $\mu = \delta_{(x,s)}$, then we write $\mathbb{P}_{x,s}$ instead of $\mathbb{P}_{\delta_{x,s}}$.

Consider now the process $(Z_t^J)_{t \geq 0} = (U_{t/J})_{t \geq 0}$, taking values in $\mathcal{S} = [0.1] \times E$. Its generator acts on f in $\mathcal{C}^1(\mathcal{S})$ as :

$$\begin{aligned} Lf(x, s) &= \frac{sx(1-x)}{(1+sx)J} \frac{\partial}{\partial x} f(x, s) + \sum_{s' \in E} \frac{\alpha_s Q_{s,s'}}{J} (f(x, s') - f(x, s)) \\ &= L_C f(x, s) + L_D f(x, s) \end{aligned}$$

Recall that our aim is to compare $(\tilde{U}_t^J)_{t \geq 0}$ with $(U_t)_{t \geq 0}$. We will be interested in quantities of the type

$$\mathbb{E}_{x,s} \left[f \left(\tilde{U}_t^J \right) - f(U_t) \right],$$

for $f : \mathcal{S} \rightarrow \mathbb{R}$ regular enough and $(x, s) \in I_J \times E$, where $I_J = \{\frac{i}{J} : i = 0, 1, 2, \dots, J\}$ is the state space of $(X_n^J)_{n \geq 0}$. On the space of continuous functions $f : \mathcal{S} \rightarrow \mathbb{R}$, we consider the semi-norm $\|f\|_J = \max_{(x,s) \in I_J \times E} |f(x, s)|$. For $k \geq 1$, we say that $f : \mathcal{S} \rightarrow \mathbb{R}$ is of class C^k if for all s , the map $f_s : x \mapsto f(x, s)$ is of class C^k . In that case, we denote by $f^{(k)}$ the application defined on \mathcal{S} by $f^{(k)}(x, s) = f_s^{(k)}(x)$.

The following theorem gives an estimation of the error of approximation of our initial Moran process by our PDMP.

Theorem 2. *There exist a function $q : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ at most exponential and a function $k : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ linear in time such that for all $f \in C^3(\mathcal{S})$, for all $t \geq 0$,*

$$\begin{aligned} \max_{(x,s) \in I_J \times E} \mathbb{E}_{x,s} [f(\tilde{U}_t^J) - f(U_t)] &\leq \frac{qt}{J} \left(\|f\|_J + \|f^{(1)}\|_J + \|f^{(2)}\|_J \right) \\ &\quad + k_t \max_{s,s' \in E} \left| JP_{s,s'} - \alpha_s Q_{s,s'} \right| \|f\|_J + O\left(\frac{1}{J^2}\right) \end{aligned}$$

The sketch of the proof is the same as in the article [23]. The complete proof is in appendix. To understand the general dynamic of the PDMP, we first study the vector field of the equation (2) for a non random environment. The following section is dedicated to this study.

2. VECTOR FIELD FOR CONSTANT PARAMETERS.

In all this section, we assume that s is a constant process. In particular, $(X_t)_{t>0}$ is a deterministic process, solution of the ODE

$$\begin{pmatrix} \frac{dX_t^1}{dt} \\ \vdots \\ \frac{dX_t^S}{dt} \end{pmatrix} = \begin{pmatrix} X_t^1 \frac{s^1 - \sum_{k \in \mathbb{S}} X_t^k s^k}{1 + \sum_{k \in \mathbb{S}} X_t^k s^k} \\ \vdots \\ X_t^S \frac{s^S - \sum_{k \in \mathbb{S}} X_t^k s^k}{1 + \sum_{k \in \mathbb{S}} X_t^k s^k} \end{pmatrix} \quad (3)$$

Let us first define the space where the process X_t evolves:

$$\mathcal{E} = \{X \in \mathbb{R}_+^S : \sum_{i=1}^S X^i \leq 1\}.$$

Note that \mathcal{E} can also be seen as the unit simplex in dimension $S + 1$: $\mathcal{E} \simeq \Delta = \{X \in \mathbb{R}_+^{S+1} : \sum_{i=1}^{S+1} X^i = 1\}$. That is why, for $X \in \mathcal{E}$, we set $X^{S+1} = 1 - \sum_{i=1}^S X^i$.

For $1 \leq i \leq S + 1$, we let \mathcal{E}_0^i be the extinction set of species i :

$$\mathcal{E}_0^i = \{X \in \mathcal{E} : X^i = 0\}.$$

We also denote by \mathcal{E}_0 the extinction set, i.e the set where at least one species is extinct:

$$\mathcal{E}_0 = \bigcup_{i=1}^{S+1} \mathcal{E}_0^i.$$

For $1 \leq S$, let e_i denote the i^{th} vector of the standard basis and set $e_{S+1} = 0$. The point e_i correspond to the invasion of species i , that is, species i is the only species in the system. Note that when we see the process as a process in Δ , e_{S+1} is the $(S + 1)^{\text{th}}$ vector of the standard basis. Finally, we set $\mathcal{E}_+^i = \mathcal{E} \setminus \mathcal{E}_0^i$, the set where species i is not extinct and $\mathcal{E}_+ = \mathcal{E} \setminus \mathcal{E}_0$ the set where none of the species is extinct.

Let us remark that \mathcal{E}_0 corresponds to the edges of the set \mathcal{E} , and \mathcal{E}_+ to the interior of \mathcal{E} . It is also easily seen that \mathcal{E} , \mathcal{E}_0^i , \mathcal{E}_0 , \mathcal{E}_+^i and \mathcal{E}_+ are invariant sets for X_t i.e $X_t \in \mathcal{E}$ (respectively \mathcal{E}_0^i , \mathcal{E}_0 , \mathcal{E}_+^i , \mathcal{E}_+) if and only if $X_0 \in \mathcal{E}$ (respectively \mathcal{E}_0^i , \mathcal{E}_0 , \mathcal{E}_+^i , \mathcal{E}_+).

The following theorem states that when the environment does not switch, the species with the highest fitness will invade the community.

Theorem 3.

Let X_t be the solution of (3). Assume that $s^k \neq s^j$ for all $j \neq k$ and set $m = \arg \max_{i \leq S+1} s^i$.

Then if $X_0^m > 0$, X_t converges to e_m .

Proof. By assumption, $s^m > s^j$ for all $j \neq m$. In particular, this implies that $s^m \geq \sum_{j=1}^S s^j X^j$,

with strict inequality as soon as $X^m \neq 1$. In particular, $\frac{dX_t^m}{dt} \geq 0$, and thus X_t^m is non-decreasing. Since X_t^m is bounded above by 1, we conclude that X_t^m converges to some X^m and $\frac{dX_t^m}{dt}$ goes to 0. Now assume that $X_0^m > 0$, then since X_t^m is increasing, $X^m > 0$. Thus

$\lim_{t \rightarrow \infty} \frac{dX_t^m}{dt} = 0$ implies that $\lim_{t \rightarrow \infty} \sum_{j=1}^{S+1} (s^m - s^j) X_t^j = 0$, which due to $s^m > s^j$ implies that $\lim_{t \rightarrow \infty} X_t^j = 0$ for all $j \neq m$. This concludes the proof. \square

Remark 1. One can actually prove that X_t converges to e_m exponentially fast, with rate $\Lambda := -\min_{k \neq m} \frac{(s^m - s^k)}{1 + s^m}$. For a proof of this result, we refer to theorem 9.

Remark 2. If some fitnesses are the same, i.e. $s^j = s^i$ for some $i \neq j$, then the same proof shows that all the species that do not have the best fitness go to extinction. In other words, for all i such that $s^i < s^m$, species i goes to extinction.

Figures 1 and 2 give some examples of vector fields and the trajectories for different initial conditions for one particular vectors field.

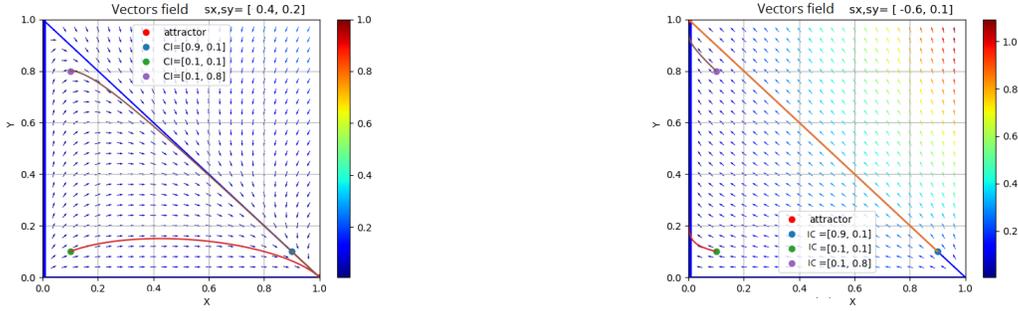


FIGURE 1. Vectors fields and trajectories for different initial conditions (3 species)

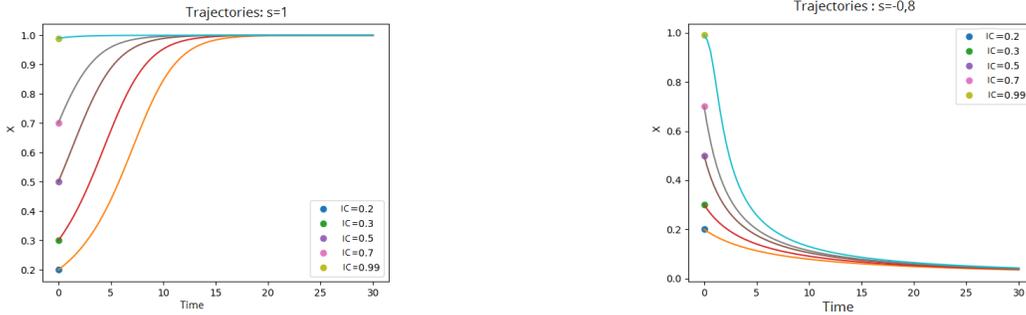


FIGURE 2. Trajectories of X_t for different initial conditions ($S=2$).

The following sections deal with the random process with switched environments. First we treat the case of two species, which is basic but essential to understand the behavior of our population with more species.

3. GENERAL FRAMEWORK AND TOOLS

In this section, $(s_t)_{t>0}$ is Markovian jump process taking values in a finite space $E = \{s_1, \dots, s_K\}$ and having for generator $(Q_{i,j})_{1 \leq i,j \leq K}$. Let s_j^i be the selection parameter of the i^{th} species in environment s_j .

In the discrete model, even if $(s_t)_{t>0}$ is a Markov chain, one species invades the community in a finite time almost surely. This property may still be preserved in weak selection (see for example [24], where examples are given on the selection process leading to a reachable boundary).

In strong selection, even if the selection is deterministic, it is impossible for a species to reach the extinction set in finite time but the process may concentrate in a neighbourhood of extinction and no longer emerge over time, i.e., extinction occurs at an infinite horizon and it is equivalent to a loss of biodiversity. In the following, we prove that under some assumptions, in strong selection it is possible to conserve biodiversity in the community. Moreover we give some information on the long time behavior of the process.

3.1. General framework. In this part, we recall some recent results of Benaïm [9] that will be used in the paper. With the notations of the previous section, we set $M = \mathcal{E} \times E$, $M_0 = \mathcal{E}_0 \times E$ and $M_+ = M \setminus M_0$. We define in a similar way M_0^i and M_+^i .

We consider the process $(U_t)_{t>0} = (X_t, s_t)$ on M starting from (x, s) and defined by :

$$\begin{cases} \frac{dX_t}{dt} = G_{s_t}(X_t) \\ \mathbb{P}_{x,s}(s_{t+h} = s_k | s_t = s_j) = q_{j,k}h + o(h) \quad \text{if } j \neq k \end{cases} \quad (4)$$

with $G_s^i(X) = X^i F_s^i(X)$ and $F_s^i(X) = \frac{s^i - \sum_{k=1}^S s^k X^k}{1 + \sum_{k=1}^S s^k X^k}$ and $q_{j,k}$ are the generator coefficients of the

Markovian jump process.

Finally let $(\Pi_t^u)_{t>0}$ be the empirical occupation measure of the process $(U_t)_{t \geq 0}$, for $U_0 = u = (x, s)$, defined by

$$\Pi_T^u(B) = \frac{1}{T} \int_0^T \mathbb{1}_{\{U_t \in B\}} ds, \quad \forall B \in \mathcal{B}(M)$$

3.2. Stochastic Persistence.

The following definition follows from [35].

Definition 1. The family $\{(U_t)_{t>0}, U_0 \in M^+\}$ is *stochastically persistent* with respect to M_0 if for all $\epsilon > 0$ there exists a compact set $K_\epsilon \in M^+$ such that for all u in M^+ :

$$\mathbf{P}(\liminf_{t \rightarrow 0} \Pi_t^u(K_\epsilon) \geq 1 - \epsilon) = 1$$

This definition means that all the species, initially present, stay away from the extinction set over arbitrary long periods of time. Persistence with respect to M_0^i is defined in the same way.

Definition 2. A probability measure is said to be ergodic for a Markovian process if it is invariant and extremal for the process, meaning that it cannot be written as a nontrivial convex combination of other invariant measures. For a Borelian set B of M , we denote by $\mathcal{P}_{erg}(B)$ the space of ergodic probability measure such as for all μ in $\mathcal{P}_{erg}(B)$, $\mu(B) = 1$.

We recall the definition given in [9] of the invasion rates with respect to an ergodic probability measure in $\mathcal{P}_{erg}(M_0)$.

Definition 3. For $\mu \in \mathcal{P}_{erg}(M_0)$, we introduce $\mu_j(B) = \mu(B \times s_j)$. The invasion rate of species i with respect to μ is defined by :

$$\lambda_i(\mu) = \sum_{1 \leq j \leq K} \int_{M_0} F_{s_j}^i(x) d\mu_j(x).$$

Remark 3. The intuition behind these quantities is the following. On the one hand, from equation (4), we see that whenever $X_0^i \neq 0$, one has

$$\frac{1}{t} \log(X_t^i) = \frac{1}{t} \int_0^t F_{s_u}^i(X_u) du + \frac{1}{t} \log(X_0^i).$$

In particular,

$$\frac{1}{t} \log(X_t^i) \sim \frac{1}{t} \int_0^t F_{s_u}^i(X_u) du$$

as $t \rightarrow \infty$. On the other hand, Birkhoff ergodic's Theorem states that for $\mu \in \mathcal{P}_{erg}(M_0)$, for μ almost every u_0 , \mathbb{P}_{u_0} almost surely,

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t F_{s_u}^i(X_u) du = \sum_{1 \leq j \leq K} \int_{M_0} F_{s_j}^i(x) d\mu_j(x) = \lambda^i(\mu).$$

Thus, $\lambda^i(\mu)$ represent an exponential growth rate of species i near M_0^i .

The following theorem is a consequence of [9, Th. 6.1]. It gives sufficient conditions for the process to be persistent with respect to M_0^i and M_0 , respectively.

Theorem 4. (1) Assume that for all $\mu \in \mathcal{P}_{erg}(M_0^i)$, $\lambda^i(\mu) > 0$. Then the process given by (4) is H -persistent with respect to M_0^i .
 (2) Assume that there exists positive numbers $\{c^i, 1 \leq i \leq S+1\}$ such that, for all $\mu \in \mathcal{P}_{erg}(M_0)$,

$$\sum_{1 \leq i \leq S+1} c^i \lambda_i(\mu) > 0.$$

Then the process given by (4) is H -persistent with respect to M_0 .

The first point of the above theorem can be interpreted as follows. If for some species i , one has $\lambda_i(\mu) > 0$ for all $\mu \in \mathcal{P}_{erg}(M_0^i)$, then the face \mathcal{E}_0^i is *repulsive* : if the process start in \mathcal{E}_+^i and close to the face \mathcal{E}_0^i , then the process is in some sense pushed away from \mathcal{E}_0^i . The second point states that the process is pushed away from every face, and thus concentrates on the interior M_+ of the domain.

3.3. Behavior near a common zero. The previous theorem gives some way to understand the behavior of the process near the boundary \mathcal{E}_0^i , which corresponds to the extinction of species i . It is also important to understand the process near the vertex e_i , which corresponds to the invasion of species i . Since the $\{e_i\}_{i < S+1}$ are common zero of the vector fields G_s , we can use the recent results of [8] and [37]. According to these papers, the behavior of the process $(U_t)_{t > 0}$ near e_i for some $1 \leq i \leq S+1$ is controlled by the behavior of the linear process $V_t = (Y_t^i, s_t)$, where $(s_t)_{t \geq 0}$ is the Markov process with generator Q and Y^i evolves according to

$$\frac{dY_t^i}{dt} = A_{s_t}^i Y_t^i,$$

where A_s is the Jacobian matrix of G_s at e_i . Assume with no loss of generality that $i = 1$. Then $A_s^i = DG_s(e_1)$ is given by

$$A_s^i = \begin{pmatrix} \frac{-s^1}{1+s^1} & * \\ 0 & D_s \end{pmatrix},$$

where $*$ is a $1 \times (S-1)$ vector and D_s is a $(S-1) \times (S-1)$ diagonal matrix given by

$$D_s = \text{diag} \left(\frac{s^2 - s^1}{1 + s^1}, \dots, \frac{s^S - s^1}{1 + s^1} \right).$$

In the particular case $i = S+1$, (recall $e_{S+1} = 0$),

$$DG_s(e_{S+1}) = \text{diag}(s^1, \dots, s^S).$$

4. STUDY FOR TWO SPECIES IN A TWO-STATES ENVIRONMENT

We consider in this section $S = 1$, i.e there is only two species in the community. The vectors field have the form:

$$\begin{cases} \frac{dX_t^1}{dt} = X_t^1 \frac{s_t - s_t X_t^1}{1 + s_t X_t^1} \\ \frac{dX_t^2}{dt} = X_t^2 \frac{-s_t X_t^1}{1 + s_t X_t^1} \end{cases} \quad (5)$$

As before, since $X_t^1 + X_t^2 = 1$, we only study $(X_t^1)_{t>0}$, that we denote simply by $(X_t)_{t>0}$. Thus we are interested in the study of

$$\frac{dX_t}{dt} = s_t \frac{X_t(1 - X_t)}{1 + s_t X_t}. \quad (6)$$

Moreover, we assume that $K = 2$, the community evolves in two different environments. The selective parameters takes values in $E = \{(s_1, 0), (s_2, 0)\}$. It is possible to take more than two values for the fitness, and the following reasoning still hold. We restrict this study to the case of two values to simplify the notations. Assume moreover $q_1 := q_{1,2} > 0$ and $q_2 := q_{2,1} > 0$, and so $(s_t)_{t>0}$ has an unique invariant probability measure $\mu = p_1 \delta_{s_1} + p_2 \delta_{s_2}$, where $p_1 = \frac{q_2}{q_1 + q_2}$ and $p_2 = \frac{q_1}{q_1 + q_2}$. We set $M = [0, 1] \times E$ and $M_0 = \{0, 1\} \times E$. It is easily checked that $\mathcal{P}_{erg}(M_0) = \{\mu_1, \mu_2\} = \{\delta_0 \otimes \mu, \delta_1 \otimes \mu\}$. To avoid trivial switching, we assume that $s_1 \neq s_2$, and without loss of generality, we assume that $s_1 > s_2$. For $i \in \{1, 2\}$, we define $g_i : [0, 1] \rightarrow \mathbb{R}$ by

$$g_i(x) = s_i \frac{x(1-x)}{1 + s_i x}.$$

We set

$$\Lambda_0 = p_1 s_1 + p_2 s_2 \quad \text{and} \quad \Lambda_1 = - \left(p_1 \frac{s_1}{1 + s_1} + p_2 \frac{s_2}{1 + s_2} \right).$$

These quantities are the average growth rate of $(X_t)_{t>0}$ at 0 and 1, respectively. The following proposition gives the behavior of the process according to the signs of Λ_0 and Λ_1 .

Proposition 5. *We can describe four regimes :*

- (1) *If $\Lambda_0 < 0$, then $\Lambda_1 > 0$, and, for all $x \in (0, 1)$ and $s \in E$,*

$$\mathbb{P}_{x,s} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log(X_t) \leq \Lambda_0 \right) = 1.$$

In particular, species 1 goes extinct.

(2) If $\Lambda_1 < 0$, then $\Lambda_0 > 0$, and, for all $x \in (0, 1)$ and $s \in E$,

$$\mathbb{P}_{x,s} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log(1 - X_t) \leq \Lambda_1 \right) = 1.$$

In particular, species 2 goes extinct.

(3) If $\Lambda_0 > 0$ and $\Lambda_1 > 0$, there exists an unique invariant probability measure π such that $\pi(\{0\} \times E) = \pi(\{1\} \times E) = 0$. Moreover, π is absolutely continuous with respect to the Lebesgue measure on $[0, 1] \times E$ with explicitly computable density, and there exist $C, \theta, \gamma > 0$ such that, for all $(x, s) \in (0, 1) \times E$ and all $t \geq 0$,

$$\|\mathbb{P}_{x,s}(X_t \in \cdot) - \pi\|_{TV} \leq C((x)^{-\theta} + (1-x)^{-\theta})e^{-\gamma t}.$$

In particular, both species persist.

(4) If $\Lambda_0 = 0$ or $\Lambda_1 = 0$, then the only invariant probability measures of the process $((X_t, s_t))_{t \geq 0}$ are μ_1 and μ_2 .

In particular, the process is not persistent.

Proof. We prove (1), the proof of (2) being the same as the one of (1) by switching species 1 and 2. Assume that $\Lambda_0 < 0$. In particular, $s_2 < 0$ and $p_1 s_1 < -p_2 s_2$, which implies that

$$-\Lambda_1 < -\left(\frac{1}{1+s_1} - \frac{1}{1+s_2} \right) p_2 s_2 < 0,$$

proving that $\Lambda_1 > 0$. Now since $\Lambda_0 > 0$, [8, Th. 3.1], implies that there exist $c > 0$ and $\eta > 0$ such that for all $x \in (0, c)$ and $s \in E$

$$\mathbb{P}_{x,s}(\limsup_{t \rightarrow \infty} \frac{1}{t} \log(X_t) \leq \frac{\Lambda_0}{2}) \geq \eta. \quad (7)$$

On the other hand, because $\Lambda_1 > 0$, there exists by Theorem 3.2 in [8] $\varepsilon > 0$ such that for all $x \neq 0$,

$$\mathbb{P}_{x,s}(\tau < \infty) = 1, \quad (8)$$

where $\tau = \inf\{t \geq 0 : X_t \leq 1 - \varepsilon\}$. Finally, because 0 is a globally asymptotically stable equilibrium of f^0 on $[0, 1)$, one can show that there exists a constant $C > 0$ such that for all $x \in [0, 1 - \varepsilon]$,

$$\mathbb{P}_{x,s}(Z_t \in \mathcal{U} \times E) \geq C. \quad (9)$$

Like in [7, Th. 3.1], Equations 7, 8 and 9 enable to conclude the proof of point 1.

We pass to the proof of point (3). Since Λ_0 and Λ_1 are positive, [8, Th. 3.2] implies that for all $\varepsilon > 0$, there exists $1 > r > 0$ such that, for all $(x, s) \in (0, 1) \times E$, almost surely

$$\liminf \frac{1}{t} \int_0^t \mathbb{1}_{r < X < 1-r} ds \geq 1 - \varepsilon.$$

This implies that the the sequence $(\Pi_t)_{t > 0}$ is almost surely tight in $(0, 1)$. Moreover, every limit point of (Π_t) is an invariant probability measure for $(X_t, s_t)_{t > 0}$ (see [9, Th. 2.1]). Thus, the process admits an invariant probability measure π on $(0, 1) \times E$. Uniqueness, absolute continuity and convergence in total variation easily follow from Theorem 4.10 in [9] and Theorem 4.4 in [6].

Point (4) is proven in the following lemma as in [26]. □

Remark 4. Note that this property still holds for any number of environments K , with $\Lambda_0 = \sum_{i \leq K} p_i s_i$ and $\Lambda_1 = - \sum_{i \leq K} p_i \frac{s_i}{1+s_i}$.

In the following lemma, we describe more precisely the case where the growth rates are positive by computing explicitly the density of the invariant probability measure concentrated on $(0, 1) \times E$.

Lemma 6. *Assume that $(U_t)_{t>0}$ admits an invariant probability measure Π on $(0, 1) \times E$. Then Π is absolutely continuous with respect to the Lebesgue measure on $(0, 1) \times E$. Moreover, denote by h_1 and h_2 the densities of $\Pi(\cdot, 0)$ and $\Pi(\cdot, 1)$, respectively. Then for all $x \in (0, 1)$,*

$$h_i(x) = \frac{H(x)}{|g_i(x)|},$$

where

$$H(x) = C(1-x)^{\beta\Lambda_1}x^{\alpha\Lambda_0},$$

with $\alpha = \frac{q_1+q_2}{|s_1s_2|}$ and $\beta = \alpha(1+s_1)(1+s_2)$ and C the positive constant such that $\int_0^1(h_1+h_2) = 1$. In particular, if $\Lambda_0 = 0$ or $\Lambda_1 = 0$, U cannot admits such an invariant probability measure.

Proof. Let us assume that $(U_t)_{t>0}$ admits an invariant probability measure Π on $(0, 1) \times E$. This implies that $s_1 > 0$ and $s_2 < 0$. Indeed, by Proposition 5, if $\Lambda_0 < 0$, X_t converges almost surely to 0, and in particular cannot admit an invariant probability measure on $(0, 1) \times E$. Thus we need $\Lambda_0 \geq 0$ and since we have assumed that $s_1 > s_2$, this implies $s_1 > 0$. For the same reason, Λ_1 must be non-negative, implying $s_2 < 0$. Thus, all the point in $[0, 1]$ are accessible, yielding that the support of Π has to be $[0, 1] \times E$ (see Proposition 3.17 in [6]). Moreover, since for every $x \in (0, 1)$, $f^1(x) > 0$, the weak bracket condition hold and Π is unique and admits a density with respect to the Lebesgue measure (see [6] or [3]). Moreover, this also implies by Theorem 1 in [4] that the densities h_i are C^∞ on $(0, 1)$. Thus, h_1 and h_2 satisfy the Fokker-Planck equations (see e.g [4, section 7.2], [7], or [19]) :

$$\begin{cases} q_1h_1 - q_2h_2 &= -(g_1h_1)' \\ q_1h_1 - q_2h_2 &= (g_2h_2)' \end{cases} \quad (10)$$

Now, one can check that the functions given above satisfy these equations. Moreover, since h_1 and h_2 are densities, they satisfy $\int_0^1 h_1 + h_2 = 1$; in particular they are integrable on $(0, 1)$. This is the case if and only if $\Lambda_0 > 0$ and $\Lambda_1 > 0$. Therefore, if you assume that $\Lambda_0 = 0$ or $\Lambda_1 = 0$, $(U_t)_{t>0}$ cannot admit an invariant probability measure on $(0, 1) \times E$, for otherwise it would have densities satisfying equations 10, hence densities that are not integrable on $(0, 1)$, a contradiction. \square

Example 1. Consider $p_1 = p_2$, i.e the jump rate are the same for both environments. So, let simplify conditions 3) of property 5 to obtain the following conditions of persistence:

$$\begin{cases} s_2 < \frac{-s_1}{1+2s_1} \\ s_2 > -s_1 \end{cases}$$

Note that if s_1 is smaller than -0.5 the first condition is automatically verified.

Then take the particular case $s_1 = 1$. Then the previous condition to have persistence becomes $s_2 < \frac{-1}{3}$.

To illustrate, we plot the comportment of the process for two values of s_2 close to $\frac{-1}{3}$, -0.3 and -0.4 .

Note that for $s_2 = -0.4$ the process seems to be persistent whereas for $s = -0.3$ it seems to be absorbed quickly. So the numerical simulations are consistent with the condition giving by Proposition 5 .

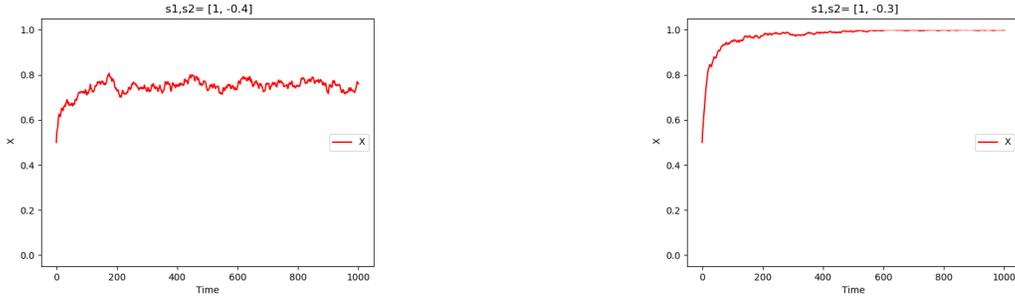


FIGURE 3. Plots of the average of $(X_t)_{t>0}$ for different fitnesses, obtained by Monte Carlo method with 500 trajectories.

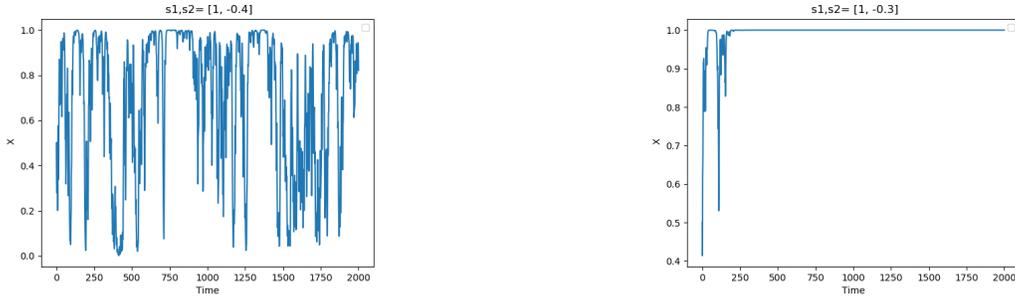


FIGURE 4. Trajectory of $(X_t)_{t>0}$ for two different fitness

Example 2. This second example illustrate the case 4) of Proposition 5. Assume as in the previous example $p_1 = p_2$ and take $s_1 = -s_2$, so $\Lambda_0 = 0$ and $\Lambda_1 = \frac{2s_1^2}{1-s_1^2} > 0$

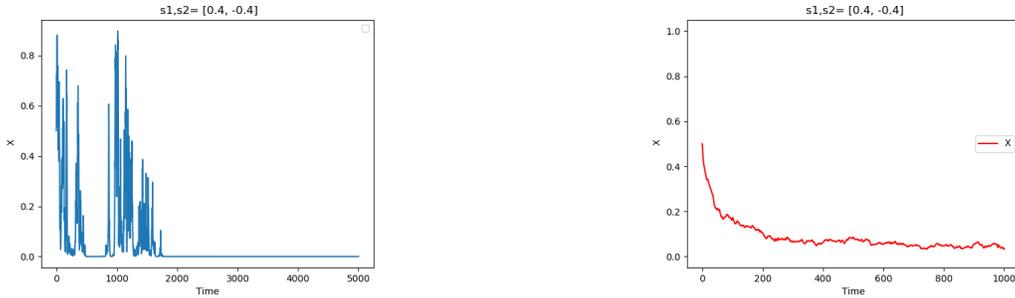


FIGURE 5. Trajectories of $(X_t)_{t>0}$ and the average of $(X_t)_{t>0}$ for different fitness, obtain by Monte Carlo method with 500 trajectories. Parameters are $s_1 = -s_2 = 0.4$, $q_{1,2} = q_{2,1} = 1/2$.

As stipulated in Proposition 5, the process is not persistent. Moreover, the fact that Λ_1 is positive prevents species 2 from extinction. The numerical simulations suggest that the first species disappears.

Example 3. In this example, we illustrate Lemma 6. Recall that if the parameters are such that the process is persistent, then the invariant distribution Π on M_+ have explicit densities,

given by

$$h_i(x) = \frac{C}{|s_i|} (1-x)^{\beta\Lambda_1-1} x^{\alpha\Lambda_0-1} (1+s_i x),$$

where $\alpha = \frac{q_1+q_2}{|s_1 s_2|}$ and $\beta = \alpha(1+s_1)(1+s_2)$. In particular, it can exhibit several behaviours at the boundaries 0 and 1, according to the sign of $\beta\Lambda_1 - 1$ and $\alpha\Lambda_0 - 1$. Let us fix $s_2 = -0.2$, and jump rates $q_1 = q_2 = q$. In particular, $p_1 = p_2$ and the process is persistent if and only if $0.2 < s_1 < 1/3$. Fix $q = 1$. Then, it is easily seen that $\beta\Lambda_1 - 1 > 0$ if and only if $s_1 < 1/4$; whereas $\alpha\Lambda_0 - 1 > 0$ if and only if $s_1 > 1/4$. In particular, if $s_1 \in (0.2, 1/4)$, then $\lim_{x \rightarrow 0} h_i(x) = +\infty$ and $\lim_{x \rightarrow 1} h_i(x) = 0$, whereas if $s_1 \in (1/4, 1/3)$, then we have the converse situation, i.e. $\lim_{x \rightarrow 0} h_i(x) = 0$ and $\lim_{x \rightarrow 1} h_i(x) = +\infty$. This is illustrated in Figure 6. Now fix $s_2 = -0.2$ and $s_1 = 0.27$. Then, once again it is easy to check that $\beta\Lambda_1 - 1 > 0$ if and only if $q > 0.259/5$; whereas $\alpha\Lambda_0 - 1 > 0$ if and only if $q > 10/7$. Thus, we have three regimes :

- (1) if $q < 0.259/5$, then $h_i(x)$ goes to infinity both at 0 and 1;
- (2) if $q \in (0.259/5, 10/7)$, then $h_i(x)$ vanishes at 0 and explodes at 1;
- (3) if $q > 10/7$, then $h_i(x)$ vanishes both at 0 and 1.

Plots of h_1 are presented in Figure 7 for situation (1) and (3), situation (2) is plot on the right of Figure 6. This example shows that even if the process is persistent, the stationary distribution Π certainly does not give mass to 0 and 1, but can be concentrated close to the extinction points. In the example with $s_1 = 0.27$, $s_2 = -0.2$ and $q < 0.259/5$, the intuition is the following. Since q is very small, the environment s takes a really long time before changing. During this time, the process is getting really close to the boundary (say 0 if we are following s_2), and spend a huge time here. When a switch occurs, the process goes away from 0 fast enough, and come close to 1 where it spends again a long time, and so on. In particular, it is much more likely that a switch occurs in the neighbourhood of 0 or 1, than in the middle. That is why, the process does not stay for a long time in the middle part, and concentrates near the boundaries.

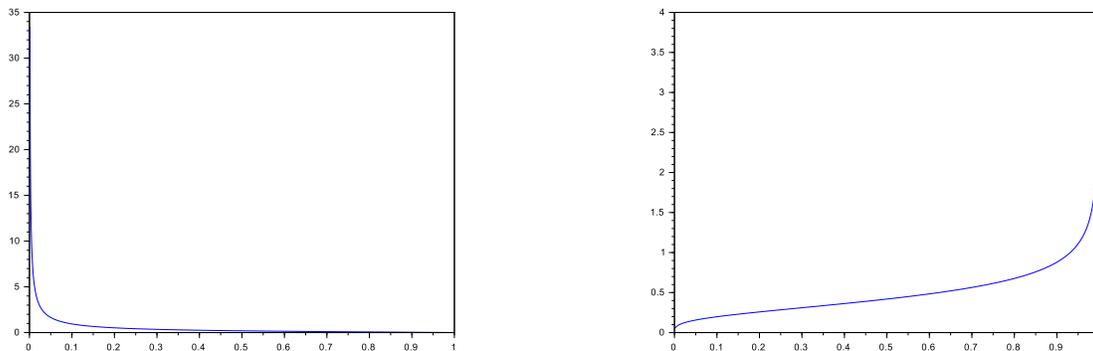


FIGURE 6. Plot of h_1 for $q = 1$ and $s_1 = 0.21$ (left) and $s_1 = 2.07$ (right)

These examples concludes the study for two species. We now generalise some properties to a larger number of species and any number of environments. The space M is no longer a line but a tetrahedron and the extinction set M_0 correspond to the face of M . Of course some intuitive behavior, as the fact that if a species has always the best fitness, it invades the

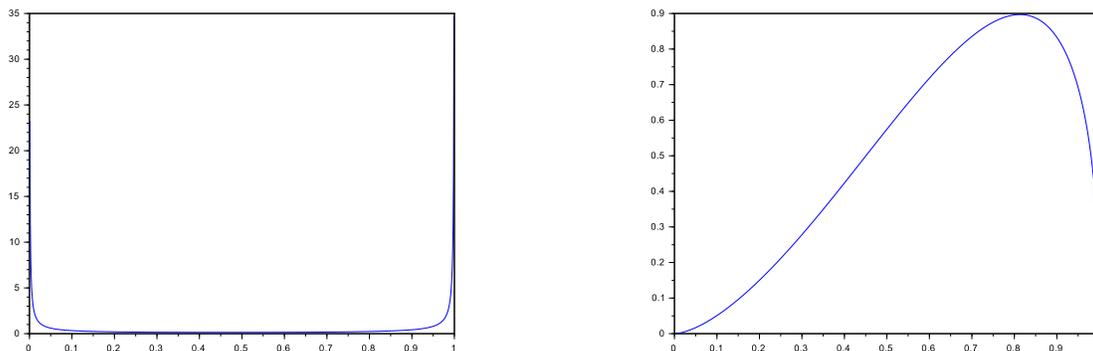


FIGURE 7. Plot of h_1 for $s_1 = 0.27$ and $q = 0.04$ (left) and $q = 2$ (right)

community, is still true. But many arguments used in previous part to prove these results are specific to dimension one and does not hold anymore.

5. GENERAL RESULTS

In this section we keep the notations of part 1.1. We assume that the Markov chain $(s_t)_{t \geq 0}$ is irreducible on E . Hence, it admits a unique invariant probability measure on E , denoted by $\mu = p_1 \delta_{s_1} + \dots + p_K \delta_{s_K}$.

We describe now some behavior of the process in some remarkable environments.

5.1. Sufficient conditions for a species to invade (or not) the community. In this section, we provide sufficient condition for a species to have a positive probability of invading the community. Furthermore, we prove that if one species have a positive probability to invade the community, then all the other ones cannot invade. For $i_0 \in \{1, \dots, S+1\}$, we set

$$\Lambda_{i_0} = \max_{i \neq i_0} \sum_{j=1}^K p_j \frac{s_j^i - s_j^{i_0}}{1 + s_j^{i_0}}$$

Theorem 7. *Assume that for some $i_0 \in \{1, \dots, S+1\}$, $\Lambda_{i_0} < 0$. Then, for all $\alpha \in (\Lambda, 0)$, there exist $\eta > 0$ and a neighbourhood \mathcal{U} of e_{i_0} such that, for all $x \in \mathcal{U}$ and all $\mathbf{s} \in E$,*

$$\mathbb{P}_{(x, \mathbf{s})} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log \|X_t - e_{i_0}\| \leq \alpha \right) \geq \eta.$$

Furthermore, for all $i \neq i_0$, we have $\Lambda_i > 0$, and there exist $b > 1$, $\varepsilon > 0$, θ and $c > 0$ such that, for all $x \in \mathcal{E} \setminus \mathcal{E}_0$, $s \in E$ and $i \neq i_0$,

$$\mathbb{E}_{(x, \mathbf{s})}(e^{b\tau_i^\varepsilon}) \leq c(1 + \|x - e_i\|^{-\theta}),$$

where

$$\tau_i^\varepsilon = \inf\{t \geq 0 : \|X_t - e_i\| \geq \varepsilon\}.$$

Proof. Without loss of generality, we assume that $i_0 = 1$, and we set $\Lambda = \Lambda_1$. We set $M_0^1 = \mathcal{E}_0^1 \times E$ and $M_1^+ = M \setminus M_0^1$.

First, we note that $e_1 = (1, 0, \dots, 0)$ is a common zero for all the G_s , $s \in E$, and that for all $i \geq 2$, \mathcal{E}_0^i is a common invariant face for the process. Moreover, the Jacobian matrix of G_s

at e_1 is given by

$$A_s = \begin{pmatrix} \frac{-s^1}{1+s^1} & * \\ 0 & D_s \end{pmatrix},$$

where $*$ is a $1 \times (S-1)$ vector and D_s is a $(S-1) \times (S-1)$ diagonal matrix given by

$$D_s = \text{diag} \left(\frac{s^2 - s^1}{1 + s^1}, \dots, \frac{s^S - s^1}{1 + s^1} \right).$$

By assumption, $\Lambda < 0$, which implies by Theorem 2.7 in [37] (or Proposition 2.5 in [37] and Theorem 3.5 in [8]) that for all $\alpha \in (\Lambda, 0)$, there exists $\eta > 0$ and a neighbourhood \mathcal{U} of e_1 such that, for all $x \in \mathcal{U}$ and all $\mathbf{s} \in E$,

$$\mathbb{P}_{(x, \mathbf{s})} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log \|X_t - e_1\| \leq \alpha \right) \geq \eta,$$

which concludes the proof of the first assertion.

We now prove the second assertion. Let $i \neq 1$. Since $\Lambda_1 < 0$, we have

$$\sum_{j=1}^K p_j \frac{s_j^i - s_j^1}{1 + s_j^1} < 0$$

As in Proposition 5, we can show that this last inequality implies that

$$\sum_{j=1}^K p_j \frac{s_j^1 - s_j^i}{1 + s_j^i} > 0$$

and thus that $\Lambda_i > 0$. Without loss of generality, we assume now that $i = S+1$. We set

$$\Lambda_{S+1}^- = \min_{k \leq S} \sum_{j=1}^K p_j s_j^k,$$

and we distinguish two cases. If $\Lambda_{S+1}^- > 0$, Proposition 2.5 in [37] and Theorem 3.5 in [8] conclude the proof. If $\Lambda_{S+1}^- < 0$, we assume without loss of generality that there exists k_0 such that $\sum_{j=1}^K p_j s_j^k > 0$ for $k \leq k_0$ and $\sum_{j=1}^K p_j s_j^k < 0$ for $k > k_0$. We set

$$\mathcal{E}_0^{1, \dots, k_0} = \bigcap_{k=1}^{k_0} \mathcal{E}_0^k,$$

which is the set of extinction of the k_0 -th first species. This set is invariant for all the vector fields G_s . Moreover, the Jacobian matrix of G_s at $e_{S+1} = 0$ is given by

$$DG_s(e_i) = \text{diag} (s^1, \dots, s^S).$$

Now, by definition of k_0 , the assumptions of Theorem 2.8 in [37], except for the accessibility of 0 from $\mathcal{E}_0^{1, \dots, k_0}$, are satisfied. However, since [37][Theorem 2.8 (iii)] is a local result, and since we get a probability of convergence to 0 which is bounded below in a neighbourhood of 0 in $\mathcal{E}_0^{1, \dots, k_0}$, a localisation argument similar to the one given in [25] enables us to conclude. \square

This theorem states that when $\Lambda_{i_0} < 0$, species i_0 has a positive probability to invade the community, while if $\Lambda_{i_0} > 0$, species i_0 cannot invade the community. Furthermore, it is only possible to have one species satisfying $\Lambda_{i_0} < 0$. Let us finish by an interesting related result that up to now we can only pose as a conjecture.

Conjecture 8. *If $\Lambda_{i_0} < 0$, then for all x with $x^{i_0} \neq 0$ and all $s \in E$,*

$$\mathbb{P}_{(x,s)} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log \|X_t - e_{i_0}\| \leq \Lambda_{i_0} \right) = 1.$$

5.2. The same species has always the best fitness.

In this section, we prove that if one of the species has always the best fitness, then this species take the upper hand on every over one. We have the following result, which generalizes Theorem 3:

Theorem 9. *Assume that for all $j \in \{1, \dots, K\}$ and $i \in \{2, \dots, S+1\}$, one has $s_j^1 > s_j^k$, and set*

$$\Lambda = \max_{2 \leq i \leq S+1} \sum_{j=1}^K p_j \frac{s_j^i - s_j^1}{1 + s_j^1} < 0.$$

Then, for all $x \in \mathcal{E}$ with $x^1 > 0$ and all $s \in E$, one has

$$\mathbb{P}_{x,s} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log \|X_t - e_1\| \leq \Lambda \right) = 1.$$

Proof. We use Theorem 3.8 in [8]. By Theorem 7, we know that for all $\alpha \in (\Lambda, 0)$, there exists $\eta > 0$ and a neighbourhood \mathcal{U} of e_{i_0} such that, for all $x \in \mathcal{U}$ and all $\mathbf{s} \in E$,

$$\mathbb{P}_{(x,s)} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log \|X_t - e_{i_0}\| \leq \alpha \right) \geq \eta.$$

Furthermore, since e_1 is an asymptotically stable equilibrium whose basin of attraction is \mathcal{E}_1^+ for each G_s , we deduce that the point e_1 is accessible from \mathcal{E}_1^+ for the PDMP. This means that each neighbourhood of e_1 can be reached with positive probability by the process (see [6] for a precise definition). Since the set \mathcal{E}_1^+ is not compact, we have to study the behavior of the process near \mathcal{E}_0^1 to conclude that the process converges to e_1 with probability one from everywhere in \mathcal{E}_1^+ . For all $s \in E$, we have

$$F_s^1(x) = \frac{s^1 - \sum_{i=1}^S s^i x^i}{1 + \sum_{i=1}^S s^i x^i}$$

By assumption, for all $x \in \mathcal{E}_0^1$, one has $F_s^1(x) > 0$. This implies that for all $\mu \in \mathcal{P}_{erg}(\mathcal{E}_0^1)$, $\lambda_1(\mu) > 0$. In particular, the process is H -persistent with respect to \mathcal{E}_0^1 . Therefore, by [9, Proposition 8.2], there exists a Lyapunov function for the process near \mathcal{E}_0^1 and thus Hypothesis 3.7 in [8] is satisfied for the set M_1^+ . This concludes the proof by Theorem 3.8 in [8]. \square

5.3. A species is always disadvantaged with respect to the other species in each environment.

With no loss of generality, we assume the species 1 is always disadvantaged with respect to the other species. More precisely for each environment, the species 1 has a negative fitness.

We assume moreover that the last species is not extinct, i.e $1 - \sum_{k=1}^S x^k > 0$.

We now prove in this situation that the species 1 is going to 0. The strategy is to show that the vector field is always entering in $E_b = \{(x^1, \dots, x^S) \in E : x_1 < b(1 - \sum_{k=2}^S x^k)\}$, for

all $b \in]0, 1[$. Hence, if the process enters in E_b , it cannot escape E_b . Then, we prove, for all $b \in]0, 1[$, the hitting time of E_b is finite.

Let us consider the hyperplane of the form $\Delta_b : \{(x^1, \dots, x^S) \in E : x_1 = b(1 - \sum_{k=2}^S x^k)\}$ for b in $]0, 1[$. This is the hyperplane passing through the points be_1, e_2, \dots, E , where e_i is the i^{th} vector of the natural base, and E_b is the area under Δ_b . The following proposition proves that for each environment, the vector field is entering in E_b .

Proposition 10. *Let s_i be such that $s_i^1 < 0$ for $i \in 1, \dots, K$, then for all b in $]0, 1[$, E_b is a trap area for the process X_t .*

Proof. Consider a fixed environment and note s^k the fitness of the k^{th} species. Let us start by remarking that $v_b = (1, b, \dots, b)$ is an orthogonal vector of the hyperplane Δ_b , pointing outward E_b . Now, we look at the sign of projection of the vector field (dX^1, \dots, dX^S) at the point $\delta_b = (b(1 - \sum_{k=2}^S x^k), x^2, \dots, x^S)$ of Δ_b on v_b . If the result is strictly negative for all x and b in $]0, 1[$, along Δ_b , the vector field is entering in E_b .

$$\begin{aligned} & \left\langle (dX^1, \dots, dX^S)(\delta_b); v_b \right\rangle < 0 \\ & \Leftrightarrow b \left(1 - \sum_{k=2}^S x^k \right) \left(s^1 - \sum_{k=1}^S s^k x^k \right) + b \left(\sum_{k=2}^S x^k \left(s^k - \sum_{k=1}^S x^k s^k \right) \right) < 0 \\ & \Leftrightarrow bs^1 \left(1 - \sum_{k=1}^S x^k \right) < 0 \\ & \Leftrightarrow s^1 < 0 \end{aligned}$$

Therefore, the vector field is entering in E_b if and only if $s^1 < 0$. But we assumed $s_i^1 < 0$ for each i , so for all environments the vector field is entering in E_b . This concludes the proof. \square

Corollary 11. *Assume that $s_i^1 < 0$ for each i . Then the process $(X_t)_{t>0}$, starting at (x^1, \dots, x^{S+1}) such that $1 - \sum_{k=1}^S x^k > 0$, verifies $\lim_{t \rightarrow \infty} X_t^1 = 0$. In particular species 1 goes to extinction.*

Proof. Denote now by b_t the intersection between the hyperplane passing through the points X_t, e_2, \dots, E and the straight line directed by e_1 . By the previous propriety, for all t , E_{b_t} is a trap area. Moreover the species 1 has in each environment a strictly negative fitness, so by the previous calculation the vector field on Δ_{b_t} is strictly entering. Consequently, b_t is strictly decreasing and b_t converges to b_{lim} . Note that by definition and the previous proposition, for all $t \geq 0$, $X_t^1 \leq b_t$. Hence, if $b_{lim} = 0$, X_t^1 converges to 0.

If $b_{lim} \neq 0$, the process converges to $\Delta_{b_{lim}}$. Necessarily the process converges to an invariant area included in $\Delta_{b_{lim}}$. But according to the previous proposition, on each point of $\Delta_{b_{lim}}$ where $\left(1 - \sum_{k=1}^S x^k \right) \neq 0$, all the vector fields are strictly entering in $E_{b_{lim}}$. So this invariant area is also included in $\left(1 = \sum_{k=1}^S x^k \right)$, which implies $X^1 = b_{lim}X^1$. Since $b_{lim} \neq 0$, we conclude that $X^1 = 0$. Thus, species one goes to extinction in all cases. \square

Remark 5. A immediate corollary of this property is, if a species has always the best fitness in each environment, then it invades the community. Note that Theorem 9 above proves this fact independently and gives the rate of convergence.

Let us now give an example to illustrate this property .

Example 4. Consider the case of three species and two environments, we take the notation of part 6.1.

Assume the species Y has always a negative fitness, and the fitness are ordered like :

$$\begin{cases} s_1 > 0 > r_1 \\ 0 > r_2 > s_2 \end{cases}$$

In Figure 4 are plotted the phase portrait of the vectors fields for each environment.



FIGURE 8. Vectors fields and trajectories for the previous configuration of fitness

In this situation Δ_b is a straight line in red on figure 9 and the v_b correspond to the direction of the green straight line.

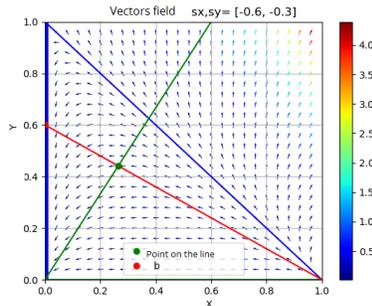


FIGURE 9. Illustration of Δ_b and v_b .

Figure 9 shows that the field is entering in E_b , and this true for each b . The conclusion follows, the Y species goes to extinction. The following figure illustrate a trajectory where the species Y has always a negative fitness.

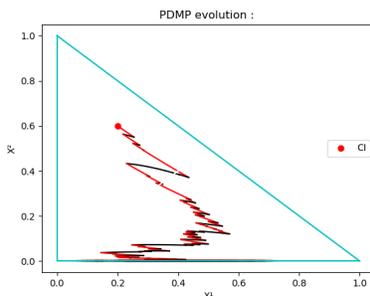


FIGURE 10. A PDMP trajectory where the 2nd species goes to extinction. The values of environments are $s_1 = [0.4, -0.1]$ and $s_2 = [-0.3, -0.2]$.

We now look at the case of three species and two jumps rates. Previous theorems find their application in this particular case. The two dimensional study made in Section 4 is also necessary to understand the long time behavior of the process. The space of extinction M_0 corresponds here to the side of the triangle defined by the apex $(0, 0)$, $(1, 0)$, $(0, 1)$. Thus understanding the long time behavior requires knowledge of the invariant measures of the process on M_0 . In particular the behaviors of the process on each side of the triangle, which corresponds to studying the process with only two species.

6. THE CASE OF 3 SPECIES

6.1. Introduction. For sake of simplicity, when there are only three species, we use the notations X , Y and Z , instead of X^1 , X^2 , X^3 . We also denote by s_k and r_k the fitness in environment $k \in \{1, \dots, K\}$ of species X and Y , respectively (remember that we have set the fitness of the third species to be 0). Since we have for all $t \geq 0$, $X_t + Y_t + Z_t = 1$, we are interested in the following equations :

$$\begin{cases} \frac{dX_t}{dt} = X_t \frac{s_t - s_t X_t - r_t Y_t}{1 + s_t X_t + r_t Y_t} \\ \frac{dY_t}{dt} = Y_t \frac{r_t - s_t X_t - r_t Y_t}{1 + s_t X_t + r_t Y_t} \end{cases} \quad (11)$$

The community still evolves in two different environments. The fitness takes values in $E = \{\mathbf{s}_1 = (s_1, r_1, 0), \dots, \mathbf{s}_K = (s_K, r_K, 0)\}$. To avoid trivial switching, we assume that $\mathbf{s}_i \neq \mathbf{s}_j$ if $i \neq j$. Assume yet that $(\mathbf{s}_t)_{t>0}$ has a unique invariant probability measure $\mu = \sum_{i=1}^K p_i \delta_{\mathbf{s}_i}$.

The set of ergodic measures of the process on M_0 , $\mathcal{P}_{erg}(M_0)$, depends on the values of the environment. This set always contains $\mu_3 = \delta_{(0,0)} \otimes \mu$, $\mu_2 = \delta_{(0,1)} \otimes \mu$ and $\mu_1 = \delta_{(1,0)} \otimes \mu$, the Dirac masses on each vertex. But on each side, it may have one other ergodic measure. It corresponds to persistence of the two remaining species on this side. Let's give more details about it:

Proposition 12. *Let define*

$$\begin{aligned}\Lambda_0^1 &= \sum_{i=1}^K p_i r_i, & \Lambda_1^1 &= \sum_{i=1}^K -p_i \frac{r_i}{1+r_i} \\ \Lambda_0^2 &= \sum_{i=1}^K p_i s_i, & \Lambda_1^2 &= \sum_{i=1}^K -p_i \frac{s_i}{1+s_i} \\ \Lambda_0^3 &= \sum_{i=1}^K p_i \frac{r_i - s_i}{1+s_i}, & \Lambda_1^3 &= \sum_{i=1}^K p_i \frac{s_i - r_i}{1+r_i}\end{aligned}$$

Then the process admits an ergodic measure, ν_i on $\text{int}(\mathcal{E}_0^i) \times E$ if and only if $\Lambda_0^i > 0$ and $\Lambda_1^i > 0$. Furthermore, this ergodic measure is unique and explicitly computable.

Proof. This property is a corollary of Proposition 5. □

When Λ_0^i and Λ_1^i are positive, we denote by ν_i the unique ergodic measure on $\text{int}(\mathcal{E}_0^i) \times E$.

Remark 6. The signs of Λ_0^i and Λ_1^i determines the behavior of the process on side i in a neighbourhood of the extinction and the invasion, respectively, for the i^{th} species.

6.2. Study for two environmental states.

Now we assume $K = 2$, then $\mu = p_1 \delta_{s_1} + p_2 \delta_{s_2}$ with $p_1 = \frac{q_2}{q_1+q_2}$ and $p_2 = \frac{q_1}{q_1+q_2}$

We now describe the different possible regimes according to the values of the parameters.

- If a species, for example Y , is always disadvantaged with respect to the same other species in each environment, by Corollary 11, this species goes to extinction.

Reorganising the order of species if necessary, it corresponds to

$$\begin{cases} s_1 > 0 > r_1 \\ 0 > r_2 > s_2 \end{cases} \quad \text{or} \quad \begin{cases} s_1 > 0 > r_1 \\ 0 > s_2 > r_2 \end{cases} \quad \text{or} \quad \begin{cases} s_1 > 0 > r_1 \\ s_2 > 0 > r_2 \end{cases} \quad \text{or} \quad \begin{cases} s_1 > 0 > r_1 \\ s_2 > r_2 > 0 \end{cases}$$

Then, there are several possibilities for the two remaining species, depending on the behavior of the process on the axis $\{y = 0\}$. If we are in the situation 1 or 2 of the Proposition 5, then a species will invade the community. However, if we are in the situation 3 of Proposition 5, there is persistence of both other species (see Figure 6.2).

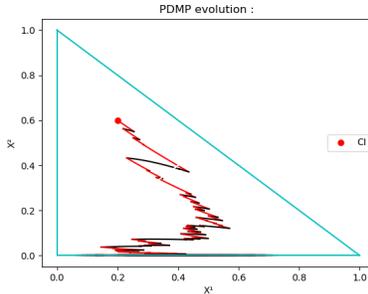


FIGURE 11. A PDMP trajectory where species Y goes to extinction and both other species persist. The values of environments are $s_1 = [0.4, -0.1]$ and $s_2 = [-0.3, -0.2]$.

- Else, reorganising if necessary the order of species, we are in the following situation :

$$\begin{cases} s_1 > 0 > r_1 \\ r_2 > 0 > s_2 \end{cases} \quad (12)$$

We see in the following that several behaviors are possible. According to the values of the fitness, each species, even the neutral, can invade the community (see Theorem 14). However, it is not possible to have persistence of all the species.

Before describing the possibilities for the case (12), we compute the invasion rates for each species.

6.2.1. *Computation of the invasion rates.* Referring to Theorem 4, it is important to describe the set of the ergodic measures on M_0 and to compute, for each species, the associated invasion rate. We know that there are at least three ergodic probability measures on M_0 , namely μ_1 , μ_2 and μ_3 . According to Proposition 12, there are at most three other ergodic probability measures on M_0 , denoted by ν_1 , ν_2 and ν_3 . We now compute the invasion rates of species i with respect to each of these ergodic measures. We detail the computations for species 1, they are similar for the other species.

Lemma 13. *We have*

$$\lambda_1(\mu_3) = \sum_{i=1}^K p_i s_i = \Lambda_0^2, \quad \lambda_1(\mu_2) = \sum_{i=1}^K p_i \frac{s_i - r_i}{1 + r_i} = \Lambda_1^3, \quad \lambda_1(\mu_1) = 0.$$

Moreover, when ν_1, ν_2 and ν_3 exist, we have

$$\lambda_1(\nu_3) = \lambda_1(\nu_2) = 0$$

and

$$\lambda_1(\nu_1) = \left(\frac{s_0}{|r_0|} + \frac{s_1}{|r_1|} \right) C_1,$$

where C_1 is an explicitly computable positive constant.

Proof. Recall that for all $\mu \in \text{Perg}(M_0)$, $\lambda_1(\mu) = \sum_{i=1}^K \int_{M_0} F^i(x, y) d\mu^i(x, y)$, with

$$F^i(x, y) = \frac{s_i - (s_i x + r_i y)}{1 + s_i x + r_i y}.$$

In particular, the formulae for $\lambda_1(\mu_3)$ and $\lambda_1(\mu_2)$ are immediate from the definitions of μ_2 and μ_3 . The fact that $\lambda_1(\mu_1) = \lambda_2(\nu_2) = \lambda_3(\nu_3) = 0$ is straightforward from [9, Theorem 5.1 (i)]. It remains to compute $\lambda_1(\nu_1)$. First, we note that by Proposition 12, ν_1 only exists if $p_0 r_0 + p_1 r_1 > 0$ and $p_0 \frac{r_0}{1+r_0} + p_1 \frac{r_1}{1+r_1} < 0$. In particular, it can only exist if r_0 and r_1 are of opposite signs. Next, we know by Lemma 6 that in this case, ν_1 admits a density with respect to the Lebesgue measure on M_0^1 , which is given by

$$g_i(y) = \frac{G(y)(1 + r_i y)}{y(1 - y)|r_i|}.$$

	μ_1	μ_2	μ_3	ν_1	ν_2	ν_3
1	0	Λ_1^3	Λ_0^2	$C_1(\frac{s_1}{ r_1 } + \frac{s_2}{ r_2 })$	0	0
2	Λ_0^3	0	Λ_0^1	0	$C_2(\frac{r_1}{ s_1 } + \frac{r_2}{ s_2 })$	0
3	Λ_1^2	Λ_1^1	0	0	0	$C^3(-\frac{r_1}{ s_1-r_1 } - \frac{r_2}{ s_2-r_2 })$

TABLE 1. Invasion rates

for some function G similar to the function H given in Lemma 6. Thus,

$$\begin{aligned} \lambda_1(\nu_1) &= \int_0^1 F^0(0, y)g_0(y) + F^1(0, y)g_1(y)dy \\ &= \int_0^1 \left(\frac{s_0 - r_0y}{|r_0|} + \frac{s_1 - r_1y}{|r_1|} \right) \frac{G(y)}{y(1-y)} dy \end{aligned}$$

Now, since r_0 and r_1 have opposite signs, we have for all $y \in (0, 1)$

$$\frac{s_0 - r_0y}{|r_0|} + \frac{s_1 - r_1y}{|r_1|} = \frac{s_0}{|r_0|} + \frac{s_1}{|r_1|},$$

which implies that

$$\lambda_1(\nu_1) = \left(\frac{s_0}{|r_0|} + \frac{s_1}{|r_1|} \right) \int_0^1 \frac{G(y)}{y(1-y)} dy.$$

and concludes the proof. \square

The invasion rates for species 1, as well as for species 2 and 3 are summed up in Table 1. As for C_1 , C_2 and C_3 are positive constant that may be computed. However, since it is sufficient to know the signs of the invasion rates, it does not really matter to have the exact expression of the C_i .

6.3. Environment favours and disadvantages alternately two species, the other one stay neutral over time. With no loss of generality, we assume the environment promotes and disadvantages alternately the first and the second species. So without regard to order, only one configuration is possible:

$$s_1 > 0 > r_1, \quad r_2 > 0 > s_2. \quad (13)$$

In this configuration, many different situations are possible for the long time behavior. In the following we highlight some of them. Mainly, we discuss about the situation where the neutral species (the third in the last configuration) invade the community. Then we prove that persistence of the three species is not possible with only two environments.

6.3.1. The neutral species invades the community. In this section, we use results of Section 5.1 to provide sufficient conditions for the invasion of the neutral species. We also give an example of parameters satisfying these conditions.

Theorem 14. *Assume that $\Lambda_0^1 < 0$ and $\Lambda_0^2 < 0$. Set*

$$\Lambda = \max(\Lambda_0^1, \Lambda_0^2) < 0$$

Then, for all $(x, y) \in \mathcal{E} \setminus \mathcal{E}_0^3$, and all $\mathbf{s} \in E$,

$$\mathbb{P}_{(x,y,\mathbf{s})} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log \|(X_t, Y_t)\| \leq \Lambda \right) = 1.$$

Proof. With the notations of Theorem 7, $\Lambda = \Lambda_3$, and thus, by this theorem, for all $\alpha \in (\Lambda, 0)$, there exists $\eta > 0$ and a neighbourhood \mathcal{U} of 0 such that, for all $(x, y) \in \mathcal{U}$ and all $\mathbf{s} \in E$,

$$\mathbb{P}_{(x,y,\mathbf{s})} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log \|(X_t, Y_t)\| \leq \alpha \right) \geq \eta.$$

Now, we prove that the point 0 is accessible from \mathcal{E}_+^3 . By Lemma 26, 0 is accessible if and only if it is accessible for the vector fields given by $g_s(x, y) = (x(s^1 - (s^1x + r^1y)), y(r^1 - (x^1x + r^1y)))$. Consider the convex combination $g_p = p_1g_{s_1} + p_2g_{s_2}$. Then $g_p = g_{\mathbf{s}_p}$, where $\mathbf{s}_p = p_1\mathbf{s}_1 + p_2\mathbf{s}_2$. Now, since Λ_0^1 and Λ_0^2 are negative, $\mathbf{s}_p = (s_p, r_p, 0)$. Hence, by Theorem 3 and Lemma 26, the flow generated by g_p converges to 0 for all initial condition in \mathcal{E}_+^3 . In particular, 0 is accessible from \mathcal{E}_+^3 with the vector fields g_s , hence it is accessible for $((X_t, Y_t))_{t>0}$.

Finally, as for the proof of Theorem 9, we have to show that the face \mathcal{E}_0^3 is repulsive. We use Theorem 4. We know that $\mathcal{P}_{erg}(\mathcal{E}_0^3)$ contain μ_1, μ_2 and possibly ν_3 . Furthermore, by Lemma 13, Proposition 5 and the assumption that $\Lambda_0^1 < 0$ and $\Lambda_0^2 < 0$, we have that

$$\lambda_3(\mu_1) = \Lambda_1^2 > 0 \quad \text{and} \quad \lambda_3(\mu_2) = \Lambda_1^1 > 0.$$

Moreover, since we are in the situation

$$\begin{cases} s_1 > 0 > r_1 \\ r_2 > 0 > s_2 \end{cases},$$

the assumption $\Lambda_0^1 = r_1 + r_2 < 0$ and $\Lambda_0^2 = s_1 + s_2 < 0$ is equivalent to $-r_1 > r_2 > 0$ and $-s_2 > s_1 > 0$, which implies $r_1s_2 > r_2s_1$. Hence, by Proposition 19 below, $\lambda_3(\nu_3) > 0$ which concludes the proof. □

Example 5. Take $s_1 = 1/3, r_1 = -1/3, s_2 = -3/8$ and $r_2 = 1/4$. Choose $q_1 = q_2$ so that $p_1 = p_2 = \frac{1}{2}$. Then

$$\Lambda_0^1 = -\frac{1}{24}; \quad \Lambda_0^2 = -\frac{1}{48}; \quad \Lambda_0^3 = -\frac{1}{5},$$

thus conclusion of Theorem 14 holds. Illustrations are given in Figure 14.

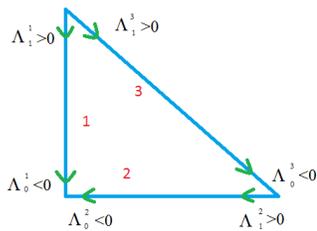


FIGURE 12. behavior of the process on a neighbourhood of each vertex.

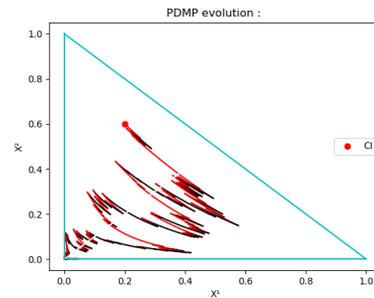


FIGURE 13. Neutral species invade the community. Environment values $[0.5, -0.7]$ and $[-0.8, 0.2]$.

An immediate corollary of Theorem 7 is the following, which gives a sufficient condition for non invasion of species 3.

Corollary 15. *Assume that $\Lambda_0^1 > 0$ or $\Lambda_0^2 > 0$. For $\varepsilon > 0$, define*

$$\tau^\varepsilon = \inf\{t \geq 0 \mid \|(X_t, Y_t)\| \geq \varepsilon\}.$$

Then, there exist $\varepsilon > 0$, $b > 1$, $\theta > 0$ and $c > 0$ such that, for all $(x, y) \in \mathcal{E} \setminus \mathcal{E}_0$, and all $\mathbf{s} \in E$,

$$\mathbb{E}_{(x,y,\mathbf{s})}(e^{\tau^\varepsilon}) \leq c(1 + \|(x, y)\|^{-\theta}).$$

In particular, species 3 cannot exclude the two other species.

6.3.2. Persistence is impossible for three species and two environments. We show in this section that persistence is not possible with only two environments. The following section will give an example of persistence for 3 environments.

The following lemma, which is a consequence of results in [9], [7] and [8], ensures us that if an edge has an attractive index, then the process converges to this face, thus preventing persistence of the process.

Lemma 16. *Assume that for some species i , ν_i exists and that $\lambda_i(\nu_i) < 0$. Then, for all $(x, y, \mathbf{s}) \in M \setminus M_0^i$,*

$$\mathbb{P}_{((x,y),\mathbf{s})} \left(\limsup_{t \rightarrow \infty} \frac{1}{t} \log(X_t^i) \leq \lambda_i(\nu_i) \right) = 1.$$

In particular, species i goes to extinction and persistence is not possible in that case.

The strategy to prove the lack of persistence is the following. First, we know by Theorem 7 that when one vertex is attractive (i.e satisfies $\Lambda_i < 0$), the corresponding species has a positive probability to invade the community, hence preventing the persistence of the process. Thus, we will assume that all the vertex are repulsive. Then, we show that under this assumption, there is always, in the configuration (12), at least one non-trivial ergodic measure (supported by an edge). Finally, we prove that among all the ergodic measure ν_1, ν_2, ν_3 , there is a species with a negative invasion rate with respect to this measure, which shows that this species has a positive probability to disappear and thus that persistence is not possible.

Proposition 17. *Assume that all the vertex of the triangle are repulsive, i.e for each $i \in \{1, 2, 3\}$, $\Lambda_i > 0$. Then necessarily there exists an invariant measure on a side of a triangle.*

Proof. We prove this result by contradiction. Refers to proposition 5, if on the edge i , Λ_0^i and Λ_1^i are positive, there exists an invariant measure on this edge. Thus the only configuration possible to obtain no invariant measure on the edges, when the vertex are repulsive is the one given in Figure 14 (or the symmetrical case). On the one hand, one has, with the configuration

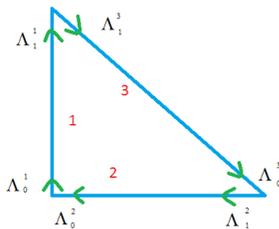


FIGURE 14. Impossible situation.

of figure 14, the following inequalities :

$$\begin{cases} \Lambda_1^1 = -p_1 \frac{r_1}{1+r_1} - p_2 \frac{r_2}{1+r_2} < 0 \\ \Lambda_1^3 = p_1 \frac{s_1 - r_1}{1+r_1} + p_2 \frac{s_2 - r_2}{1+r_2} > 0 \end{cases} \iff \begin{cases} -p_1 \frac{r_1}{1+r_1} < p_2 \frac{r_2}{1+r_2} \\ p_1 \frac{s_1}{1+r_1} > -p_2 \frac{s_2}{1+r_2} \end{cases}$$

and thus

$$r_1 s_2 < r_2 s_1.$$

But on the other hand, we have:

$$\begin{cases} \Lambda_1^2 = -p_1 \frac{s_1}{1+s_1} - p_2 \frac{s_2}{1+s_2} > 0 \\ \Lambda_0^3 = p_1 \frac{r_1 - s_1}{1+s_1} + p_2 \frac{r_2 - s_2}{1+s_2} < 0 \end{cases} \iff \begin{cases} -p_1 \frac{r_1}{1+s_1} > p_2 \frac{r_2}{1+s_2} \\ p_1 \frac{s_1}{1+s_1} < -p_2 \frac{s_2}{1+s_2} \end{cases}$$

which imply

$$r_1 s_2 > r_2 s_1,$$

a contradiction. □

The previous proposition states that there exists at least one ergodic measure on a edge of the triangle. The following proposition deals with the case where there is only one such measure :

Proposition 18. *Assume it exists exactly one invariant measure on a edge of a triangle, then a species has an negative invasion rate with respect to this measure. And this species goes to extinction.*

Proof. Two case have to be considered :

- (1) The invariant measure is on the face 3.
- (2) The invariant measure is on the face 1 (or symmetrically on the face 2).

Let us consider first the case 1, we are in the situation of the figure 15 (or in a symmetrical case):

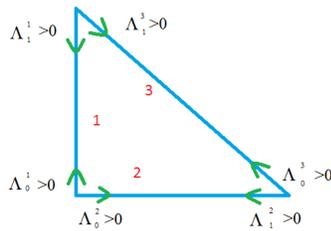


FIGURE 15. Ergodic measure on each edge.

So the following inequalities hold :

$$\begin{cases} \Lambda_1^1 = -p_1 \frac{r_1}{1+r_1} - p_2 \frac{r_2}{1+r_2} < 0 \\ \Lambda_1^3 = p_1 \frac{s_1 - r_1}{1+r_1} + p_2 \frac{s_2 - r_2}{1+r_2} > 0 \end{cases} \iff \begin{cases} -p_1 \frac{r_1}{1+r_1} < p_2 \frac{r_2}{1+r_2} \\ p_1 \frac{s_1}{1+r_1} > -p_2 \frac{s_2}{1+r_2} \end{cases}$$

we obtain $r_1 s_2 < r_2 s_1$, and so $\lambda_3(\nu_3) < 0$.

By lemma 16, species 3 goes to extinction.

For the case 2, the same reasoning is still valid. Species 1 goes to extinction. \square

The following property clarifies the conditions to obtain negative invasion rates. Moreover it states, it's impossible to obtain three positive invasion rates $\lambda_i(\nu_i)$ for $i \in \{1, 2, 3\}$:

Proposition 19. *The following equivalences hold:*

$$\lambda_1(\nu_1) < 0 \iff \lambda_2(\nu_2) < 0 \iff \lambda_3(\nu_3) > 0 \iff s_1 r_2 < s_2 r_1$$

Proof. Remember, we are in situation 6.2, it may possible to simplify the following inequalities :

$$\begin{aligned} \lambda_1(\nu_1) < 0 &\iff \frac{s_1}{|r_1|} + \frac{s_2}{|r_2|} < 0 \iff r_1 s_2 > s_1 r_2 \\ \lambda_2(\nu_2) < 0 &\iff \frac{r_1}{|s_1|} + \frac{r_2}{|s_2|} < 0 \iff r_1 s_2 > s_1 r_2 \\ \lambda_3(\nu_3) > 0 &\iff -\frac{r_1}{|s_1 - r_1|} - \frac{r_2}{|s_2 - r_2|} > 0 \iff r_1 s_2 > s_1 r_2 \end{aligned}$$

And we find the result. \square

The previous property states it impossible have persistence if we have two invariant measures on the faces 1 and 3 or 2 and 3. Because necessarily one of the invasion rates compared to one of these two measure is negative

Proposition 20. *If there exist two invariant measures on face 1 and 2, necessarily it exists one on face 3 and $\lambda_3(\nu_3) < 0$.*

Proof. Assume it exists an invariant measure on edge 1 and 2. Let's prove Λ_0^3 and Λ_1^3 are strictly positive. We are in the situation of figure 16

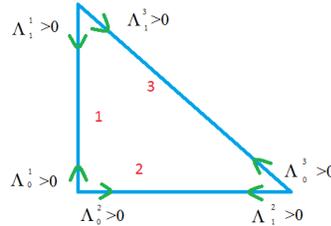


FIGURE 16. behavior of the process on a neighbourhood of each vertex.

Then we have

$$\begin{cases} \Lambda_1^2 = -p_1 \frac{s_1}{1+s_1} - p_2 \frac{s_2}{1+s_2} > 0 \\ \Lambda_1^0 = r_1 + p_1 + r_2 p_2 > 0 \end{cases}$$

and

$$\begin{aligned} \Lambda_0^3 &= p_1 \frac{r_1 - s_1}{1+s_1} + p_2 \frac{r_2 - s_2}{1+s_2} \\ &= -p_1 \frac{s_1}{1+s_1} - p_2 \frac{s_2}{1+s_2} + \frac{p_1 r_1 + p_2 r_2 + p_1 r_1 s_2 + p_2 s_1 r_1}{(1+s_1)(1+s_2)} \\ &= \Lambda_1^2 + \frac{\Lambda_0^1 + p_1 r_1 s_2 + p_2 s_1 r_1}{(1+s_1)(1+s_2)} \end{aligned}$$

Note that $p_1 r_1 s_2$ and $p_2 s_1 r_1$ are positive because r_1, s_2 are both negative and s_1, r_2 are both positive. So Λ_0^3 is positive.

A similar reasoning gives the same condition for Λ_1^3 .

Let us conclude the proof by noting that

$$\begin{cases} \Lambda_0^2 = p_1 s_1 + p_2 s_2 > 0 \\ \Lambda_1^0 = r_1 + p_1 + r_2 p_2 > 0 \end{cases} \iff s_1 r_2 > s_2 r_1 \iff \lambda_3(\nu_3) < 0$$

And species 3 goes to extinction. □

Corollary 21. *If there are exactly two or three invariant measures, at least, an invasion rate $\lambda_i(\nu_i)$, is negative.*

Proof. The proof is direct with property 19 □

It is impossible to obtain persistence with only two environments and three species. In the next section we give an example of persistence with three species and three environments.

6.4. Persistence for 3 species and 3 environments. In this part we give two examples of a system with 3 species and 3 environments which is persistent. In the first example, each species has, in one environment, the best fitness. In the second, the last species has never the best fitness.

With obvious notations, we set

$$\begin{aligned} \Lambda_0^1 &= p_1 r_1 + p_2 r_2 + p_3 r_3, & \Lambda_1^1 &= -p_1 \frac{r_1}{1+r_1} - p_2 \frac{r_2}{1+r_2} - p_3 \frac{r_3}{1+r_3} \\ \Lambda_0^2 &= p_1 s_1 + p_2 s_2 + p_3 s_3, & \Lambda_1^2 &= -p_1 \frac{s_1}{1+s_1} - p_2 \frac{s_2}{1+s_2} - p_3 \frac{s_3}{1+s_3} \\ \Lambda_0^3 &= p_1 \frac{r_1 - s_1}{1+s_1} + p_2 \frac{r_2 - s_2}{1+s_2} + p_3 \frac{r_3 - s_3}{1+s_3}, \\ \Lambda_1^3 &= p_1 \frac{s_1 - r_1}{1+r_1} + p_2 \frac{s_2 - r_2}{1+r_2} + p_3 \frac{s_3 - r_3}{1+r_3}. \end{aligned}$$

To prove persistence, with theorem 4, we need to calculate the invasion rates $\lambda_i(\nu_i)$ for possible ergodic measures ν_i (remember if $k \neq i$, $\lambda_k(\nu_i) = 0$). Thus, we need to obtain an explicit formula for the ν_i density. We could follow the same reasoning as in lemma 6. If $(U_t)_{t>0}$ admits an invariant measure on $(0, 1) \times E$, Π , it is absolutely continuous with respect

to the Lebesgue measure and admits a density. We still define h_i the density of $\Pi(\cdot, i)$ for $i \in \{1, 2, 3\}$. The h_i are in \mathcal{C}^∞ and verify the Fokker-Planck equation :

$$\begin{cases} -h_1(q_{1,2} + q_{1,3}) + q_{2,1}h_2 + q_{3,1}h_3 &= -(g_1h_1)' \\ -h_2(q_{2,1} + q_{2,3}) + q_{1,2}h_1 + q_{3,2}h_3 &= (g_2h_2)' \\ -h_3(q_{3,2} + q_{3,1}) + q_{1,3}h_1 + q_{2,3}h_2 &= (g_3h_2)' \end{cases} \quad (14)$$

Unfortunately, the explicit computation of (h_i) now becomes tedious, and thus we have no explicit expression for the invasion rates $\lambda_i(\nu_i)$. In the following example, we compute numerically the invasions rates $\lambda_i(\nu_i)$ and show that we are in the situation of Theorem 4.

Example 6. In this example, we assume $q_{i,j} = q_{k,l}, \forall i, j, k, l \in \{1, 2, 3\}$, and $\mathbf{s}_1 = \{1, \frac{1}{2}\}$, $\mathbf{s}_2 = \{\frac{-1}{4}, \frac{-1}{2}\}$, $\mathbf{s}_3 = \{\frac{-1}{3}, \frac{1}{3}\}$.

And it follows

$$\Lambda_0^1 = \frac{1}{6}, \quad \Lambda_1^1 = \frac{5}{36}, \quad \Lambda_0^2 = \frac{5}{36}, \quad \Lambda_1^2 = \frac{1}{6}, \quad \Lambda_0^3 = \frac{5}{36}, \quad \Lambda_1^3 = \frac{1}{6}.$$

Then there are exactly 3 ergodic measures $\nu_i, i \in \{1, 2, 3\}$, so we are in the same situation than picture 16.

For each of them, we approximate the invasion rate, i.e the quantity $\lambda_i(\nu_i) = \int_{\mathcal{E}_0^i \times E} F_s^i(x) d\nu_i(x)$. A way of doing it, since the measure is ergodic, is to use the ergodic theorem. So if $(X_t, s_t)_{t>0}$ is the PDMP define by equation 2 and starting in $\text{int}(\mathcal{E}_0^i) \times E$, $\frac{1}{T} \int_0^T F_{s_t}^i(X_t) dt \xrightarrow{T \rightarrow +\infty} \lambda_i(\nu_i)$.

Note the initial point (X_0, s_0) has no influence on the previous result. In the following we chose arbitrary initial conditions, others would have led to the same results.

We proceed as follows:

- Simulate a large number of PDMP trajectories (1000), on $[0, T]$ for T big enough and starting in $\text{int}(\mathcal{E}_0^i) \times E$.
- For each simulation calculate $\frac{1}{T} \int_0^T F_{s_t}^i(X_t) dt$.
- Take the average on the trajectories to improve our result.

Results :

In each simulation we take $T = 80$ and the number of trajectories simulated is 1000.

- (1) For $X_0 = [0, 0.5], s_0 = \mathbf{s}_1$ we obtain $\lambda_1(\nu_1) = 0.0191$
- (2) For $X_0 = [0.5, 0], s_0 = \mathbf{s}_1$ we obtain $\lambda_2(\nu_2) = 0.0594$
- (3) For $X_0 = [0.5, 0.5], s_0 = \mathbf{s}_1$ we obtain $\lambda_3(\nu_3) = 0.090$

For this configuration of environments we obtain positive invasion rates. So it proves, using 4, that persistence is possible for 3 species and 3 environments.

Example 7. We now give an example of persistence in which a species has never the best fitness. Let us choose as parameters $q_{i,j} = q_{k,l}, \forall i, j, k, l \in \{1, 2, 3\}$, and $\mathbf{s}_1 = \{0.1, -0.3\}$, $\mathbf{s}_2 = \{-0.33, 0.1\}$, $\mathbf{s}_3 = \{0.27, 0.25\}$.

So that,

$$\Lambda_0^1 = 0.5, \quad \Lambda_1^1 = 0.13, \quad \Lambda_0^2 = 0.04, \quad \Lambda_1^2 = 0.19, \quad \Lambda_0^3 = 0.26, \quad \Lambda_1^3 = 0.20.$$

As in the previous example, there are exactly 3 ergodic measures $\nu_i, i \in \{1, 2, 3\}$ and we are in the same situation than Figure 16.

Let us calculate the invasion rate, with the same method :

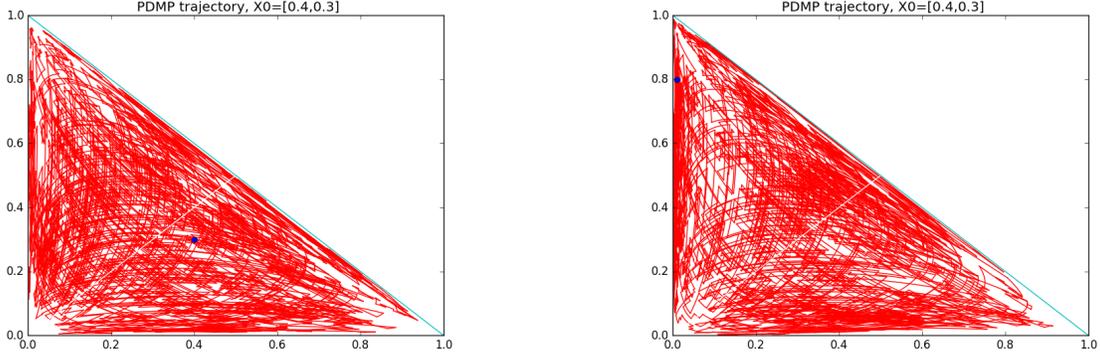


FIGURE 17. A PDMP trajectory. $T = 1000$. Left figure: $X_0 = [0.4, 0.3]$. Right figure: $X_0 = [0.01, 0.8]$

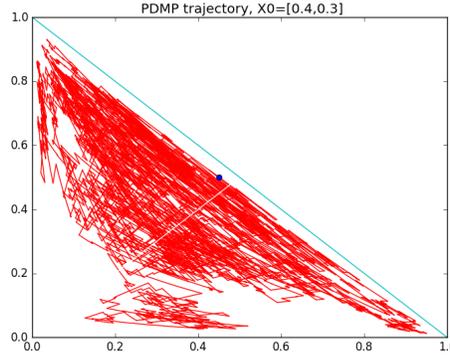


FIGURE 18. PDMP trajectory, $T=1000$, $X_0 = [0.45, 0.5]$.

- (1) For $X_0 = [0, 0.5]$, $s_0 = \mathbf{s}_1$ we obtain $\lambda_1(\nu_1) = 0.016$
- (2) For $X_0 = [0.5, 0]$, $s_0 = \mathbf{s}_1$ we obtain $\lambda_2(\nu_2) = 0.019$
- (3) For $X_0 = [0.5, 0.5]$, $s_0 = \mathbf{s}_1$ we obtain $\lambda_3(\nu_3) = 0.009$

The invasion rates are strictly positive so we conclude that in this example; we have persistence, even if the last species has never the best fitness. A trajectory of the PDMP is plotted in Figure 18.

In the two previous examples, the process is persistent, and thus admits at least one stationary distribution Π such that $\Pi(M_+) = 1$. The numerical simulations presented in Figure 6 suggest that in the case of Example 6, that Π has full support, i.e. its support is the whole space M . The following proposition proves this fact, as well as the exponential convergence of the process towards Π for general coefficients.

Proposition 22. *Assume that $\mathbf{s}_1, \mathbf{s}_2, \mathbf{s}_3$ are such that*

$$\begin{cases} s_1 > 0 > r_1 \\ r_2 > s_2 > 0 \\ 0 > r_3 > s_3 \end{cases} \quad (15)$$

or

$$\begin{cases} s_1 > r_1 > 0 \\ r_2 > 0 > s_2 \\ 0 > s_3 > r_3 \end{cases} \quad (16)$$

Then, if the process is persistent :

- (1) The stationary distribution Π satisfying $\Pi(M_+) = 1$ is unique and absolutely continuous with respect to the Lebesgue measure;
- (2) Π has full support;
- (3) If furthermore $\alpha := s_2 r_3 - r_2 s_3 + s_3 r_1 - s_1 r_3 + s_1 r_2 - s_2 r_1 \neq 0$, then there exist $C, \theta, \gamma > 0$ such that, for all $(x, y, s) \in M_+$ and all $t \geq 0$,

$$\|\mathbb{P}_{(x,y,s)}(U_t \in \cdot) - \Pi\|_{TV} \leq C \left(\frac{1}{x^\theta} + \frac{1}{y^\theta} + \frac{1}{(1-x-y)^\theta} \right) e^{-\gamma t}.$$

Proof. We only do the proof in the case (15); it can be proved in the same way for (16).

For $i \in \{1, 2, 3\}$, we denote by $(\varphi_t^i(x))_{t \geq 0}$ the flow generated by $G_i := G_{s_i}$ and started at x . That is, $\varphi_t^i(x)$ is solution to

$$\begin{cases} \frac{\partial \varphi_t^i(x)}{\partial t} = G_i(\varphi_t^i(x)) \\ \varphi_0^i(x) = x. \end{cases}$$

For $m \geq 1$, $\mathbf{i} = (i_1, \dots, i_m) \in \{1, 2, 3\}^m$ and $\mathbf{u} = (u_1, \dots, u_m) \in \mathbb{R}_+^m$, we denote by $\Phi_{\mathbf{u}}^{\mathbf{i}}$ the composite flow: $\Phi_{\mathbf{u}}^{\mathbf{i}} = \varphi_{u_m}^{i_m} \circ \dots \circ \varphi_{u_1}^{i_1}$. For $x \in M$ and $t \geq 0$, we denote by $\mathcal{O}_t^+(x)$ (resp. $\mathcal{O}^+(x)$) the set of points that are reachable from x at time t (resp. at any nonnegative time) with a composite flow:

$$\mathcal{O}_t^+(x) = \{\Phi_{\mathbf{v}}^{\mathbf{i}}(x), (\mathbf{i}, \mathbf{v}) \in E^m \times \mathbb{R}_+^m, m \in \mathbb{N}, v_1 + \dots + v_m = t\},$$

$$\mathcal{O}^+(x) = \bigcup_{t \geq 0} \mathcal{O}_t^+(x).$$

We define the set of points that are accessible from \mathcal{E}_+ as

$$\Gamma = \bigcap_{x \in \mathcal{E}_+} \overline{\mathcal{O}^+(x)}.$$

According to Corollary 4.6 and Remark 14 in [9] and to Theorem 3.4 and Proposition 3.11 in [6], $\Gamma \times E$ is included in the support of Π for all stationary distribution Π such that $\Pi(M_+) = 1$. Thus, point (2) is proved if we show that $\Gamma = \mathcal{E}$.

For $x \in \mathcal{E}$ and $i \in \{1, 2, 3\}$, we let $\gamma_+^i(x)$ and $\gamma_-^i(x)$ denote the positive and negative orbit, respectively, of x under the flow φ^i , namely :

$$\gamma_+^i(x) = \{\varphi_t^i(x), t \geq 0\}, \quad \gamma_-^i(x) = \{\varphi_t^i(x), t \leq 0\}.$$

In situation (15), for all $x \in \mathcal{E}_+$, $\gamma_+^i(x)$ is a regular curve linking x to e_i , while $\gamma_-^i(x)$ is a curve linking x to e_{i+1} , where $i+1$ is taken modulo 3. We claim that for all $x, y \in \mathcal{E}_+$ with $x \neq y$, there exist $i, j \in \{1, 2, 3\}$ such that $\gamma_+^i(x) \cap \gamma_-^j(y) \neq \emptyset$. In that case, let $z \in \gamma_+^i(x) \cap \gamma_-^j(y) \neq \emptyset$. Then, there exist $t, s > 0$ such that $z = \varphi_t^i(x) = \varphi_{-s}^j(y)$. Hence, by the flow property of φ^j , we get $y = \varphi_s^j \circ \varphi_t^i(x)$, and thus y is accessible from x . This shows that $\mathcal{E}_+ \subset \mathcal{O}^+(x)$, for all $x \in \mathcal{E}_+$, hence $\mathcal{E} \subset \Gamma$ and point (2) is proven since $\mathcal{E} \supset \Gamma$. We now prove the claim. Let $x, y \in \mathcal{E}_+$ with $x \neq y$. Then the $\gamma_+^i(x), i \in \{1, 2, 3\}$ are three regular curves linking x to each vertex of \mathcal{E}_0 , while the $\gamma_-^j(y), j \in \{1, 2, 3\}$ are three regular curves linking y to each vertex of

\mathcal{E}_0 . In particular, at least one of these three first curves has to cross one of the three other, which proves the claim.

We pass to the proof of point (1). Let $x \in \mathcal{E}_+$. Then, there must exist a point $y \in \gamma_+^1(x)$ such that $G_1(y)$ and $G_2(y)$ are linearly independent. If not, one would have for all $y \in \gamma_+^1(x)$, $G_1(y) = \alpha(y)G_2(y)$ for some negative function α , which would imply that $\gamma_+^1(x) = \gamma_-^2(x)$. This is a contradiction since $\gamma_+^1(x)$ is a curve linking x to e_1 while $\gamma_-^2(x)$ is a curve linking x to e_3 . Hence, the weak bracket condition holds at y which belongs to Γ , thus Π has to be unique and absolutely continuous with respect to the Lebesgue measure by Corollary 6.3 in [9].

To prove point (3), we also use Corollary 6.3 in [9]. According to this corollary (which is a consequence of results in [6] and [3]), it suffices to find an accessible point (x, y) (thus a point in \mathcal{E}) such that $G_1(x, y) - G_2(x, y)$ and $G_2(x, y) - G_3(x, y)$ are linearly independent. One can check that

$$\det(G_1 - G_2, G_2 - G_3)(x, y) = \frac{xy(1-x-y)}{h(x, y)}(s_2r_3 - r_2s_3 + s_3r_1 - s_1r_3 + s_1r_2 - s_2r_1),$$

where $h(x, y) = (1 + s_1x + r_1y)(1 + s_2x + r_2y)(1 + s_3x + r_3y) > 0$. In particular, if $s_2r_3 - r_2s_3 + s_3r_1 - s_1r_3 + s_1r_2 - s_2r_1 \neq 0$; $G_1(x, y) - G_2(x, y)$ and $G_2(x, y) - G_3(x, y)$ are linearly independent and point (3) is proven. \square

Remark 7. Using the same kind of proof, it can be shown that Π has full support in more general situation. Indeed, the assumption that the process is persistent implies that each of the species has exactly once the worst fitness. Indeed, if one species (say 1) has never the worst fitness, it has to be better than another one (say 2) in each environment, which implies that species 2 will go to extinction according to Corollary 11. Moreover, if the process is persistent, by Theorem 9, none of the species can have the best fitness in every environment. Thus, in the persistent case, we are either in case 15 or 16, that are handled by the previous proposition, or in a situation like in Example 7. That is

$$\begin{cases} s_1 > 0 > r_1 \\ r_2 > 0 > s_2 \\ s_3 > r_3 > 0 \end{cases} \quad (17)$$

With the same notations as in the proof of the previous proposition, one can see that the $\gamma_-^i(y)$ for $i \in \{1, 2, 3\}$ are still three regular curves linking one to each vertex of \mathcal{E}_0 . However, now $\gamma_+^1(x)$ and $\gamma_+^3(x)$ are curves linking x to e_1 , while $\gamma_+^2(x)$ is a curve linking x to e_2 . To be able to conclude as in the previous proof, we need $e_3 = 0$ to be accessible from x . This is for example the case if one can find $a_1, a_2, a_3 \geq 0$ such that

$$a_1s_1 + a_2s_2 + a_3s_3 < 0 \quad \text{and} \quad a_1r_1 + a_2r_2 + a_3r_3 < 0, \quad (18)$$

by the argument given in the proof of Theorem 14. In this case, $e_2 \in \mathcal{O}^+(x)$ and as before, $r^+(x)$ has to have a nonempty intersection with one of the $\gamma_-^i(y)$, and we can conclude that in this situation, Π is unique and has full support. In Example 7, take $a_1 = a_2 = 1/2$ and $a_3 = 0$, then (18) is satisfied and thus Π is unique and has full support. Note also that the condition $s_2r_3 - r_2s_3 + s_3r_1 - s_1r_3 + s_1r_2 - s_2r_1 \neq 0$ is satisfied, thus the process converges exponentially fast to Π .

6.5. Conclusion. In this part, we treat the whole case of tree species and two environments, and we prove persistence is impossible in this situation. On the other hand, if we deal with 3 species and 3 environments, we are able to exhibit configurations where persistence is possible.

Of course many other configurations of fitness gives persistence to. But, we actually are unable to give explicit conditions on fitness to characterize them. However numerical (deterministic) approximations may be used for each environment.

In view of the results of the previous sections, we formulate the following conjecture, that we have proved for 2 and 3 species.

Conjecture 23. *Persistence of the system is possible if and only if there are at least as many environments as there are species.*

7. APPENDIX

7.1. Proof of Theorem 2. Let $(U_n^J)_{n \geq 0} = (X_n^J, s_n^J)_{n \geq 0}$ be the Moran model described in section 1.1, $(U_t)_{t \geq 0} = (X_t, s_t)_{t \geq 0}$ the PDMP given by equation 2 and $(Z_t^J)_{t \geq 0} = (X_{\lfloor tJ \rfloor}, s_{\lfloor tJ \rfloor})_{t \geq 0}$ the PDMP in the time scale of the discrete process, whose generator is given by L .

Our goal is to quantify the difference

$$\mathbb{E}_{x,s} \left(f(U_t) - f(\tilde{U}_t^J) \right)$$

for $f : \mathcal{S} \rightarrow \mathbb{R}$ regular enough. First note that, since $U_t = Z_{\lfloor tJ \rfloor}^J$, we can rewrite this difference as

$$\mathbb{E}_{x,s} \left(f(Z_{\lfloor tJ \rfloor}^J) - f(Z_{\lfloor tJ \rfloor}^J) \right) + \mathbb{E}_{x,s} \left(f(Z_{\lfloor tJ \rfloor}^J) - f(U_{\lfloor tJ \rfloor}^J) \right) + \mathbb{E}_{x,s} \left(f(U_{\lfloor tJ \rfloor}^J) - f(\tilde{U}_{\lfloor tJ \rfloor}^J) \right).$$

We first show that the first and last term of the above quantity can easily be controlled. For all $t \geq 0$ and $J \geq 1$, one has $0 \leq t - \frac{\lfloor tJ \rfloor}{J} < \frac{1}{J}$, hence $\frac{\lfloor tJ \rfloor}{J}$ converges to t . The probability that $(s_u)_{u \geq 0}$ performs a jump at time t is zero, hence, almost surely, for J big enough, $s_{\frac{\lfloor tJ \rfloor}{J}} = s_t$.

In particular, if f is C^1 , one has

$$\left| f(Z_{tJ}) - f(Z_{\lfloor tJ \rfloor}) \right| \leq \|f^{(1)}\| \left| X_t - X_{\frac{\lfloor tJ \rfloor}{J}} \right|,$$

where $\|f^{(1)}\| = \max_{(x,s) \in \mathcal{S}} |f'_s(x)|$. Let $C_G = \max_{(x,s) \in \mathcal{S}} |G_s(x)|$, then

$$\begin{aligned} \left| X_t - X_{\frac{\lfloor tJ \rfloor}{J}} \right| &= \left| \int_{\frac{\lfloor tJ \rfloor}{J}}^t G_{s_u}(X_u) du \right| \\ &\leq \left(t - \frac{\lfloor tJ \rfloor}{J} \right) C_G \leq \frac{C_G}{J}, \end{aligned}$$

which implies

$$\left| f(Z_{tJ}) - f(Z_{\lfloor tJ \rfloor}) \right| \leq \|f^{(1)}\| \frac{C_G}{J}.$$

Furthermore, $\tilde{U}_t^J = (\tilde{X}_t^J, \tilde{s}_t^J)$ and by definition, $\tilde{s}_t^J = s_{\lfloor tJ \rfloor}^J$ and

$$\begin{aligned} \left| \tilde{X}_t^J - X_{\lfloor tJ \rfloor}^J \right| &= J \left(t - \frac{\lfloor tJ \rfloor}{J} \right) \left| X_{\lfloor tJ \rfloor + 1}^J - X_{\lfloor tJ \rfloor}^J \right| \\ &\leq \left| X_{\lfloor tJ \rfloor + 1}^J - X_{\lfloor tJ \rfloor}^J \right|. \end{aligned}$$

Thus,

$$\left| \mathbb{E}_{x,s} \left(f(U_{\lfloor tJ \rfloor}^J) - f(\tilde{U}_{\lfloor tJ \rfloor}^J) \right) \right| \leq \|f^{(1)}\| \mathbb{E}_{x,s} \left| X_{\lfloor tJ \rfloor + 1}^J - X_{\lfloor tJ \rfloor}^J \right| \leq \frac{\|f^{(1)}\|}{J}$$

because the difference between X_{n+1}^J and X_n^J is at most $1/J$. Therefore, one can look at the difference

$$\mathbb{E}_{x,s} \left(f(Z_{[tJ]}^J) - f(U_{[tJ]}^J) \right)$$

because

$$\left| \mathbb{E}_{x,s} \left(f(U_t) - f(U_{[tJ]}^J) \right) \right| \leq \|f^{(1)}\| \frac{C_G + 1}{J} + \mathbb{E}_{x,s} \left(f(Z_{[tJ]}^J) - f(U_{[tJ]}^J) \right).$$

We set $T_u^J f(x, s) = \mathbb{E}_{x,s} (f(Z_t^J))$ and $S_k^J f(x, s) = \mathbb{E}_{x,s} (f(X_n^J))$. When there is no ambiguity, we shall drop the exponent J on T^J and S^J . With these notations, our aim is to control $\|T_n f - S_n f\|_J$, where $n = [tJ]$. For this, we can use the following inequality, proved in [23] :

$$\|S_n f - T_n f\|_J \leq \sum_{k=0}^{n-1} \|(S_1 - T_1) T_k f\|_J \quad (19)$$

Thus we are reduced to the study of $\|(S_1 - T_1)g\|_J$ for g regular enough. We start by the following lemma :

Lemma 24. *There exists $\gamma_0, \gamma_1, \gamma_2 > 0$, such that for all $g \in C^3(\mathcal{I})$,*

$$\|(S_1 - T_1)g\|_J \leq \gamma_0 \|g\|_J + \gamma_1 \frac{\|g^{(1)}\|_J}{J^2} + \gamma_2 \frac{\|g^{(2)}\|_J}{J^2} + 2 \sum_{s' \neq s} \left| P_{s,s'}^J - \frac{\alpha_s Q_{s,s'}}{J} \right| \|g\|_J + O\left(\frac{1}{J^3}\right).$$

Proof. We first show that for g which is C^3 ,

$$T_1 g(x, s) = g(x, s) + Lg(x, s) + \frac{1}{2} L^2 g(x, s) + O\left(\frac{1}{J^3}\right)$$

Let $(\mathcal{P}_t)_{t \geq 0}$ be the semigroup associated with the PDMP $(U_t)_{t \geq 0} : Q_t g(x, s) = \mathbb{E}_{x,s}(g(U_t))$ and \mathcal{L} its generator :

$$\mathcal{L}g(x, s) = \frac{sx(1-x)}{(1+sx)} \frac{\partial}{\partial x} g(x, s) + \sum_{s' \in E} \alpha_s Q_{s,s'} (f(x, s') - f(x, s)).$$

Then, one has $T_t = \mathcal{P}_{t/J}$ and $L = \frac{1}{J} \mathcal{L}$. It is well known that for g in the domain of \mathcal{L} ,

$$\frac{\partial}{\partial t} \mathcal{P}_t g(x, s) = \mathcal{P}_t \mathcal{L}g = \mathcal{L} \mathcal{P}_t g$$

In particular, if g and $\mathcal{L}g$ are in the domain of \mathcal{L} , then $\mathcal{P}_t g$ is twice differential with respect to time and

$$\frac{\partial^2}{\partial t^2} \mathcal{P}_t g(x, s) = \mathcal{P}_t \mathcal{L}^2 g = \mathcal{L}^2 \mathcal{P}_t g,$$

where $\mathcal{L}^2 g = \mathcal{L}(\mathcal{L}g)$. In the case of PDMP, it is possible to prove that when g is C^3 , then both g and $\mathcal{L}g$ are in C^3 .

Thus, we obtain the following Taylor development :

$$\begin{aligned} T_1 g(x, s) &= \mathcal{P}_{1/J} g(x, s) \\ &= g(x, s) + \frac{1}{J} \mathcal{L}g(x, s) + \frac{1}{2J^2} \mathcal{L}^2 g(x, s) + O\left(\frac{1}{J^3}\right) \\ &= g(x, s) + Lg(x, s) + \frac{1}{2} L^2 g(x, s) + O\left(\frac{1}{J^3}\right). \end{aligned}$$

Hence,

$$S_1 g - T_1 g = S_1 g - g - Lg - \frac{1}{2} L^2 g + O\left(\frac{1}{J^3}\right).$$

Moreover, we have

$$\begin{aligned} S_1 g(x, s) &= \mathbb{E}_{x,s} (g(X_1^J, s_1^J)) \\ &= P_{s,s}^J \mathbb{E}_{x,s} (g(X_1^J, s)) + \sum_{s' \neq s} P_{s,s'}^J \mathbb{E}_{x,s} (g(X_1^J, s')), \end{aligned}$$

which leads to (we drop the J in $P_{s,s'}$ for better readability)

$$\begin{aligned} S_1 g(x, s) - T_1 g(x, s) &= \mathbb{E}_{x,s} (g(X_1^J, s)) - g(x, s) - L_C g(x, s) \\ &\quad (P_{s,s'} - 1) (\mathbb{E}_{x,s} (g(X_1^J, s)) - g(x, s)) \\ &\quad + \sum_{s' \neq s} P_{s,s'} (\mathbb{E}_{x,s} (g(X_1^J, s')) - g(x, s')) \\ &\quad + \sum_{s' \neq s} \left(P_{s,s'} - \frac{\alpha_s Q_{s,s'}}{J} \right) (g(x, s') - g(x, s)) \\ &\quad - \frac{1}{2} L^2 g(x, s) + O\left(\frac{1}{J^3}\right). \end{aligned}$$

We now prove that the three first terms are of order $1/J^2$, with bounds controllable by the derivative of g . Note that by definition of L^2 , it is immediate that there exist some constants γ'_0 , γ'_1 and γ'_2 such that

$$\|L^2 g\|_J \leq \gamma'_0 \frac{\|g\|_J}{J^2} + \gamma'_1 \frac{\|g^{(1)}\|_J}{J^2} + \gamma'_2 \frac{\|g^{(2)}\|_J}{J^2}.$$

Since in one step, the difference $X_1^J - x$ is of order $1/J$, we have the following Taylor development :

$$\mathbb{E}_{x,s} (g(X_1^J, s')) = g(x, s') + \frac{\partial g}{\partial x}(x, s') \mathbb{E}_{x,s} [X_1^J - x] + \frac{\partial^2 g}{\partial x^2}(x, s') \frac{1}{2} \mathbb{E}_{x,s} [(X_1^J - x)^2] + O\left(\frac{1}{J^3}\right)$$

By Proposition 1 and definition of L_C , we thus have

$$|\mathbb{E}_{x,s} (g(X_1^J, s)) - g(x, s) - L_C g(x, s)| \leq \frac{\|g^{(2)}\|}{2J^2} + O\left(\frac{1}{J^3}\right).$$

The previous Taylor development also gives that

$$|\mathbb{E}_{x,s} (g(X_1^J, s')) - g(x, s')| \leq \frac{\|g^{(1)}\|}{J} + O\left(\frac{1}{J^2}\right)$$

Now, since for all $s' \neq s$, $\lim_{J \rightarrow \infty} P_{s,s'}^J J = \alpha_s Q_{s,s'}$, we have $P_{s,s'} = O(1/J)$, which concludes the proof. \square

Let $f \in C^3(\mathcal{I})$. In view of inequality 19, we want to apply Lemma 24 to $T_k f$, for $0 \leq k \leq n-1$. For this, we need to prove that $T_t f$ is regular for all $t \geq 0$, and to give an estimate on the derivative of $T_t f$:

Lemma 25. *Let $C = \max_{(x,s) \in \mathcal{I}} |\frac{\partial G_s}{\partial x}(x)|$ and $K = \max_{(x,s) \in \mathcal{I}} |D^2 G_s(x)|$. Then for all $f \in C^2(\mathcal{I})$, for all $t \geq 0$,*

$$\|(\mathcal{P}_t f)^{(1)}\| \leq \exp(Ct) \|f^{(1)}\|,$$

and

$$\|(\mathcal{P}_t f)^{(2)}\| \leq \exp(2Ct) \left(\|f^{(1)}\| + K \|f^{(2)}\| \right).$$

In particular,

$$\|(T_t f)^{(1)}\| \leq \exp\left(C \frac{t}{J}\right) \|f^{(1)}\|,$$

and

$$\|(T_t f)^{(2)}\| \leq \exp\left(2C \frac{t}{J}\right) \left(\|f^{(1)}\| + K\|f^{(2)}\|\right).$$

Proof. For $s \in E$, we denote by $\varphi_t^s(x)$ the flow generated by G_s and started at x . That is, $\varphi_t^s(x)$ is solution to

$$\begin{cases} \frac{\partial \varphi_t^s(x)}{\partial t} = G_s(\varphi_t^s(x)) \\ \varphi_0^s(x) = x. \end{cases}$$

By C^∞ regularity of G_s , for every $t \geq 0$, $x \mapsto \varphi_t^s(x)$ is C^∞ . Let $(\tilde{S}_n)_{n \geq 0}$ and $(\tilde{T}_n)_{n \geq 0}$ denote the sequence of postjump locations and of jump times of $(s_t)_{t \geq 0}$, respectively. Under $\mathbb{P}_{x,s}$, one has

$$X_t^x = \varphi_{t-\tilde{T}_{N_t}}^{\tilde{S}_{N_t}} \circ \dots \circ \varphi_{\tilde{T}_1}^s(x),$$

where we have denoted X_t^x the process X_t to emphasis the dependence on x . From this equation, since the sequences $(\tilde{S}_n)_{n \geq 0}$ and $(\tilde{T}_n)_{n \geq 0}$ do not depend on x and since every φ^s is C^∞ , one deduce that $x \mapsto X_t^x$ is C^∞ almost surely. We can also write

$$X_t^x = x + \int_0^t G_{s_u}(X_u^x) du,$$

that we can differentiate with respect to x to find

$$\frac{\partial}{\partial x} X_t^x = 1 + \int_0^t DG_{s_u}(X_u^x) \frac{\partial}{\partial x} X_u^x du.$$

Using Gronwall's inequality, we deduce that

$$\left| \frac{\partial}{\partial x} X_t^x \right| \leq e^{Ct}.$$

Differentiating once again, we find

$$\frac{\partial^2}{\partial x^2} X_t^x = \int_0^t D^2 G_{s_u}(X_u^x) \left(\frac{\partial}{\partial x} X_u^x \right)^2 du + \int_0^t DG_{s_u}(X_u^x) \frac{\partial^2}{\partial x^2} X_u^x du,$$

which leads to

$$\left| \frac{\partial^2}{\partial x^2} X_t^x \right| \leq K(e^{Ct} - 1) + C \int_0^t \left| \frac{\partial^2}{\partial x^2} X_u^x \right| du.$$

Using once again Gronwall's inequality, we deduce that

$$\left| \frac{\partial^2}{\partial x^2} X_t^x \right| \leq K(e^{Ct} - 1)e^{Ct} \leq Ke^{2Ct}.$$

Now let $f \in C^2(\mathcal{J})$, then

$$\frac{\partial}{\partial x} f(X_t^x, s_t) = \left(\frac{\partial}{\partial x} f \right) (X_t^x, s_t) \frac{\partial}{\partial x} X_t^x,$$

and thus

$$\left| \frac{\partial}{\partial x} f(X_t^x, s_t) \right| \leq \|f^{(1)}\| e^{Ct}.$$

Furthermore,

$$\frac{\partial^2}{\partial x^2} f(X_t^x, s_t) = \left(\frac{\partial^2}{\partial x^2} f \right) (X_t^x, s_t) \left(\frac{\partial}{\partial x} X_t^x \right)^2 + \left(\frac{\partial}{\partial x} f \right) (X_t^x, s_t) \frac{\partial^2}{\partial x^2} X_t^x,$$

hence

$$\left| \frac{\partial^2}{\partial x^2} f(X_t^x, s_t) \right| \leq e^{2Ct} \left(\|f^{(2)}\| + K\|f^{(1)}\| \right)$$

□

We can now finish the proof of Theorem 2. Using inequality (19) and Lemma 24 applied to $g = T_k f$, we have :

$$\begin{aligned} \|S_n f - T_n f\| &\leq \sum_{k=0}^{n-1} \|(S_1 - T_1)T_k f\| \\ &\leq \frac{1}{J^2} \sum_{k=0}^{n-1} \left(\gamma_0 \|T_k f\| + \gamma_1 \|T_k^{(1)} f\| + \gamma_2 \|T_k^{(2)} f\| \right) \\ &\quad + \sum_{k=0}^{n-1} \left[2 \sum_{s' \neq s} \left| P_{s,s'}^J - \frac{\alpha_s Q_{s,s'}}{J} \right| \|T_k f\| + O\left(\frac{1}{J^3}\right) \right]. \end{aligned}$$

Now, since $n = \lfloor tJ \rfloor$, we get that $\sum_{k=0}^{n-1} O\left(\frac{1}{J^3}\right) = O\left(\frac{1}{J^2}\right)$. Moreover, by Lemma 25, we have

$$\sum_{k=0}^{n-1} \|(T_k f)^{(1)}\| \leq \|f^{(1)}\| \sum_{k=0}^{n-1} e^{k\frac{C}{J}} = \|f^{(1)}\| \frac{e^{n\frac{C}{J}} - 1}{e^{\frac{C}{J}} - 1}$$

Since $e^{\frac{C}{J}} - 1 \geq \frac{C}{J}$ and $n = \lfloor tJ \rfloor \leq tJ$, we get

$$\sum_{k=0}^{n-1} \|(T_k f)^{(1)}\| \leq \|f^{(1)}\| J \frac{e^{tC} - 1}{C}.$$

For the same reason, we get that

$$\sum_{k=0}^{n-1} \|(T_k f)^{(2)}\| \leq \left(\|f^{(1)}\| + K\|f^{(2)}\| \right) J \frac{e^{2tC} - 1}{2C},$$

hence

$$\begin{aligned} &\frac{1}{J^2} \sum_{k=0}^{n-1} \left(\gamma_0 \|T_k f\| + \gamma_1 \|T_k^{(1)} f\| + \gamma_2 \|T_k^{(2)} f\| \right) \\ &\leq \frac{1}{J} \left(t\gamma_0 \|f\| + \gamma_1 \frac{e^{tC} - 1}{C} \|f^{(1)}\| + \gamma_2 K \frac{e^{2tC} - 1}{2C} \|f^{(2)}\| \right) \end{aligned}$$

This, together with the fact that

$$\sum_{k=0}^{n-1} \sum_{s' \neq s} \left| P_{s,s'}^J - \frac{\alpha_s Q_{s,s'}}{J} \right| \|T_k f\| \leq |JP_{s,s'}^J - \alpha_s Q_{s,s'}| \|f\|$$

conclude the proof of Theorem 2.

7.2. A lemma for accessibility. This section is devoted to the statement and the proof of a lemma which is useful for accessibility issue. Let E be a finite set, and for all $i \in E$, let $f_i : \mathbb{R}^d \rightarrow \mathbb{R}^d$ be a globally integrable vector field. For $i \in E$, we denote by $(\varphi_t^i(x))_{t \geq 0}$ the flow generated by f_i and started at x . That is, $\varphi_t^i(x)$ is solution to

$$\begin{cases} \frac{\partial \varphi_t^i(x)}{\partial t} = f_i(\varphi_t^i(x)) \\ \varphi_0^i(x) = x. \end{cases}$$

For $m \geq 1$, $\mathbf{i} = (i_1, \dots, i_m) \in \{1, 2, 3\}^m$ and $\mathbf{u} = (u_1, \dots, u_m) \in \mathbb{R}_+^m$, we denote by $\Phi_{\mathbf{u}}^{\mathbf{i}}$ the composite flow: $\Phi_{\mathbf{u}}^{\mathbf{i}} = \varphi_{u_m}^{i_m} \circ \dots \circ \varphi_{u_1}^{i_1}$. For $x \in \mathbb{R}^d$ and $t \geq 0$, we denote by $\mathcal{O}_{f,t}^+(x)$ (resp. $\mathcal{O}_f^+(x)$) the set of points that are reachable from x at time t (resp. at any nonnegative time) with a composite flow:

$$\mathcal{O}_{f,t}^+(x) = \{\Phi_{\mathbf{v}}^{\mathbf{i}}(x), (\mathbf{i}, \mathbf{v}) \in E^m \times \mathbb{R}_+^m, m \in \mathbb{N}, v_1 + \dots + v_m = t\},$$

$$\mathcal{O}_f^+(x) = \bigcup_{t \geq 0} \mathcal{O}_{f,t}^+(x).$$

For $B \subset \mathbb{R}^d$, We define the set of points that are accessible from B (with the vector fields $(f_i)_{i \in E}$) as

$$\Gamma_{f,B} = \bigcap_{x \in B} \overline{\mathcal{O}_f^+(x)}.$$

These accessible sets are linked to the support of invariant probability measure of PMDP, see e.g. [6, Proposition 3.17]. With these notations, we have the following lemma :

Lemma 26. *Let $(f_i)_{i \in E}$ and $(g_i)_{i \in E}$ be two families of globally integrable vector fields on \mathbb{R}^d . Assume that for all i , there exists a positive, Lipschitzian, bounded function $h_i : \mathbb{R}^d \rightarrow \mathbb{R}$ such that $g_i = h_i f_i$. Then, for all $x \in \mathbb{R}^d$, one has*

$$\mathcal{O}_f^+(x) = \mathcal{O}_g^+(x).$$

In particular, for all $B \subset \mathbb{R}^d$

$$\Gamma_{f,B} = \Gamma_{g,B}.$$

Proof. Since $g_i = h_i f_i$, one can find, for all $i \in E$ and $x \in \mathbb{R}^d$ an increasing bijection $\alpha_x^i : [0, +\infty) \rightarrow [0, +\infty)$ such that, for all $t \geq 0$, $\psi_t^i(x) = \varphi_{\alpha_x^i(t)}^i(x)$, where ψ^i and φ_i are the flow generated by g_i and f_i , respectively. Now, let $y \in \mathcal{O}_f^+(x)$. Then, there exists $(\mathbf{i}, \mathbf{v}) \in E^m \times \mathbb{R}_+^m$ such that

$$y = \Phi_{\mathbf{u}}^{\mathbf{i}}(x) = \varphi_{u_m}^{i_m} \circ \dots \circ \varphi_{u_1}^{i_1}(x).$$

Hence,

$$y = \psi_{\alpha_{\varphi_{u_{m-1}}^{i_{m-1}} \circ \dots \circ \varphi_{u_1}^{i_1}(x)}^{i_m}}^{i_m}(u_m) \circ \dots \circ \psi_{\alpha_x^{i_1}}^{i_1}(u_1)(x),$$

and so $y \in \mathcal{O}_g^+(x)$. Since the functions α are bijective, we can prove the converse inclusion, hence the equality of $\mathcal{O}_f^+(x)$ and $\mathcal{O}_g^+(x)$ \square

With the notations of the main sections of this paper, one has

$$G_s(x) = h_s(x) f_s(x),$$

where $h_s(x) = 1 + s^1 x^1 + \dots + s^S x^S$ and $f_s^i(x) = x^i (s^i - (s^1 x^1 + \dots + s^S x^S))$. The particular interest of the lemma lies in the fact that a convex combination of the f_s is given by the

function with the convex combination of the coefficients. That is, if $(a_s)_{s \in E}$ are nonnegative such that $\sum_s a_s = 1$, and if we set for $s_a = \sum_{s \in E} a_s s$, then $\sum_s a_s f_s = f_{s_a}$.

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REFERENCES

- [1] Robert A. Armstrong and Richard McGehee. Coexistence of species competing for shared resources. *Theoretical Population Biology*, 9(3):317 – 328, 1976.
- [2] R. Azaïs, J.-B. Bardet, A. Génadot, N. Krell, and P.-A. Zitt. Piecewise deterministic Markov process—recent results. In *ESAIM: Proceedings*, volume 44, pages 276–290. EDP Sciences, 2014.
- [3] Y. Bakhtin and T. Hurth. Invariant densities for dynamical systems with random switching. *Nonlinearity*, 25(10):2937–2952, 2012.
- [4] Y. Bakhtin, T. Hurth, and J. C. Mattingly. Regularity of invariant densities for 1d systems with random switching. *Nonlinearity*, 28(11):3755, 2015.
- [5] J.-B. Bardet, A. Christen, A. Guillin, F. Malrieu, and P.-A. Zitt. Total variation estimates for the TCP process. *Electron. J. Probab.*, 18:no. 10, 21, 2013.
- [6] M. Benaïm, S. Le Borgne, F. Malrieu, and P.-A. Zitt. Qualitative properties of certain piecewise deterministic Markov processes. *Ann. Inst. Henri Poincaré Probab. Stat.*, 51(3):1040–1075, 2015.
- [7] M. Benaïm and C. Lobry. Lotka Volterra in fluctuating environment or “how switching between beneficial environments can make survival harder”. *Ann. Appl. Probab.*, 26(6):3754–3785, 2016.
- [8] M. Benaïm and E. Strickler. Random switching between vector fields having a common zero. *Ann. Appl. Probab.*, 29(1):326–375, 2019.
- [9] M. Benaïm. Stochastic persistence. *arXiv:1806.08450v2*, June 2018.
- [10] D. Chafaï, F. Malrieu, and K. Paroux. On the long time behavior of the TCP window size process. *Stochastic Process. Appl.*, 120(8):1518–1534, 2010.
- [11] Peter Chesson and Robert Warner. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, 117:923–943, 06 1981.
- [12] Peter L. Chesson. The stabilizing effect of a random environment. *Journal of Mathematical Biology*, 15(1):1–36, Sep 1982.
- [13] B. Cloez, R. Dossalles, A. Genadot, F. Malrieu, A. Marguet, and R. Yvinec. Probabilistic and piecewise deterministic models in biology. *ESAIM: Proceedings and Surveys*, 60:225–245, 2017.
- [14] A. Crudu, A. Debussche, A. Muller, and O. Radulescu. Convergence of stochastic gene networks to hybrid piecewise deterministic processes. *Ann. Appl. Probab.*, 22(5):1822–1859, 2012.
- [15] M. Danino, D.A. Kessler, and N.M. Shnerb. Stability of two-species communities: drift, environmental stochasticity, storage effect and selection. *Theoretical population biology*, 119:57–71, 2018.
- [16] M. Danino and N.M. Shnerb. Fixation and absorption in a fluctuating environment. *Journal of theoretical biology*, 441:84–92, 2018.
- [17] M. H. A. Davis. Piecewise-deterministic Markov processes: a general class of nondiffusion stochastic models. *J. Roy. Statist. Soc. Ser. B*, 46(3):353–388, 1984.
- [18] P. de Mottoni and A. Schiaffino. Competition systems with periodic coefficients: A geometric approach. *Journal of Mathematical Biology*, 11(3):319–335, Mar 1981.
- [19] N. H. Du, N. H. Dang, and W. Feng. Asymptotic behavior of Kolmogorov systems with predator-prey type in random environment. *Communications on Pure & Applied Analysis*, 13(6), 2014.
- [20] S. N. Ethier and Thomas Nagylaki. Diffusion approximations of the two-locus wright-fisher model. *Journal of Mathematical Biology*, 27(1):17–28, Feb 1989.
- [21] J. Fontbona, H. Guérin, and F. Malrieu. Quantitative estimates for the long-time behavior of an ergodic variant of the telegraph process. *Adv. in Appl. Probab.*, 44(4):977–994, 2012.
- [22] J. Fontbona, H. Guérin, and F. Malrieu. Long time behavior of telegraph processes under convex potentials. *Stochastic Process. Appl.*, 126(10):3077–3101, 2016.

- [23] G. Gackou, A. Guillin, and A. Personne. When can the discrete moran process be replaced by wright-fisher diffusion?, 2019. (hal-02116608).
- [24] A. Guillin, F. Jabot, and A. Personne. On the simpson index for the moran process with random selection and immigration, 2018. arXiv:1809.08890.
- [25] A. Hening and E. Strickler. On a predator-prey system with random switching that never converges to its equilibrium. *SIAM Journal on Mathematical Analysis*, 51(5):3625–3640, 2019.
- [26] T. Hurth and C. Kuehn. Random switching near bifurcations. *Stochastics and Dynamics*, page 2050008, 2019.
- [27] F. Jabot and T. Lohier. Non-random correlation of species dynamics in tropical tree communities. *Oikos*, 125(12):1733–1742, 2016.
- [28] M. Kalyuzhny, R. Kadmon, and N.M. Shnerb. A neutral theory with environmental stochasticity explains static and dynamic properties of ecological communities. *Ecology letters*, 18(6):572–580, 2015.
- [29] Motoo Kimura. Diffusion models in population genetics. *Journal of Applied Probability*, 1(2):177–232, 1964.
- [30] P. A. P. Moran. Random processes in genetics. *Mathematical Proceedings of the Cambridge Philosophical Society.*, 54(1):60–71, 1958.
- [31] K. Pakdaman, M. Thieullen, and G. Wainrib. Fluid limit theorems for stochastic hybrid systems with application to neuron models. *Adv. in Appl. Probab.*, 42(3):761–794, 2010.
- [32] K. Pakdaman, M. Thieullen, and G. Wainrib. Intrinsic variability of latency to first-spike. *Biol. Cybernet.*, 103(1):43–56, 2010.
- [33] K. Pakdaman, M. Thieullen, and G. Wainrib. Asymptotic expansion and central limit theorem for multi-scale piecewise-deterministic Markov processes. *Stochastic Process. Appl.*, 122(6):2292–2318, 2012.
- [34] Kluth S and Baake E. The moran model with selection: fixation probabilities, ancestral lines, and an alternative particle representation. *Theor Popul Biol*, 12:90–104, 2013.
- [35] S. Schreiber. Persistence for stochastic difference equations: A mini review. (18):1381–1403., 2012.
- [36] S. Schreiber, M. Benaïm, and KAS Atchadé. Persistence in fluctuating environments. *Journal of Mathematical Biology*, 62:655–683, 2011.
- [37] E. Strickler. Randomly switched vector fields sharing a zero on a common invariant face. *arXiv preprint arXiv:1810.06331*, 2018.

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