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Research article

Comparison principles and applications to mathematical modelling of vegetal meta-communities†

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Abstract: This article partakes of the PEGASE project the goal of which is a better understanding of the mechanisms explaining the behaviour of species living in a network of forest patches linked by ecological corridors (hedges for instance). Actually we plan to study the effect of the *fragmentation* of the habitat on biodiversity. A simple neutral model for the evolution of abundances in a vegetal metacommunity is introduced. Migration between the communities is explicitely modelized in a deterministic way, while the reproduction process is dealt with using Wright-Fisher models, independently within each community. The large population limit of the model is considered. The hydrodynamic limit of this split-step method is proved to be the solution of a partial differential equation with a deterministic part coming from the migration process and a diffusion part due to the Wright-Fisher process. Finally, the diversity of the metacommunity is adressed through one of its indicators, the mean extinction time of a species. At the limit, using classical comparison principles, the exchange process between the communities is proved to slow down extinction. This shows that the existence of corridors seems to be good for the biodiversity.

Keywords: comparison principle; mathematical modelling for metacommunities; Markov chains; diffusion equations

1. Introduction

This article partakes of a research program aimed at understanding the dynamics of a fragmented landscape composed of forest patches connected by hedges, which are ecological corridors. When dealing with the dynamics of a metacommunity at a landscape scale we have to take into account the local competition between species and the possible migration of species.

We are interested here in the mathematical modelling of two species, on two forest patches linked by some ecological corridor. We model the evolution by a *splitting method*, performing first the exchange process (see the definition of the corresponding Markov chain in the sequel) on a small time step, and then we perform independently on each station a birth/death process according to the Wright-Fisher model, and we reiterate.

Our first mathematical result is to compute the limit equation of this modelling when the time step goes to 0 and the size of the population diverges to ∞. This issue, the *hydrodynamic limit*, i.e., to pass from the mesoscopic scale to the macroscopic one received increasing interest in the last decades (see for instance in various contexts [2, 11, 17]). As our main results on extinction times do not require the convergence in law of the processes, instead of using a martingale problem ([8]), we prove directly the convergence of operators towards a diffusion semi-group ([10]). We find a deterministic diffusion-convection equation, where the drift comes from the exchange process, while the diffusion comes from the limit of the Wright-Fisher process. We point out here that the fact that the diffusion operator L_d satisfies a non standard *comparison principle* (or a maximum principle) is instrumental: first the comparison principle ensures the uniqueness of the limit of the approximation process and then the definition of the Feller diffusion process. Then this comparison principle yields our second result that is concerned with the comparison of the extinction time of one species for a system with exchange and a system without exchanges. Assuming that the discrete extinction time converges, we prove that the limit is solution of the equation $-L_d\tau = 1$. Taking advantage once again of comparison principles, we prove that the exchange process slows down the extinction time of one species. Thus, the fragmentation of the habitat seems to be good to the biodiversity.

This article outlines as follows. In a second section we describe the modelling at mesoscopic scale. We couple a Wright-Fisher model for the evolution of the abundances together with an exchange process. The third section is devoted to the large population limit of the discrete process. In a fourth section we discuss the issues related to the extinction time; we compare the extinction time of one species with and without exchange process. In a final section we draw some conclusion and prospects for ecological issues, and we address the question of convergence in law for our model.

2. The mathematical model

2.1. Modelling the exchange between patches

Consider two patches that have respectively the capacity to host (N_1, N_2) individuals, to be chosen into two different species α and β. Set (y_1^n, y_2^n) for the numbers of individuals of type α, respectively in patch 1 and 2, at time $n\delta t$, i.e., after n iterations and δt is the time that will be defined below.

The exchange process is then simply modelled by

$$\begin{aligned} y_1^{n+1} &= (1-\kappa d\delta t)y_1^n + \kappa\delta t y_2^n, \\ y_2^{n+1} &= (\kappa d\delta t)y_1^n + (1-\kappa\delta t)y_2^n, \end{aligned} \tag{2.1}$$

where κ is the instantaneous speed of exchanges and $d = \frac{N_2}{N_1}$ represents the distortion between the patches (the ratio between the hosting capacities); we may assume without loss of generality that $d \leq 1$. With this modelling, and assuming that $\kappa\delta t \leq 1$, it is easy to check that

- The set $[0, N_1] \times [0, N_2]$ is mapped into itself, i.e., stable, by the exchange process.
- The total population of individuals of type α, $y_1^n + y_2^n$, is conserved.
- If we start with only individuals of species α (respectively β) then we remain with only individuals from α (respectively β); this reads $(N_1, N_2) \mapsto (N_1, N_2)$ (respectively $(0, 0) \mapsto (0, 0)$).

Set $x = (x_1 = \frac{y_1}{N_1}, x_2 = \frac{y_2}{N_2})$ belonging to $\mathcal{D} = [0, 1]^2$ for the population densities of a species α on two separate patches and $x^n = (x_1^n, x_2^n)$ for these densities at time $n\delta t$. Then we have alternatively

$$\begin{aligned} x_1^{n+1} &= (1-\kappa d\delta t)x_1^n + \kappa d\delta t x_2^n, \\ x_2^{n+1} &= \kappa\delta t x_1^n + (1-\kappa\delta t)x_2^n. \end{aligned} \tag{2.2}$$

This reads also $x^{n+1} = Ax^n$ where A is a stochastic matrix.

Consider now the piecewise constant càdlàg process with jumps $X \mapsto AX$ at each time step δt. In other words, for any continuous function f defined on $\mathcal{D} = [0, 1]^2$ then $P_{\delta t}^{\mathrm{ex}}(f)(x) = f(Ax)$, where $P_{\delta t}^{\mathrm{ex}}$ is the transition kernel of the exchange process.

2.2. *Wright-Fisher reproduction model*

On each patch we now describe the death/birth process that is given by the Wright-Fisher model. The main assumption is that the death/birth process on one patch is *independent* of the other one.

Consider then the first patch that may host N_1 individuals. The Markov chain is then defined by the transition matrix, written for $z_1 = \frac{j_1}{N_1} \in [0, 1]$

$$\mathbb{P}(x_1^{n+1} = z_1 | x_1^n = x_1) = \binom{N_1}{j_1} x_1^{j_1}(1-x_1)^{N_1-j_1}. \tag{2.3}$$

Since the two Wright-Fisher processes are independent, the corresponding transition kernel reads

$$P_{\delta t}^{\mathrm{wf}}(f)(x) = \sum_{j_1=0}^{N_1}\sum_{j_2=0}^{N_2} \binom{N_1}{j_1}\binom{N_2}{j_2} x_1^{j_1}(1-x_1)^{N_1-j_1} x_2^{j_2}(1-x_2)^{N_2-j_2} f\left(\frac{j_1}{N_1}, \frac{j_2}{N_2}\right), \tag{2.4}$$

for any function f defined on $\mathcal{D} = [0, 1]^2$. Notice that $P_{\delta t}^{\mathrm{wf}}$ is a two-variable version of the usual Bernstein polynomials. In the sequel, we will also use the notation $B_N(f)$ and write for the sake of conciseness

$$\binom{N}{j} x^j (1-x)^{N-j} f\left(\frac{j}{N}\right) = \binom{N_1}{j_1}\binom{N_2}{j_2} x_1^{j_1}(1-x_1)^{N_1-j_1} x_2^{j_2}(1-x_2)^{N_2-j_2} f\left(\frac{j_1}{N_1}, \frac{j_2}{N_2}\right).$$

2.3. The full disrete model

Starting from the state $x = (x_1, x_2)$, during a time step, we apply first the exchange process and then the Wright-Fisher reproduction process. In this way, the sequence of random variables x^n is a Markov chain with state space $\{0, \frac{1}{N_1}, \cdots, 1\} \times \{0, \frac{1}{N_2}, \cdots, 1\}$ and the transition kernel reads as follows

$$\mathbb{E}(f(x^{n+1})|x^n = x) = P^{\text{wf}}_{\delta t} P^{\text{ex}}_{\delta t}(f)(x) = \sum_j \binom{N}{j} x^j (1-x)^{N-j} f \circ A\left(\frac{j}{N}\right) = B_N(f \circ A)(x).$$

3. From discrete model to continuous one

We consider the same scaling as for the Wright-Fisher usual model, that is $N_1 \delta t = 1$. We set $N = N_1$ in the sequel to simplify the notations. We may consider either the càdlàg process associated to the reproduction-exchange discrete process defined by $\overline{x}^t = x^n$ if $n\delta t \leq t < (n+1)\delta t$ or the continuous piecewise linear function x^t such that $x^t = x^n$ for $t = n\delta t$. We consider an analogous interpolation in space in order to deal with function that are defined on $[0, T] \times \mathcal{D}$ where $T > 0$ is given.

We set $M = \begin{pmatrix} d & -d \\ -1 & 1 \end{pmatrix}$ and then $A = Id - \frac{\kappa}{N} M$. For a given continuous function f that vanishes at $(0,0)$ and $(1,1)$, we now define the sequence of functions

$$u_N(t, x) = \mathbb{E}(f(x^t)|x^0 = x). \tag{3.1}$$

We may also use analogously $\overline{u}_N(t, x) = \mathbb{E}(f(\overline{x}^t)|x^0 = x) = (P^{\text{wf}}_{\delta t} P^{\text{ex}}_{\delta t})^n(f)(x)$. The fonctions u_N and $\overline{u}_N$ represent the average densities of the species at a macroscopic level. If X^N is the Lagrangian representation of the densities, then u_N represents the densities in Eulerian variables.

3.1. Statement of the result

Theorem 3.1. *Let T>0 be fixed. Assume f is a function of class C^2 on $\mathcal{D}$, that vanishes at $(0,0)$ and $(1,1)$. The sequence u_N converges uniformly in $[0, T] \times \mathcal{D}$ to the unique solution u of the diffusion equation*

$$\partial_t u = L_d u,$$

where L_d is defined as, for $x = (x_1, x_2)$,

$$L_d u(x) = \frac{x_1(1-x_1)}{2} u_{x_1 x_1}(x) + \frac{x_2(1-x_2)}{2d} u_{x_2 x_2}(x) - \kappa M x.\nabla u(x),$$

and with initial data $u(0, x) = f(x)$.

Remark 3.1. *We may have proved that the càdlàg process associated to the reproduction-exchange process $\overline{u}_N$ converges to a diffusion equation. We will discuss this in the sequel. Besides, we prove the convergence results for a sufficiently smooth f, and we will extend in the sequel the definition of a mild solution to the equation for functions f in the Banach space $E = \{f \in C(\mathcal{D}); f(0,0) = f(1,1) = 0\}$. The theory for Markov diffusion process and the related PDE equations is well developed in the litterature (see [1, 9, 16] and the references therein). The particularity of our diffusion equation is that the boundary of the domain is only two points.*

3.2. Proof of Theorem 3.1

The proof of the theorem is divided into several lemmata. The first lemma describes in a way how the discrete process is close to a martingale.

Lemma 3.1. *The conditional expectation of the discrete reproduction-exchange process is*

$$\mathbb{E}(x^{n+1}|x^n) = Ax^n. \tag{3.2}$$

As a consequence $\mathbb{E}(x^{n+1} - x^n|x^n) = o(1)$ *when* N *diverges to* ∞.

Proof. Using the properties of the Bernstein polynomials,

$$\mathbb{E}(x^{n+1}|x^n) = \sum_j \binom{N}{j} (x^n)^j (1 - x^n)^{N-j} A \begin{pmatrix} \frac{j_1}{N_1} \\ \frac{j_2}{N_2} \end{pmatrix} = Ax^n.$$

Then the proof of the lemma is completed, observing that $A - Id = o(1)$.

□

The following lemma is useful to prove that x^t and $\overline{x}^t$ are close.

Lemma 3.2. *There exists a constant* C *such that*

$$\mathbb{E}(|x^{n+1} - x^n|^2) \leq CN^{-1}.$$

Proof. Since $|A\frac{j}{N}|^2 = |\frac{j}{N}|^2(1 + O(||A - Id||)$, then the following conditional expectation reads

$$\mathbb{E}(|x^{n+1}|^2|x^n) = \sum_j \binom{N}{j} x^j(1 - x)^{N-j}|A\frac{j}{N}|^2 = |x^n|^2 + O(||A - Id||).$$

We expand the ℓ^2 norm in $\mathbb{R}^2$ as

$$|x^{n+1} - x^n|^2 = |x^{n+1}|^2 - 2(x^n, x^{n+1}) + |x^n|^2.$$

We first have by linearity and by the Lemma 3.1 above that

$$\mathbb{E}((x^{n+1}, x^n)|x^n) = (Ax^n, x^n).$$

Therefore

$$\mathbb{E}(|x^{n+1} - x^n|^2|x_n) = 2(x^n, x^n - Ax^n) + O(||I - A||) = O(||I - A||) \tag{3.3}$$

that completes the proof of the lemma.

□

The next statement is a consequence of the inequality $|\overline{x}^t - x^t| \leq |x^n - x^{n+1}|$ for $t \in (n\delta t, (n+1)\delta t)$ and of the previous lemma

Corollary 3.1. *The processes* x^t *and* $\overline{x}^t$ *are asymptotically close, i.e., there exists a constant* C *such that*

$$\mathbb{E}(|\overline{x}^t - x^t|^2) \leq CN^{-1}.$$

As a consequence, when looking for the limit when N diverges towards $+\infty$ of the process, we may either work with x^t or $\overline{x}^t$.

The next lemma is a compactness result on the bounded sequence u_N defined in (3.1).

Lemma 3.3. *There exists a constant C that depends on $\|f\|_{lip}$ and on T such that for any, x, y in $\mathcal{D}$ and s, t in $[0, T]$,*

$$|u_N(t, x) - u_N(t, y)| \leq C|x - y|,$$

$$|u_N(t, x) - u_N(s, x)| \leq C|t - s|^{\frac{1}{2}}.$$

Remark 3.2. *Since the constants C do not depend on N we can infer letting $N \to \infty$ some extra regularity results for u, assuming that f is Lipschitz.*

Proof. We begin with the first estimate. Introduce n such that $n\delta t \leq t < (n+1)\delta t$. Set y^t for the process that starts from $y = y^0$.

$$|x^t - y^t| \leq \max(|x^n - y^n|, |x^{n+1} - y^{n+1}|),$$

therefore, proving the first inequality for $\overline{u}_N$ (which amounts to controlling $|x^n - y^n|$)) will imply the inequality for u_N. Due to the properties of Bernstein's polynomials we have that

$$|\partial_{x_1} P^{\mathrm{wf}}_{\delta t}(f)(Ax)| \leq N\|A\|\omega(f, \frac{1}{N}), \tag{3.4}$$

where $\omega(f, \frac{1}{N})$ is the modulus of continuity of f. Then, using that $\|A - Id\| \leq CN^{-1}$, we infer that

$$|\partial_{x_1} P^{\mathrm{wf}}_{\delta t}(f)(Ax)| \leq \|f\|_{lip}(1 + \frac{C}{N}). \tag{3.5}$$

Iterating in time we have that,

$$|\partial_{x_1} (P^{\mathrm{wf}}_{\delta t} P^{\mathrm{ex}}_{\delta t})^m(f)(x)| \leq \|f\|_{lip}(1 + \frac{C}{N})^m \leq \exp(CT)\|f\|_{lip}. \tag{3.6}$$

The other derivative is similar and then we infer from this computation that the first inequality in the statement of Lemma 3.3 is proved.

We now proceed to the proof of the second one. Introduce the integers m, n such that $m\delta t \leq s < (m+1)\delta t$ and $n\delta t \leq t < (n+1)\delta t$. Using that

$$|x^t - x^s|^2 \leq 9(|x^{m+1} - x^s|^2 + |x^{m+1} - x^n|^2 + |x^n - x^t|^2),$$

and that $|x^n - x^t| \leq (t - \frac{n}{\delta t})|x^n - x^{n+1}|$ we just have to prove the inequality for $\frac{t}{\delta t}$ and $\frac{s}{\delta t}$ in $\mathbb{N}$. Introduce the increment $y^j = x^{j+1} - x^j$. We have that, for $m \leq i, j \leq n$

$$\mathbb{E}(|x^n - x^m|^2) = \sum_j \mathbb{E}(|y^j|^2) + 2\sum_{i<j} \mathbb{E}(y^i, y^j). \tag{3.7}$$

On the one hand, by Lemma 3.2 we have that the first term in the right hand side of (3.7) is bounded by above by $\frac{C(m-n)}{N}$. On the other hand, using that the $\mathbb{E}(y^j|x^j) = (A - Id)x^j$ then

$$\sum_{i<j} \mathbb{E}(y^i, y^j) = \sum_{i<j} \mathbb{E}(y^i, (A - Id)x^j) = \sum_j \mathbb{E}(x^j - x^m, (Id - A)x^j). \tag{3.8}$$

Since $\|Id - A\| \leq CN^{-1}$ then the right hand side of (3.8) is also bounded by above by $\frac{C(m-n)}{N}$. This completes the proof of the lemma.

□

Thanks to Ascoli's theorem, up to a subsequence extraction, u_N converges uniformly to a continuous function $u(t,x)$. We now prove that u is solution of a diffusion equation whose infinitesimal generator is defined as the limit of $N(P^{\mathrm{wf}}_{\delta t} P^{\mathrm{ex}}_{\delta t} - Id)$.

Lemma 3.4. *Consider f a function of class C^2 on $\mathcal{D}$ that vanish at $(0,0)$ and $(1,1)$. Then*

$$\lim_{\delta t \to 0^+} N(P^{\mathrm{wf}}_{\delta t} P^{\mathrm{ex}}_{\delta t}(f(x)) - f(x)) = \lim_{N\to\infty} N(B_N(f\circ A(x) - f(x)) = L_d f(x),$$

where L_d is defined in Theorem 3.1.

Proof. Due to Taylor formula

$$P^{\mathrm{ex}}_{\delta t}(f)(x) = f(x) - \kappa\delta t(Mx.\nabla f)(x) + O((\delta t)^2), \tag{3.9}$$

where $(O(\delta t)^2)$ is valid uniformly in x in $\mathcal{D}$.
Using that the linear operator $P^{\mathrm{wf}}_{\delta t}$ is positive and bounded by 1 we then have

$$P^{\mathrm{wf}}_{\delta t} P^{\mathrm{ex}}_{\delta t}(f)(x) = (P^{\mathrm{wf}}_{\delta t} f)(x) - \kappa\delta t P^{\mathrm{wf}}_{\delta t}(Mx.\nabla f)(x) + O((\delta t)^2), \tag{3.10}$$

The well-known properties of Bernstein polynomials (see [6]) entail that uniformly in x

$$[P^{\mathrm{wf}}_{\delta t}(Mx.\nabla f)(x) - Mx.\nabla f(x)| \leq C\sqrt{\delta t}.$$

On the other hand, the operator $P^{\mathrm{wf}}_{\delta t}$ is the tensor product of two one-dimensional Bernstein operators. Then by Voronovskaya-type theorem (see [6]), for $f(x) = f_1(x_1)f_2(x_2)$ we have the uniform convergence of $N((P^{\mathrm{wf}}_{\delta t} f)(x) - f(x))$ to $\frac{x_1(1-x_1)}{2} f_{x_1x_1} + \frac{x_2(1-x_2)}{2d} f_{x_2x_2}$. By density of the linear combinations of tensor products $f_1(x_1)f_2(x_2)$ this result extend to general f as

$$\lim_{\delta t\to 0^+} \frac{P^{\mathrm{wf}}_{\delta t}(f)(x) - f(x)}{\delta t} = \frac{x_1(1-x_1)}{2} f_{x_1x_1} + \frac{x_2(1-x_2)}{2d} f_{x_2x_2}. \tag{3.11}$$

Denoting Δ_d the diffusion operator defined by the right hand side of (3.11), the Kolmogorov limit equation of our coupled Markov process is

$$\partial_t u - \Delta_d u = -\kappa(Mx.\nabla u)(x), \tag{3.12}$$

with initial data $u(0,x) = f(x)$. Let us observe that u, the limit of $\mathbb{E}(f(x^t)|x^0 = x)$, vanishes at two points $(0,0)$ and $(1,1)$ in the boundary $\partial\mathcal{D}$.

□

We now complete the proof of the Theorem. Considering f such that the convergence in Lemma 3.4 holds. Then, for $n \leq tN < n+1$,

$$\overline{u}_N(t,x) = f(x) + \sum_{k=0}^{n-1} \int_{k\delta t}^{(k+1)\delta t} (N(P^{\mathrm{wf}}_{\delta t} P^{\mathrm{ex}}_{\delta t} - Id)(\overline{u}_N(s,.)))(x)ds. \tag{3.13}$$

Using the uniform convergence of $\overline{u}_N$, Lemma 3.4 and a recurrence on n we may prove that at the limit

$$u(t) = f + \int_0^t L_d u(s)ds, \tag{3.14}$$

where we have omitted the variable x for the sake of convenience.

We now state a result that ensures the uniqueness of a solution to the diffusion equation (3.14). Such a solution is a solution to the diffusion equation in a weak PDE sense.

Introduce $D(L_d) = \{f \in E; \frac{P^{\mathrm{wf}}_{\delta t} P^{\mathrm{ex}}_{\delta t}(f)(x) - f(x)}{\delta t} \to L_d f \text{ in } E\}$.

Remark 3.3. *We precise here the regularity of the functions f in $D(L_d)$. Since L_d is a strictly elliptic operator on any compact subset of the interior of $\mathcal{D}$ then f is $C^2(\mathring{\mathcal{D}}) \cap C(\mathcal{D})$ (see [12]). The regularity of f up to the boundary is a more delicate issue (see [14, 15]). Besides, to determine exactly what is the domain of L_d is a difficult issue. For PDEs the unbounded operator is also determinated by its boundary conditions. Here we have boundary conditions of Ventsel'-Vishik type, that are integro-differential equations on each side of the square linking the trace of the function f and its normal derivative. This is beyond the scope of this article.*

Theorem 3.2 (Comparison Principle).

- *Parabolic version: Consider a function u in $C(\mathbb{R}^+, D(L_d))$ that satisfies*
  - $u_t - L_d u \geq 0$ *in* $\mathbb{R}^+ \times [0,1]^2$,
  - $u(0,x) = f(x) \geq 0$ *for x in* $[0,1]^2$,

  then $u(t,x) \geq 0$.
- *Elliptic version: Consider $u(x)$ in $D(L_d)$ that satisfies $-L_d u \geq 0$ in $[0,1]^2$. Then $u(x) \geq 0$.*

We postpone the proof of this theorem until the end of this section. We point out that a comparison principle for L_d is not standard since it requires only information on two points $\{(0,0),(1,1)\}$ in $\partial\mathcal{D}$ and not on the whole boundary.

Theorem 3.2 implies uniqueness of the limit solution. Therefore the whole sequence u_N converge and the semigroup is well defined. Actually, setting $S(t)f = u(t)$ we then have defined for smooth f the solution to a Feller semigroup (see [1]) as follows

1). $S(0) = Id$.
2). $S(t+s) = S(t)S(s)$.
3). $\|S(t)f - f\|_E \to 0$ when $t \to 0^+$
4). $\|S(t)f\|_E \leq \|f\|_E$.

The second property comes from uniqueness, the last one passing to the limit in

$$\|(P^{\mathrm{wf}}_{\delta t} P^{\mathrm{ex}}_{\delta t})^n f\|_{L^\infty} \leq \|f\|_{L^\infty}.$$

The third one is then simple. The third property allows us to extend the definition of $S(t)$ to functions in E by a classical density argument. Then we have a Feller semigroup in E that satisfies the assumptions of the Hille-Yosida theorem (see [5]).

3.3. Proof of the comparison principle

We begin with the comparison principle for the parabolic operator. We use that $C^2(\mathcal{D})$ is dense in $D(L_d)$, i.e., that any function u in $D(L_d)$ can be approximated in E by smooth functions u_k up to the boundary, and such that Lu_k converges uniformly on any compact subset of $\mathring{\mathcal{D}}$. We then prove the comparison principle for smooth functions and we conclude by density.

Consider u as in the statement of the Theorem for a C^2 initial data f. Consider ε small enough. Set $\mathcal{P} = \partial_t - L_d$. Set $\psi(x) = (x_1 + dx_2)(d + 1 - x_1 - dx_2)$ and $\theta(x) = (x_1 - x_2)^2$. Introduce the auxiliary function

$$v(t, x) = u(t, x) + \varepsilon\psi(x) + \varepsilon^2\theta(x) + \varepsilon^3. \tag{3.15}$$

We prove below that $v(t, x) \geq 0$ for all t and x. Since u belongs to $D(L_d)$ then $v(t, x) = \varepsilon^3$ at the corners $x \in \{(0, 0), (1, 1)\}$. We also have $v(0, x) \geq \varepsilon^3$.

Let us then argue by contradiction. Introduce $t_0 = \inf\{t > 0; \exists x \in [0, 1];\ v(t, x) < 0\}$. Then there exists x_0 such that $v(t_0, x_0) = 0$. Notice that $x_0 \notin \{(0, 0), (1, 1)\}$. We shall discuss below different cases according to the location of x_0.

First case: x_0 belongs to the interior of $\mathcal{D}$.

We then have $v_t(t_0, x_0) \leq 0$, $v_{x_1}(t_0, x_0) = v_{x_2}(t_0, x_0) = 0$, and $v_{x_1x_1}(t_0, x_0), v_{x_2x_2}(t_0, x_0) \geq 0$. Therefore $\mathcal{P}v(t_0, x_0) \leq 0$

$$0 \leq \mathcal{P}u(t_0, x_0) \leq \mathcal{P}v(t_0, x_0) + \varepsilon L_d(\psi + \varepsilon\theta)(x_0). \tag{3.16}$$

Let us observe that if ε is chosen small enough

$$\begin{aligned} L_d(\psi + \varepsilon\theta)(x_0) = &- (x_1(1 - x_1) + dx_2(1 - x_2)) + \\ \varepsilon\left(x_1(1 - x_1) + \frac{1}{d}x_2(1 - x_2)\right) &- \kappa\varepsilon(d + 1)\theta(x)^2 < 0. \end{aligned} \tag{3.17}$$

Second case: x_0 belongs to $\partial\mathcal{D}$ but the four corners.

We may assume that $x_0 = (0, x_2)$ the other cases being similar. We have that $v_t(t_0, x_0) \leq 0$, $v_{x_2}(t_0, x_0) = 0$, $v_{x_1}(t_0, x_0) \geq 0$ and $v_{x_2x_2}(t_0, x_0) \geq 0$. Therefore $\mathcal{P}v(t_0, x_0) \leq 0$.

We then have as in (3.16) that $0 \leq L_d(\psi + \varepsilon\theta)(x_0)$. Computing $L_d(\psi + \varepsilon\theta)(x_0) = -\varepsilon\kappa(d + 1)\theta^2(x_0) < 0$ gives the contradiction.

Third case: $x_0 = (0, 1)$ (the case $(1, 0)$ is similar).

We have that $v_t(t_0, x_0) \leq 0$, $v_{x_2}(t_0, x_0) \leq 0 \leq v_{x_1}(t_0, x_0)$. Therefore $\mathcal{P}v(t_0, x_0) \leq 0$. We then have as in (3.16) that $0 \leq L_d(\psi + \varepsilon\theta)(x_0)$. Computing $L_d(\psi + \varepsilon\theta)(x_0) = -\varepsilon\kappa(d + 1)\theta^2(x_0) < 0$ gives the contradiction.

We now conclude. since v is nonnegative we have

$$\inf_{[0,+\infty)\times\mathcal{D}} u \geq -\varepsilon\|\psi + \varepsilon\theta\|_{L^\infty} - \varepsilon^3. \tag{3.18}$$

Letting ε goes to 0 completes the proof.

Let us prove the elliptic counterpart of the result for a smooth function u (we also proceed by density). Set as above $v(x) = u(x) + \varepsilon\psi(x) + \varepsilon^2\theta(x)$. Introduce x_0 where v achieves its minimum, i.e.,

$v(x_0) = \min_{\mathcal{D}} v(x)$. First if x_0 belongs to the interior of $\mathcal{D}$, then $L_d v(x_0) > 0$ and we have a contradiction. We disprove the case where x_0 belongs to the boundary but $\{(0,0),(1,1)\}$ exactly as in the evolution equation case. Assume first that x_0 belongs to $\partial\mathcal{D}$ but the four corners; for instance $x_0 = (0, x_2)$. We have that $v_{x_2}(x_0) = 0$, $v_{x_1}(x_0) \geq 0$ and $v_{x_2x_2}(x_0) \geq 0$. Therefore $L_d v(x_0) \geq 0$. Then $L_d(\psi + \varepsilon\theta)(x_0) =< 0$ gives the contradiction. Assume then that $x_0 = (0,1)$. We have that $v_{x_2}(x_0) \leq 0 \leq v_{x_1}(x_0)$. Therefore $-L_d v(x_0) \leq 0$. We then have that $0 \leq L_d(\psi + \varepsilon\theta)(x_0)$. Computing $L_d(\psi + \varepsilon\theta)(x_0) =< 0$ gives the contradiction.

Corollary 3.2. *Actually L_d satisfies the positive maximum principle (PMP). If u in $D(L_d)$ achieves its minimum in x_0 in the interior of $\mathcal{D}$ then $L_d u(x_0) \geq 0$. This is standard for infinitesimal generator of Feller semigroups (see [3]).*

4. Extinction time

4.1. Hydrodynamic limit of the extinction time

We handle here the convergence of the discrete extinction time towards the solution of an elliptic equation. To begin with, recall that the discrete process describing the evolution of the densities of population (migration and reproduction at each time step) is a Markov chain with state space $\{0, \frac{1}{N}, \ldots, 1\} \times \{0, \frac{1}{N}, \ldots, 1\}$ for which $(0,0)$ and $(1,1)$ are absorbing states. These two absorbing states correspond to the extinction of a species. Let us introduce the hitting time Θ_N that is the random time when the Markov chain reaches the absorbing states, i.e., the *extinction time*. Since the restriction of the chain to the non absorbing states is irreducible and since there is at least one positive transition probability from the non absorbing states to the absorbing states then this hitting time is almost surely finite. This result is standard for Markov chains with finite state space (see [4, 7] and the references therein).

Let U be the complement of the trapping states $(0,0)$ and $(1,1)$. Consider the vector T_N defined as the conditional expectation $(T_N)_{\frac{j}{N}\in U} = \mathbb{E}_{\frac{j}{N}}(\Theta_N)$ of this hitting time and denote by $\tilde{P}_N$ or $\tilde{P}$ the restriction of the transition matrix to U.

Then for $x \in U$, denoting $\mathbb{P}_x$ the conditional probability, we have using Markov property and time translation invariance

$$
\begin{aligned}
\mathbb{E}_x(\Theta_N) &= \sum_{k=1}^{\infty} \frac{k}{N}\mathbb{P}_x(\Theta_N = \frac{k}{N}) = \frac{1}{N}\mathbb{P}_x(\Theta_N = \frac{1}{N}) + \sum_{k=2}^{\infty} \frac{k}{N}\mathbb{P}_x(\Theta_N = \frac{k}{N}) \\
&= \frac{1}{N}\mathbb{P}_x(\Theta_N = \frac{1}{N}) + \sum_{k=2}^{\infty} \frac{k}{N} \sum_{y\in U} \mathbb{P}_x(\Theta_N = \frac{k}{N}, x^1 = y) \\
&= \frac{1}{N}\mathbb{P}_x(\Theta_N = \frac{1}{N}) + \sum_{k=2}^{\infty} \frac{k}{N} \sum_{y\in U} \mathbb{P}(\Theta_N = \frac{k}{N} | x^1 = y)\mathbb{P}_x(x^1 = y) \\
&= \frac{1}{N}\mathbb{P}_x(\Theta_N = \frac{1}{N}) + \sum_{y\in U} \tilde{P}_{x,y} \sum_{k=2}^{\infty} (\frac{k-1}{N} + \frac{1}{N})\mathbb{P}_y(\Theta_N = \frac{k-1}{N}) \\
&= \left(\frac{1}{N}\mathbb{P}_x(\Theta_N = \frac{1}{N}) + \frac{1}{N}\sum_{y\in U} \tilde{P}_{x,y}\right) + \sum_{y\in U} \tilde{P}_{x,y}\mathbb{E}_y(\Theta_N)
\end{aligned}
$$

$$= \frac{1}{N} + \sum_{y \in U} \tilde{P}_{x,y} \mathbb{E}_y(\Theta_N).$$

This is equivalent to

$$N(Id - \tilde{P}_N)T_N = \begin{pmatrix} 1 \\ \dots \\ 1 \end{pmatrix}. \tag{4.1}$$

We are now interested in the limit of T_N when N diverges towards ∞.

Let us recall that for the one dimensional Wright-Fisher process the expectation of the hitting time starting from x converges towards the entropy $H(x)$ (see [16]) defined by

$$H(x) = -2\left(x \ln x + (1-x)\ln(1-x)\right). \tag{4.2}$$

The entropy is a solution to the equation $-\frac{x(1-x)}{2}H_{xx} = 1$ that vanishes at the boundary. The proof, that can be found in Section 10 of [9], uses probability tools like the convergence in distribution of the processes and the associated stochastic differential equation. We believe that the same kind of tools would give the convergence of τ_N in dimension two but this is beyond the scope of this article. Besides, for the sake of completeness we provide a proof for the convergence in distribution of our processes in Section 5.2 below.

Set now τ_N for the polynomial of degree N in x_1 and x_2 that interpolates T_N at the points of the grid. We have

Theorem 4.1 (Extinction time)**.** *When N diverges to $+\infty$ the sequence τ_N converges towards τ that is solution to the elliptic equation $-L_d\tau = 1$.*

Assuming the convergence of τ_N, the proof of the theorem is straightforward by passing to the limit in (4.1) using Lemma 3.4.

Remark 4.1. *We expect the function τ to be smooth up to the boundary but at the two points $(0,0)$ and $(1,1)$. We admit here this result. This allows us to use the previous comparison result.*

The solution of this elliptic equation in E, i.e., that vanishes at $\{(0,0),(1,1)\}$ is unique due to comparison principle (see Theorem 3.2 above).

4.2. Exchanges slow down extinction

Consider now a single patch whose hosting capacity is $N_1 + N_2 = (d+1)N$ for $N = \frac{1}{\delta t}$. The limit equation for the classical Wright-Fisher related process is

$$\partial_t u = \frac{z(1-z)}{2(1+d)}\partial_z^2 u. \tag{4.3}$$

Then the corresponding extinction time for the Wright-Fisher process without exchange is $\underline{\tau} = (d+1)H(z)$, where $z = \frac{x_1 + dx_2}{1+d}$ is the corresponding averaged starting density (see [16]) and where H is the entropy defined above (4.2). We shall prove in the sequel

Theorem 4.2. *The extinction time $\underline{\tau}$ is a subsolution to the equation $-L_d\tau = 1$. Besides, the operator L_d satisfies the comparison principle and then $\underline{\tau} \leq \tau$.*

Proof. We point out that to check that $-L_d$ satisfies the comparison result is not obvious (see Theorem 3.2). We first observe that the entropy (4.2) vanishes at the boundary points $\{(0,0),(1,1)\}$. Setting $\underline{\tau}(x_1,x_2) = g(z)$, we have

$$(Mx.\nabla g)(z) = (x_1 - x_2)g'(z)\,(d\partial_{x_1}z - \partial_{x_2}z) = 0, \tag{4.4}$$

We then have

$$-L_d\underline{\tau} = \frac{x_1(1-x_1) + dx_2(1-x_2)}{(1+d)z(1-z)}. \tag{4.5}$$

Observing that by a mere computation

$$\frac{x_1(1-x_1) + dx_2(1-x_2)}{(1+d)z(1-z)} = 1 - \frac{d(x_1-x_2)^2}{(1+d)^2 z(1-z)}, \tag{4.6}$$

we have that $\underline{\tau}$ is a subsolution to the equation. □

4.3. More comparison results

We address here the issue of the convergence of the limit extinction time $\tau = \tau_{d,\kappa}$ defined in Section 4 when κ or d converges towards 0. This extinction time depends on the starting point x.

Proposition 4.1. *Assume d be fixed. When κ converges to* 0 *then* $\lim \tau_{d,\kappa}(x) = +\infty$ *everywhere but in* $x = (0,0)$ *or* $x = (1,1)$.

Proof. Consider here the function $V = \frac{x_1(1-x_2)+x_2(1-x_1)}{12\kappa}$. This function vanishes at $x = (0,0)$ and $x = (1,1)$ and satisfies

$$-L_d V = \frac{(x_1 - x_2)(d(1-2x_2) - (1-2x_1))}{12} \leq 1. \tag{4.7}$$

Then V is a subsolution to the equation $-L_d\tau = 1$ and by the comparison principle $V \leq \tau_{d,\kappa}$ everywhere. Letting $\kappa \to 0$ completes the proof of the Proposition. □

Proposition 4.2. *Assume κ be fixed. Then*

$$\lim_{d\to 0} \tau = H(x_1) = -2x_1 \ln x_1 - 2(1-x_1)\ln(1-x_1),$$

that is the extinction time for one patch.

Proof. We begin with

$$-L_d(\tau - \underline{\tau}) = \frac{d(x_1-x_2)^2}{(1+d)^2 z(1-z)}. \tag{4.8}$$

Let us observe that due to (4.6)

$$\frac{d(x_1-x_2)^2}{(1+d)^2 z(1-z)} \leq 1. \tag{4.9}$$

The strategy is to seek a supersolution X to the equation $-L_d\tilde{X} = \frac{1}{d}$ that is bounded when d converges to 0. We first have, using the entropy function $H_2(x_1,x_2) = H(x_2)$

$$-L_d H_2 = \frac{1}{d} + 2\kappa(x_1 - x_2)\ln\frac{x_2}{1-x_2} \geq \frac{1}{d} + 2\kappa(x_1 \ln x_2 + (1-x_1)\ln(1-x_2)). \tag{4.10}$$

Setting $D(x_1, x_2) = x_1 x_2^d + (1-x_1)(1-x_2)^d$, we have

$$-L_d D = \frac{1-d}{2}(x_2^{d-1}x_1(1-x_2) + (1-x_2)^{d-1}x_2(1-x_1)) - \kappa d(x_1 - x_2)^2(x_2^{d-1} + (1-x_2)^{d-1}). \tag{4.11}$$

Therefore, since we have

$$\frac{1-d}{2}x_2^{d-1}x_1(1-x_2) - \kappa d(x_1^2 - 2x_1x_2 + x_2^2)x_2^{d-1} \geq x_2^{d-1}x_1\left(\frac{1-d}{2} - \kappa d\right) - \frac{1-d}{2} - \kappa d,$$

we obtain, for d small enough to have $(1+2\kappa)d < 1$,

$$-L_d D \geq -1 - 2d\kappa + \frac{1-(1+2\kappa)d}{2}\left(x_1 x_2^{d-1} + (1-x_1)(1-x_2)^{d-1}\right).$$

Gathering this inequality with (4.10) and chosing d small enough such that $\frac{1-(1+2\kappa)d}{2} \geq \frac{1}{4}$ holds true, we then have

$$-L_d(H_2 + D) \geq (\frac{1}{d} - 1 - 2d\kappa) + x_1(2\kappa \ln x_2 + \frac{x_2^{d-1}}{4}) + (1-x_1)(2\kappa\ln(1-x_2) + \frac{(1-x_2)^{d-1}}{4}). \tag{4.12}$$

Using the estimate

$$\frac{1}{4x_2^{1-d}} + 2\kappa \ln x_2 \geq \frac{2\kappa}{1-d}(1 + \ln(\frac{8\kappa}{1-d}).$$

we have that if d is small enough depending on κ then $-L_d(H_2 + D) \geq \frac{1}{2d}$. Using the comparison principle we then have that

$$0 \leq \tau - \underline{\tau} \leq 2d(H_2 + D), \tag{4.13}$$

and we conclude by letting d converge to 0 since $\underline{\tau}$ converges towards $H(x_1)$. □

5. Miscellaneous results and comments

5.1. Discussion and prospects for ecological issues

To begin with, we have introduced a split-step model that balances between the local reproduction of species and the exchange process between patches. This split-step model at a mesoscopic scale converges towards a diffusion model whose drifts terms come from the exchanges. This has been also observed for instance in [19].

Here we deal with a neutral metacommunity model with no exchange with an external pool. Hence the dynamics converge to a fixation on a single species for large times. The average time to extinction of species is therefore an indicator of biodiversity. Here for our simple neutral model, Theorem 4.2

provides a strong reckon that the exchange process is good for the biodiversity. In some sense, the presence of two patches allows each species to establish itself during a larger time lapse.

In a forthcoming work we plan to numerically study a similar model but with more than two patches and several species. We plan also to calibrate this model with data measured in the south part of Hauts-de-France. The main interest is to assess the role of ecological corridors to maintain biodiversity in an area. The question of the benefit of maintaining hedges arises when the agricultural world works for their removal to enlarge the cultivable plots. This is one of the issue addresses by the Green and Blue Frame in Hauts-de-France.

5.2. Convergence un distribution

We address here the convergence in law/in distribution of the infinite dimensional processes related to the x_N^t. This is related to the convergence of the process towards the solution of a stochastic differential equations; we will not develop this here. Following [18] or [13], it is sufficient to check the tightness of the process and the convergence of the finite m-dimensional law.

Dealing with $\overline{x}_N^t$ instead of x_N^t, the second point is easy. Indeed, Theorem 3.1 implies the convergence of the m-dimensional law for $m = 1$. We can extend the result for arbitrary m by induction using the Markov property. For the tightness, we use the so-called Kolmogorov criterion that is valid for continuous in time processes (see [18] chapter 2 and [13] chapter 14); this criterion reads in our case

$$\mathbb{E}(|x_N^s - x_N^t|^4) \leq C|t-s|^2. \tag{5.1}$$

This is a consequence of the following discrete estimate, since x_N^t is piecewise linear with respect to t,

Proposition 5.1. *There exists a constant C such that for any $m < n$*

$$\mathbb{E}(|x^n - x^m|^4) \leq C\frac{|n-m|^2}{N^2}. \tag{5.2}$$

Proof. First step: using that x^n is close to a true martingale.

Let us set $A = Id - \frac{\kappa}{N}M = Id - B$. Introduce $z^0 = x^0$ and $z^n = x^n + B\sum_{k<n} x^k$. Then since $\mathbb{E}(x^{n+1}|x^n) = x^n - Bx^n$, we have that z^n is a martingale. Moreover we have the estimate, for $0 \leq m < n$

$$|(z^n - x^n) - (z^m - x^m)| \leq (n-m)\|B\| \leq C\frac{n-m}{N}. \tag{5.3}$$

Second step: computing the fourth moment.

To begin with we observe that, due to (5.3)

$$|x^n - x^m|^4 \leq 4\left(|z^n - z^m|^4 + C(\frac{n-m}{N})^4\right). \tag{5.4}$$

Therefore we just have to prove that (5.2) is valid with z^n replacing x^n. We introduce the increment $y^j = z^{j+1} - z^j$. We then expand as follows, setting $|.|$ and $(.,.)$ respectively for the euclidian norm and the scalar product in $\mathbb{R}^2$.

$$\mathbb{E}(|z^n - z^m|^4) = \sum_{i,j,k,l} \mathbb{E}\left((y^i, y^j)(y^k, y^l)\right). \tag{5.5}$$

Since y^l is independent of the past, if for instance $l > \max(i, j, k)$ then $\mathbb{E}((y^i, y^j)(y^k, y^l)) = 0$. Therefore, (5.5) reads also

$$\begin{aligned}\mathbb{E}(|z^n - z^m|^4) = 2\sum_{i,j<k}\mathbb{E}\left((y^i, y^j)|y^k|^2\right) + 4\sum_{i,j<k}\mathbb{E}\left((y^i, y^k)(y^j, y^k)\right) + \\ 4\sum_{i<k}\mathbb{E}\left((y^i, y^k)|y^k|^2\right) + \sum_k \mathbb{E}(|y^k|^4) = D_1 + D_2 + D_3 + D_4.\end{aligned} \tag{5.6}$$

Third step: handling D_4 and D_3.

The key estimate reads as follows

$$\mathbb{E}(|y^k|^4|x^k) \leq CN^{-2}. \tag{5.7}$$

Let us check that (5.7) is valid. Due to the very properties of Bernstein polynomials we know that $B_N(1) = 1, B_N(X) = x, B_N(X^2) = x^2 + \frac{x(1-x)}{N}$ and that $B_N(X^3) = x^3 + \frac{3x^2(1-x)}{N} + 0(\frac{1}{N^2})$ and $B_N(X^4) = x^4 + \frac{6x^3(1-x)}{N} + 0(\frac{1}{N^2})$. Therefore $B_N((X-x)^4) \leq CN^{-2}$ and since for any function h we have that $\mathbb{E}(h(x^{k+1})|x^k) = h(Ax^k)$ then, due to the very definition of z^k

$$\mathbb{E}(|y^k|^4) \leq 4\left(\mathbb{E}(|x^{k+1} - x^k|^4) + \frac{C}{N^4}\right) = O(N^{-2}). \tag{5.8}$$

Therefore $D_4 = O((n-m)N^{-2})$ and then the result.

For D_3 thanks to Hölder inequality, we have the estimate

$$D_3 = 4\sum_{j<k}\mathbb{E}\left((y^j, y^k)|y^k|^2\right) \leq C(n-m)D_4 = O((n-m)^2N^{-2}). \tag{5.9}$$

Fourth step: handling D_1 and D_2.

Using the conditional expectation we have

$$\begin{aligned}D_1 &= 2\sum_{i,j<k}\mathbb{E}\left((y^i, y^j)|y^k|^2\right) = 2\sum_{i,j<k}\mathbb{E}\left((y^i, y^j)\mathbb{E}\left(|y^k|^2|x^k\right)\right) \\ &= 2\sum_{m<k\leq n}\mathbb{E}\left(|z^m - z^k|^2\mathbb{E}(|y^k|^2|x^k)\right).\end{aligned} \tag{5.10}$$

Due to (5.7) and Cauchy-Schwarz inequality $\mathbb{E}(|y^k|^2|x^k)) = O(N^{-1})$ and it follows

$$D_1 \leq CN^{-1}\sum_k \mathbb{E}(|z^m - z^k|^2) = CN^{-1}\sum_k(\sum_j \mathbb{E}(|y^j|^2)) \leq CN^{-1}\sum_k \frac{k-m}{N} \leq CN^{-2}(n-m)^2. \tag{5.11}$$

We now handle D_2 exactly as we did for D_1. This completes the proof. □

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Conflict of interest

The authors declare no conflict of interest.

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