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Invasion and adaptive evolution for individual-based spatially structured populations

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Abstract

The interplay between space and evolution is an important issue in population dynamics, that is in particular crucial in the emergence of polymorphism and spatial patterns. Recently, biological studies suggest that invasion and evolution are closely related. Here we model the interplay between space and evolution starting with an individual-based approach and show the important role of parameter scalings on clustering and invasion. We consider a stochastic discrete model with birth, death, competition, mutation and spatial diffusion, where all the parameters may depend both on the position and on the trait of individuals. The spatial motion is driven by a reflected diffusion in a bounded domain. The interaction is modelled as a trait competition between individuals within a given spatial interaction range. First, we give an algorithmic construction of the process. Next, we obtain large population approximations, as weak solutions of nonlinear reaction-diffusion equations with Neumann's boundary conditions. As the spatial interaction range is fixed, the nonlinearity is nonlocal. Then, we make the interaction range decrease to zero and prove the convergence to spatially localized nonlinear reaction-diffusion equations, with Neumann's boundary conditions. Finally, simulations based on the microscopic individual-based model are given, illustrating the strong effects of the spatial interaction range on the emergence of spatial and phenotypic diversity (clustering and polymorphism) and on the interplay between invasion and evolution. The simulations focus on the qualitative differences between local and nonlocal interactions.

1 Introduction

The spatial aspect of population dynamics is an important ecological issue that has been extensively studied (Murray [31], Durrett and Levin [12], Tilman and Kareiva [44], McGlade [26], Dieckmann et al. [9]). It is in particular crucial in environmental problems, such as spatial invasions and epidemics (Mollison [30], Murray [31], Rand et al. [36], Tilman and Kareiva [44], Lewis and Pacala [25]), and clustering or agglomeration of the population, i.e. the organization as isolated patches (Hassel and May [19], Hassel and Pacala [20], Niwa [32], Flierl et al. [14], Young et al. [45]). The combination of space and phenotype is also known for a long time to have important effects on population dynamics (Mayr [27], Endler [13]). In particular, it can strongly favor the coexistence of several types of individuals and the emergence and stability of polymorphism (Durrett and Levin [11], Dieckmann and Doebeli [7]). More recently, several biological studies (Thomas et al. [43], Phillips et al. [33]) observed that classical models could underestimate the invasion speed and suggested that evolution and invasion are closely related. Namely, the evolution of morphology can have strong impact on the expansion of invading species, such as insect species ([43]) or cane toads ([33]). In this context, the study of space-related traits, such as dispersal speed (PrÃľvost [34], Desvillettes et al. [6]), or sensibility to heterogeneously distributed resources (Bolker and Pacala [3], Grant and Grant [18]), is fundamental.

In this paper, we propose and construct stochastic and deterministic population models describing the interplay between evolution and spatial structure. We show how helpful these models can reveal to understand and predict several specific behaviors concerning clustering and invasion.

We study the dynamics of a spatially structured asexual population with adaptive evolution, in which individuals can move, reproduce with possible phenotypic mutation, or die of natural death or from the competition between individuals. The individuals are characterized both by their position and by one or several phenotypical adaptive traits (such as body size, rate of food intake, age at maturity or dispersal speed). The interaction is modelled as a trait competition between individuals in some spatial range. Our approach is based on a stochastic microscopic description of these individuals' mechanisms, involving both space and traits. This approach has already been developed in simpler ecological contexts. For populations undergoing dispersal, Bolker and Pacala [2, 3] and Dieckmann and Law [8], offered the first microscopic heuristics and simulations. Their individual-based model has been rigourously constructed in Fournier and Méléard [15]. If one thinks of the dispersion in the physical space as a mutation in a trait space, this model translates into an evolutionary model. The generalization to adaptive population with general mutation and competition phenomena is achieved by Champagnat, Ferrière and Méléard [5, 4]. In these papers, different large population deterministic or stochastic approximations have been obtained, depending on several scalings on the microscopic parameters.

The basic mechanisms of the population dynamics we consider combine spatial motion and evolutionary dynamics (Section 2). The birth, mutation and death parameters of each individual depend on its position and trait. An offspring, appearing at the same position as its progenitor, usually inherits the trait value of the latter, except when a mutation causes the offspring to take an instantaneous mutation step at birth to new trait values. As soon as it is alive, an individual moves in the spatial domain according to a reflected diffusion process. Moreover, each individual dies because of natural death or is eliminated in the competition (selecting the fittest traits) between individuals living in a given spatial range $\delta > 0$.

Section 3 starts with the algorithmic construction of a stochastic Markov point process whose generator captures the individual migration and ecological mechanisms in the population. Then the existence of this measure-valued process and its martingale properties are proved under some moment condition on the initial data.

Next (Section 4), we study approximations of this model based on large-population limits. We consider a large number N of individuals at initial time and assume that a fixed amount of available resources has to be partitioned between individuals. When N tends to infinity, the conveniently normalized point process converges to a deterministic finite measure, solution of a nonlinear nonlocal integro-differential equation with Neumann's boundary conditions, parameterized by the spatial range. The proof is based on the martingale properties of the process and on limit theorems for measure-valued jump processes. We moreover prove that for sufficiently smooth and non-degenerate diffusion coefficients, assuming that the initial condition has a density, the limiting measure has at each time a density with respect to the Lebesgue measure. That is due to the regularizing effect of the reflected diffusion process. The proof mainly uses analytic tools, and is based on the mild formulation of the limiting nonlinear equation.

In Section 5, we study the behavior of this density function as the interaction range tends to 0. We show its convergence to the solution of a spatially local nonlinear integro-differential equation with Neumann's boundary conditions. This equation has been introduced and studied in Prévost [34] in an analytic point of view (see also Desvillettes et al. [6]). In this spatially local case, numerical simulations by finite element methods are given and show the influence of diffusion and mutation parameters on the invasion of the domain by the population.

In Section 6, we give simulations of the microscopic process illustrating the time-dependent interplay between space and adaptation. We address the effect of the population size, and the crucial role of the interaction range with respect to spatial organization (clustering) and polymorphism. We focus on the qualitative differences between nonlocal and local interactions. In a first example, we show that, when migrations and mutations are not too strong, a large interaction range induces a spatial organization of the population as a finite set of isolated clusters, as assumed in classical metapopulation models ([11]). Such a spatial organization is related to the ecological notion of "niches" (different types of individuals settle different regions of space, Roughgarden [39]). Conversely, for sufficiently small interaction range, the clustering phenomenon is no more observed. Next, we propose another example where a similar phase transition occurs for spatial clustering and in which the critical interaction range can be identified. In our last example, we investigate a model describing the invasion of a species with evolving dispersal speed (as in [6]). The diffusion coefficient and the trait are assumed to be proportional and a triangular invasion pattern is observed, indicating that the invasion front is composed of faster individuals ([33]).

Notation

The individuals live in the closure of a bounded domain $\mathcal{X}$ of $\mathbb{R}^d$ of class C^3 and their trait values belong to a compact set $\mathcal{U}$ of $\mathbb{R}^q$.

- For $x \in \partial\mathcal{X}$, we denote by $n(x)$ the outward normal to the boundary $\partial\mathcal{X}$ at point x.
- For a sufficiently smooth function f and $(x,u) \in \partial\mathcal{X} \times \mathcal{U}$, we denote by $\partial_n f(x,u)$ the scalar product $\nabla_x f(x,u) \cdot n(x)$.
- We denote by $C_0^{2,b}$ the space of measurable functions $f(x,u)$ of class C^2 in x and

bounded in u satisfying $\partial_n f(x,u) = 0$ for all $(x,u) \in \partial\mathcal{X} \times \mathcal{U}$ and by $C_0^{2,0}$ the subspace of functions $f(x,u)$ which are moreover continuous in u.
- For each $p \geq 1$, the L^p-norm on $\bar{\mathcal{X}} \times \mathcal{U}$ is denoted by $\| \cdot \|_p$.
- We denote by $M_F(\bar{\mathcal{X}} \times \mathcal{U})$ the set of finite measures on $\bar{\mathcal{X}} \times \mathcal{U}$, endowed by the weak topology, and by $\mathcal{M}$ the subset of $M_F(\bar{\mathcal{X}} \times \mathcal{U})$ composed of all finite point measures, that is

$$\mathcal{M} = \left\{ \sum_{i=1}^{n} \delta_{(x^i,u^i)},\ n \in \mathbb{N},\ x^1, \dots, x^n \in \bar{\mathcal{X}}\ ,\ u^1, ..., u^n \in \mathcal{U} \right\}$$

where $\delta_{(x,u)}$ denotes the Dirac measure at (x,u). (If $n = 0$, one obtains by extension the null measure). For any $\nu \in M_F(\bar{\mathcal{X}} \times \mathcal{U})$ and for any measurable function f on $\bar{\mathcal{X}} \times \mathcal{U}$, we write indifferently $\langle \nu, f \rangle$ or $\int_{\bar{\mathcal{X}} \times \mathcal{U}} f d\nu$. If $\nu = \sum_{i=1}^{n} \delta_{(x^i,u^i)}$, then $\langle \nu, f \rangle = \sum_{i=1}^{n} f(x^i, u^i)$.
- We denote by $\mathbb{D}([0,\infty), M_F(\bar{\mathcal{X}} \times \mathcal{U}))$ the Skorohod space of left limited and right continuous functions from $\mathbb{R}_+$ to $M_F(\bar{\mathcal{X}} \times \mathcal{U})$, endowed with the Skorohod topology.
- The constant C will be a constant which can change from line to line.

Remark 1.1 *Let us remark that the space of $C^2(\bar{\mathcal{X}})$-functions with a vanishing normal derivative is dense, for the uniform norm, in $C(\bar{\mathcal{X}})$. Indeed, let us consider the Cauchy problem for the parabolic differential equation $\frac{\partial u}{\partial t}(t,x) = \Delta u(t,x)$; $t > 0$; $x \in \mathcal{X}$ with the boundary condition $\frac{\partial u}{\partial n}(t,x) = 0$; $t > 0$; $x \in \partial\mathcal{X}$. Since $\mathcal{X}$ is of class C^3, we may apply Sato-Ueno [40] Theorem 2.1. There exists a smooth fundamental solution $q(t,x,y)$ to this problem and each $f \in C(\bar{\mathcal{X}})$ is the uniform limit of the sequence $\int_{\bar{\mathcal{X}}} q(t,x,y)f(y)dy$ of $C^2(\bar{\mathcal{X}})$-functions with vanishing normal derivative, as t tends to 0.*

We easily extend this result and show that the space $C_0^{2,0}$ is dense in the space of continuous functions on $\bar{\mathcal{X}} \times \mathcal{U}$.

2 The model

Let us now describe the evolutionary process we are interested in. The population will be described at any time by a finite point measure $\nu \in \mathcal{M}$. Each individual, characterized by its position and trait (x,u), may move, give birth or die, as described below.

1. The **migration** is described as a diffusion process normally reflected at the boundary of the domain $\mathcal{X}$. Biologists usually assume that the random behavior is isotropic, so the diffusion matrix is chosen with the form $m(x,u)\mathrm{Id}$ (Id is the identity matrix on $\mathbb{R}^d$) and the nonnegative coefficient $m(x,u)$ (depending on the position x and the trait value u), is the diffusion coefficient. We moreover model the environment heterogeneity (resources, topography, external effects,...) by a drift term driven by a $\mathbb{R}^d$-vector $b(x,u)$.

2. **Births and mutations**. We consider a population with asexual reproduction. An individual with position x and trait u can give birth either to a clonal child at rate $\lambda(x,u)$, or to a mutant with trait v at rate $M(x,u,v)$, both at position x.

3. The **death** rate μ of an individual depends on its position x and trait u and on the spatial and phenotypic competition with the individuals located around x. Let us call $\delta > 0$ the **range** of this spatial interaction.

   For a population $\nu = \sum_{i=1}^{n} \delta_{(x^i,u^i)} \in \mathcal{M}$, the death rate is given by

$$\begin{aligned}\mu(x,u,I^\delta W \star \nu(x,u)) &= \mu\Big(x,u,\int_{\mathcal{X}\times\mathcal{U}} I^\delta(x-y)W(u-v)\nu(dy,dv)\Big)\\ &= \mu\Big(x,u,\sum_{i=1}^{n} I^\delta(x-x^i)W(u-u^i)\Big).\end{aligned}$$

   The function $\mu(x,u,r)$ is assumed to be measurable on $\mathcal{X}\times\mathcal{U}\times\mathbb{R}$.

This interaction assumes that spatial and phenotypic interactions are independent, which is realistic in many biological situations. One could of course consider a more complicated interaction. Since our ultimate goal is to make the spatial interaction range go to zero, we have chosen this particular form.

Hypotheses (H):
1) The coefficients $m(x,u)$ and $b(x,u)$ depend Lipschitz continuously on the position and measurably on the trait, and there exist constants $m^\star > 0$ and $b^* > 0$ such that for all $(x,u) \in \bar{\mathcal{X}}\times\mathcal{U}$

$$\begin{aligned}0 \le m(x,u) \le m^\star\\ |b(x,u)| \le b^*.\end{aligned} \tag{2.1}$$

2) It is natural from a biological point of view to assume that all birth rates are bounded. There exists λ^* such that

$$0 \le \lambda(x,u) \le \lambda^*, \quad \forall (x,u) \in \bar{\mathcal{X}}\times\mathcal{U}. \tag{2.2}$$

The kernel M is nonnegative and symmetric in (u,v) for each $x \in \bar{\mathcal{X}}$ and

$$\sup_{x\in\bar{\mathcal{X}},u\in\mathcal{U}} M(x,u,v) = M^*(v) \in L^1(\mathcal{U}). \tag{2.3}$$

3) There exists a positive constant μ^* such that

$$\forall (x,u,r) \in \mathcal{X}\times\mathcal{U}\times\mathbb{R}, \quad 0 \le \mu(x,u,r) \le \mu^*(1+|r|) \tag{2.4}$$

4) For each $\delta > 0$, the spatial kernel I^δ is nonnegative and bounded and for each $x \in \bar{\mathcal{X}}$,

$$\int_{\mathcal{X}} I^\delta(x-y)dy = 1.$$

5) The competition kernel W is nonnegative and bounded on $\mathbb{R}^q$.

Let us remark that if I^δ is proportional to $1_{\{|x|\leq\delta\}}$, then (H-4) means that the interaction is proportional to the surface in $\mathcal{X}$ around x. This is a natural biological assumption, especially if x lies on the boundary of $\mathcal{X}$. We will later assume that the measure $I^\delta(y)dy$ weakly converges to the Dirac measure δ_0 as δ tends to 0.

Hypotheses (H) will be assumed in all the sequel. They imply in particular that for each $\nu \in M_F(\bar{\mathcal{X}} \times \mathcal{U})$ and each $(x,u) \in \bar{\mathcal{X}} \times \mathcal{U}$,

$$\mu(x,u,I^\delta W \star \nu(x,u)) \leq \mu^*(1 + \|I^\delta W\|_\infty \langle \nu, 1\rangle) \tag{2.5}$$

which yields

$$\begin{aligned}\mu(x,u,I^\delta W \star \nu(x,u)) + \lambda(x,u) + \int_{\mathcal{U}} M(x,u,v)dv \\ \leq \mu^*(1 + \|I^\delta W\|_\infty \langle \nu, 1\rangle) + \lambda^* + \|M^*\|_1 \leq C_\delta(\langle \nu, 1\rangle + 1)\end{aligned} \tag{2.6}$$

and the total jump rate for a population ν is bounded by

$$C_\delta \langle \nu, 1\rangle(\langle \nu, 1\rangle + 1). \tag{2.7}$$

We are interested in the evolution of the stochastic point process (ν_t), taking its values in $\mathcal{M}$ and describing the evolution of the population at each time t. We define

$$\nu_t = \sum_{i=1}^{N_t} \delta_{(X_t^i, U_t^i)} \ ,$$

$N_t \in \mathbb{N}$ standing for the number of living individuals at time t, $X_t^1, ..., X_t^{N_t}$ describing their positions (in $\bar{\mathcal{X}}$) and $U_t^1, ..., U_t^{N_t}$ their trait values (in $\mathcal{U}$).

The dynamics of the population can be roughly summarized as follows. The initial population is characterized by a measure $\nu_0 \in \mathcal{M}$ at time $t = 0$, and any individual located at $x \in \bar{\mathcal{X}}$ with trait u at time t has four independent exponential clocks: a "clonal reproduction" clock with parameter $\lambda(x,u)$, a "mutant reproduction" clock with parameter $M(x,u,v)$, and a "mortality" clock with parameter $\mu(x,u,\sum_{j=1}^{N_t} I^\delta(x - X_t^j)W(u - U_t^j))$. If the "mortality" clock of an individual rings, then this individual disappears; if the "clonal reproduction" clock of an individual rings, then it produces at the same location an individual with the same trait as itself; if the "mutant reproduction" clock of an individual rings, then it produces at the same location an individual with characteristics (x,v).

The living individuals evolve in the domain, according to diffusion processes with diffusion coefficient $m(x,u)$ and drift $b(x,u)$, normally reflected at the boundary of $\mathcal{X}$.

The measure-valued process $(\nu_t)_{t\geq0}$ is a Markov process whose infinitesimal generator L captures this dynamics. This generator is the sum of a jump part L_1 corresponding to the phenotypic evolution and of a diffusion part L_2. The generator L_1 is defined for bounded and measurable functions ϕ from $\mathcal{M}$ into $\mathbb{R}$ and for $\nu = \sum_{i=1}^n \delta_{(x^i,u^i)}$ by

$$\begin{aligned} L_1\phi(\nu) = &\sum_{i=1}^{\langle \nu,1\rangle} \lambda(x^i,u^i)(\phi(\nu+\delta_{(x^i,u^i)})-\phi(\nu)) \\ &+ \int_{\mathcal{U}} \sum_{i=1}^{\langle \nu,1\rangle} (\phi(\nu+\delta_{(x^i,v)})-\phi(\nu))M(x^i,u^i,v)dv \\ &+ \sum_{i=1}^{\langle \nu,1\rangle} (\phi(\nu-\delta_{(x^i,u^i)})-\phi(\nu))\mu(x^i,u^i,I^\delta W\star\nu(x^i,u^i)). \end{aligned} \tag{2.8}$$

A standard class of cylindrical functions generating the set of bounded and measurable functions from $M_F(\bar{\mathcal{X}}\times\mathcal{U})$ into $\mathbb{R}$ is the class of functions

$$F_f(\nu) = F(\langle \nu, f\rangle), \tag{2.9}$$

for bounded and measurable functions F and f.

For such functions F_f, with $F \in C_b^2(\mathbb{R})$ and $f \in C_0^{2,0}$, the diffusive part L_2 of the generator can easily be deduced from Itô's formula. Its form is similar to the one obtained in the whole space for branching diffusing processes (cf. Roelly-Rouault [38]) and is given by

$$L_2F_f(\nu) = \langle \nu, m\Delta_x f + b.\nabla_x f\rangle F'(\langle \nu,f\rangle) + \langle \nu, m|\nabla_x f|^2\rangle F''(\langle \nu, f\rangle). \tag{2.10}$$

Hence,

$$\begin{aligned} LF_f(\nu) &= L_1F_f(\nu) + L_2F_f(\nu) \\ &= \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ \lambda(x,u)\big(F(\langle \nu,f\rangle + f(x,u)) - F(\langle \nu,f\rangle)\big) \\ &\qquad + \int_U \big(F(\langle \nu,f\rangle + f(x,v)) - F(\langle \nu,f\rangle)\big)M(x,u,v)dv \\ &\qquad + \mu(x,u,I^\delta W\star\nu(x,u))\big(F(\langle \nu,f\rangle - f(x,u)) - F(\langle \nu,f\rangle)\big) \\ &\qquad + \big(m(x,u)\Delta_x f(x,u) + b(x,u).\nabla_x f(x,u)\big)F'(\langle \nu,f\rangle)) \\ &\qquad + m(x,u)|\nabla_x f(x,u)|^2 F''(\langle \nu,f\rangle)\Big\}\ \nu(dx,du) \end{aligned} \tag{2.11}$$

3 Construction of the particle system and martingale properties

In this section, we construct a Markov process on the path space $\mathbb{D}([0,\infty), M_F(\bar{\mathcal{X}}\times\mathcal{U}))$ with infinitesimal generator L. Then we prove some martingale properties satisfied by this process, which are the key point to obtain large population approximations.

Let us firstly present an iterative construction of the process, which gives an effective simulation algorithm, if combined with a diffusion simulation step such as an Euler scheme for reflected diffusions (see Lépingle [24], Gobet [17] and Section 6).

The initial number of individuals is equal to some natural integer $N \in \mathbb{N}^*$ and the vector of random variables $(X_0, U_0) = (X_0^i, U_0^i)_{1\leq i\leq N} \in (\bar{\mathcal{X}} \times \mathcal{U})^N$ denotes the position and trait values of these individuals. More generally, we denote by N_t the number of individuals at time t and by (X_t, U_t) the vector of their positions and traits. Let us introduce the following sequences of independent random variables, independent of (X_0, U_0).

- $(B^{j,k})_{k,j\in\mathbb{N}^*}$ are d-dimensional Brownian motions,

- $(\theta_k)_k$ are uniform random variables on $[0, 1]$,

- $(V_k)_k$ take values in $\mathcal{U}$ with law $\frac{M^*(v)}{\|M^*\|_1}dv$,

- $(\tau_k)_k$ are exponential random variables with law $C_\delta e^{-C_\delta t}1_{t\geq 0}$. (The constant C_δ is defined in (2.6)).

The system is obtained inductively for $k \geq 1$ as described below. We set $T_0 = 0$ and $N_0 = N$. Assume that $(T_{k-1}, N_{k-1}, X_{T_{k-1}}, U_{T_{k-1}})$ are given. If $N_{k-1} = 0$, then $\nu_t = 0$ for all $t \geq T_{k-1}$. If not, let

- $T_k = T_{k-1} + \frac{\tau_k}{N_{k-1}(N_{k-1}+1)}$. Notice that $\frac{\tau_k}{N_{k-1}(N_{k-1}+1)}$ represents the time between possible jumps for N_{k-1} individuals and that $C_\delta N_{k-1}(N_{k-1}+1)$ gives an upper-bound on the total jump rate for a population with N_{k-1} individuals, as seen in (2.7).

- On the time-interval $[T_{k-1}, T_k)$, the number of particles remains equal to N_{k-1}, their trait values are equal to $U^j_{T_{k-1}}$, $1 \leq j \leq N_{k-1}$ and their positions $(X^j_t,\ 1 \leq j \leq N_{k-1})$ evolve according to the following stochastic differential equation with normal reflection : $\forall t \in [T_{k-1}, T_k]$,
$$\begin{aligned}
&X^j_t \in \bar{\mathcal{X}},\\
&X^j_t = X^j_{T_{k-1}} + \int_{T_{k-1}}^t \sqrt{2m(X^j_s, U^j_{T_{k-1}})}dB^{j,k}_s + \int_{T_{k-1}}^t b(X^j_s, U^j_{T_{k-1}})ds - k^j_t\ ,\\
&|k^j|_t = \int_{T_{k-1}}^t \mathbf{1}_{\{X^j_s\in\partial\mathcal{X}\}}d|k^j|_s\ ;\ k^j_t = \int_{T_{k-1}}^t n(X^j_s)d|k^j|_s.
\end{aligned}\tag{3.1}$$

- At time T_k, one chooses at random an individual $I_k = i$ uniformly among the N_{k-1} individuals living during the time-interval $[T_{k-1}, T_k)$. Its position and trait are $(X^i_{T_k}, U^i_{T_{k-1}})$.
  - If $0 \leq \theta_k \leq \frac{\mu(X^i_{T_k}, U^i_{T_{k-1}}, \sum_{j=1}^{N_{k-1}} I^\delta(X^i_{T_k} - X^j_{T_k})W(U^i_{T_{k-1}} - U^j_{T_{k-1}}))}{C_\delta(N_{k-1}+1)} = \theta^i_1(X_{T_k}, U_{T_{k-1}})$, then the individual i dies and $N_k = N_{k-1} - 1$.
  - If $\theta^i_1(X_{T_k}, U_{T_{k-1}}) < \theta_k \leq \theta^i_1(X_{T_k}, U_{T_{k-1}}) + \frac{\lambda(X^i_{T_k}, U^i_{T_{k-1}})}{C_\delta(N_{k-1}+1)} = \theta^i_2(X_{T_k}, U_{T_{k-1}})$, then the individual i gives birth to an offspring with characteristics $(X^i_{T_k}, U^i_{T_{k-1}})$ and $N_k = N_{k-1} + 1$.

- If $\theta_2^i(X_{T_k}, U_{T_{k-1}}) < \theta_k \leq \theta_2^i(X_{T_k}, U_{T_{k-1}}) + \frac{M(X^i_{T_k}, U^i_{T_{k-1}}, V_k)\|M^*\|_1}{M^*(V_k)C_\delta(N_{k-1}+1)} = \theta_3^i(X_{T_k}, U_{T_{k-1}}, V_k)$, then the individual i gives birth to a mutant offspring with trait V_k at the position $X^i_{T_k}$, and $N_k = N_{k-1} + 1$.
- If $\theta_k > \theta_3^i(X_{T_k}, U_{T_{k-1}}, V_k)$, nothing happens and $N_k = N_{k-1}$.

The total number N_t of individuals at time t is equal to $N_t = \sum_{k\geq 0} 1_{\{T_k \leq t < T_{k+1}\}} N_k$, and $\nu_t = \sum_{k\geq 0} 1_{\{T_k \leq t < T_{k+1}\}} \sum_{i=1}^{N_k} \delta_{(X_t^i, U^i_{T_k})} = \sum_{i=1}^{N_t} \delta_{(X_t^i, U_t^i)}$.

This stochastic individual-based process ν can be rigorously expressed as solution of a stochastic differential equation driven by d-dimensional Brownian motions $(B^i)_{i\in\mathbb{N}^*}$ and the $\mathbb{R}_+ \times \mathbb{N} \times [0,1] \times \mathcal{U}$-valued multivariate point process

$$Q(dt, di, d\theta, dv) = \sum_{k\geq 1} \delta_{(T_k, I_k, \theta_k, V_k)}(dt, di, d\theta, dv)$$

associated with the birth, mutation and death of individuals. We will prove its existence on $\mathbb{R}^+$, deduced from moment properties, and develop some martingale properties that we will use below.

Let us consider $\nu_0 \in \mathcal{M}$. For each $C_0^{2,0}$-function f, we define the process $\langle \nu_t, f\rangle$ as solution of the stochastic differential equation

$$\begin{aligned}
&\langle \nu_t, f\rangle = \langle \nu_0, f\rangle + \int_0^t \langle \nu_r, m(x,u)\Delta_x f + b(x,u).\nabla_x f\rangle dr \\
&+ \int_0^t \sum_{i=1}^{\langle \nu_{r-}, 1\rangle} \sqrt{2m(X_r^i, U_r^i)} \nabla_x f(X_r^i, U_r^i) dB_r^i \\
&+ \int_{[0,t]\times\mathbb{N}\times[0,1]\times U^2} \Big\{ - f(X_r^i, U_r^i)\mathbf{1}_{\{\theta \leq \theta_1^i(X_r, U_r)\}} + f(X_r^i, U_r^i)\mathbf{1}_{\{\theta_1^i(X_r,U_r) < \theta \leq \theta_2^i(X_r,U_r)\}} \\
&\qquad\qquad + f(X_r^i, v)\mathbf{1}_{\{\theta_2^i(X_r,U_r) < \theta \leq \theta_3^i(X_r,U_r,v)\}} \Big\} Q(dr, di, d\theta, dv), \qquad (3.2)
\end{aligned}$$

where θ_1^i, θ_2^i and θ_3^i have been defined previously.

By Remark 1.1, the knowledge of $\langle \nu_t, f\rangle$ for $f \in C_0^{2,0}$ is enough to characterized the finite measure-valued process ν.

We introduce the canonical filtration

$$\mathcal{F}_t = \sigma\{\nu_0;\ B_r^j, j \in \mathbb{N}^*;\ Q([0,r]\times A),\ A \in \mathcal{P}(\mathbb{N}) \otimes \mathcal{B}([0,1]\times\mathcal{U}),\ r \leq t\},$$

where $\mathcal{B}([0,1]\times\mathcal{U})$ is the Borel σ-field on $[0,1]\times\mathcal{U}$.

Lemma 3.1 *The measure*

$$\begin{aligned}
q(dt, di, d\theta, dv) &= C_\delta \sum_{k\geq 0} 1_{\{T_k < t \leq T_{k+1}\}}(N_k + 1) \sum_{j=1}^{N_k} \delta_j(di) dt d\theta \frac{M^*(v)}{\|M^*\|_1} dv \\
&= C_\delta (N_t + 1) \sum_{j=1}^{N_t} \delta_j(di) dt d\theta \frac{M^*(v)}{\|M^*\|_1} dv
\end{aligned}$$

is the (predictable) compensator of the multivariate point process Q.

Proof. For $k \geq 0$, a regular version of the conditional law of $(T_{k+1}, I_{k+1}, \theta_{k+1}, V_{k+1})$ with respect to $\sigma\{\nu_0,\ (B^j_{\cdot}),\ j \in \mathbb{N}^*,\ (T_p, I_p, \theta_p, V_p),\ 1 \leq p \leq k\}$ is given by the measure

$$C_\delta(N_k+1)1_{\{T_k<t\}}e^{-C_\delta N_k(N_k+1)(t-T_k)}\sum_{j=1}^{N_k}\delta_j(di)dtd\theta\frac{M^*(v)}{\|M^*\|_1}dv.$$

The conclusion is thus a consequence of [21] Theorem 1.33 p.136. □

Using Lemma 3.1 and Itô's formula, one can immediately show that any solution ν of (3.2), such that $E(\sup_{t\leq T}\langle\nu_t,1\rangle^2) < +\infty$, is a Markov process with infinitesimal generator L defined by (2.11). Moreover, we also deduce the following existence, moment and martingale properties.

Proposition 3.2 *1) Assume Hypotheses (H) and that $E(\langle\nu_0,1\rangle) < +\infty$.*
Then $E(\sup_{t\leq T}\langle\nu_t,1\rangle) < +\infty$ for each $T > 0$ and the process ν defined by (3.2) is well defined on $\mathbb{R}^+$.
2) If furthermore for some $p \geq 1$, $E(\langle\nu_0,1\rangle^p) < +\infty$, then for each $T > 0$

$$E(\sup_{t\leq T}\langle\nu_t,1\rangle^p) < +\infty.$$

Proof. We firstly prove 2). For each integer k, define $S_k = \inf\{t \geq 0,\ \langle\nu_t,1\rangle \geq k\}$. A simple computation using (3.2), and dropping the non-positive death terms, gives

$$\begin{aligned}E(\sup_{s\in[0,t\wedge S_k]}\langle\nu_s,1\rangle^p) &\leq E\left(\langle\nu_0,1\rangle^p + C\int_0^{t\wedge S_k}(1+\langle\nu_s,1\rangle^p)ds\right)\\ &\leq C\left(1+E\left(\int_0^t\langle\nu_{s\wedge S_k},1\rangle^p ds\right)\right).\end{aligned}$$

Gronwall's lemma implies that for any $T > 0$, there exists a constant C independent of k, such that $E(\sup_{t\in[0,T\wedge S_k]}\langle\nu_t,1\rangle^p) \leq C$. One easily deduces that S_k tends a.s. to infinity when k tends to infinity and next, Fatou's lemma yields $E(\sup_{t\in[0,T]}\langle\nu_t,1\rangle^p) < +\infty$.

Point 1) is a consequence of point 2). Indeed, one builds the solution $(\nu_t)_{t\geq 0}$ step by step. One only has to check that the sequence of jump instants $(T_k)_k$ goes to infinity a.s. as k tends to infinity. But this follows from $E(\sup_{t\leq T}\langle\nu_t,1\rangle) < +\infty$. □

The following martingale properties are the key point to study large population approximations.

Theorem 3.3 *Assume Hypotheses (H) and that for some $p \geq 2$, $E(\langle\nu_0,1\rangle^p) < +\infty$.*

1) Then, for F and $f \in C_0^{2,0}$ such that for all $\nu \in \mathcal{M}$, $|F_f(\nu)| + |LF_f(\nu)| \leq C(1 + \langle \nu, 1\rangle^p)$, the process

$$F_f(\nu_t) - F_f(\nu_0) - \int_0^t LF_f(\nu_s)ds$$

is a càdlàg martingale starting from 0. It is in particular true for $F(y) = y^{p-1}$.

2) The process Z^f defined for $f \in C_0^{2,0}$ by

$$Z_t^f = \langle \nu_t, f\rangle - \langle \nu_0, f\rangle - \int_0^t \int_{\bar{\mathcal{X}}\times U} \Big\{ m(x,u)\Delta_x f(x,u) + b(x,u).\nabla_x f(x,u) \\ + \big(\lambda(x,u) - \mu(x,u,I^\delta W \star \nu_s(x,u))\big) f(x,u) + \int_U f(x,v)M(x,u,v)dv \Big\}\nu_s(dx,du)ds \tag{3.3}$$

is a càdlàg L^2-martingale starting from 0 with predictable quadratic variation

$$\langle Z^f\rangle_t = \int_0^t \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ 2m(x,u)|\nabla_x f|^2 + \big(\lambda(x,u) + \mu(x,u,I^\delta W \star \nu_s(x,u))\big) f^2(x,u) \\ + \int_{\mathcal{U}} f^2(x,v)M(x,u,v)dv \Big\}\nu_s(dx,du)ds \tag{3.4}$$

Proof. Point 1) is immediate. For point 2), we first assume that $E(\langle \nu_0, 1\rangle^3) < +\infty$. Applying point 1) with $F(y) = y$ (or (3.2) and Lemma 3.1) leads to Z^f. Then one applies 1) again with $F(y) = y^2$, and thus

$$\langle \nu_t, f\rangle^2 - \langle \nu_0, f\rangle^2 - \int_0^t \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ 2(m(x,u)\Delta_x f(x,u) + b(x,u).\nabla_x f(x,u))\langle \nu_s, f\rangle \\ + 2m(x,u)|\nabla_x f|^2 + \lambda(x,u)(2\langle \nu_s, f\rangle f(x,u) + f^2(x,u)) \\ + \int_{\mathcal{U}} (2f(x,v)\langle \nu_s, f\rangle + f^2(x,v))M(x,u,v)dv \\ + \mu(x,u,I^\delta W \star \nu_s(x,u))(-2\langle \nu_s, f\rangle f(x,u) + f^2(x,u)) \Big\}\nu_s(dx,du)ds \tag{3.5}$$

is a càdlàg martingale. In another hand, Itô's formula allows us to compute $\langle \nu_t, f\rangle^2$ from (3.3): the process

$$\langle \nu_t, f\rangle^2 - \langle \nu_0, f\rangle^2 - \int_0^t \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ 2(m(x,u)\Delta_x f(x,u) + b(x,u).\nabla_x f(x,u))\langle \nu_s, f\rangle \\ + 2(\lambda(x,u) - \mu(x,u,I^\delta W \star \nu_s(x,u)))\langle \nu_s, f\rangle f(x,u) \\ + \int_{\mathcal{U}} 2f(x,v)\langle \nu_s, f\rangle M(x,u,v)dv \Big\}\nu_s(dx,du)ds - \langle Z^f\rangle_t \tag{3.6}$$

is a càdlàg martingale. Comparing (3.5) and (3.6) leads to (3.4). The extension to the case where $E(\langle \nu_0, 1\rangle^2) < +\infty$ is straightforward, noticing that $E(\langle Z^f\rangle_t) < +\infty$. □

4 Large population approximation for a fixed interaction range

We are now interested in deterministic approximations of the population point process when the size of the population increases. We assume in this section that the interaction range $\delta > 0$ is fixed.

Let us consider a sequence of initial measures $(\nu_0^N)_{N\in\mathbb{N}^*}$ belonging to $\mathcal{M}$. For each $N \in \mathbb{N}^*$, we keep all parameters (m, b, λ, M) unchanged, except the competition kernel. We assume that for each N,

$$\mu_N(x, u, r) = \mu(x, u, \frac{r}{N}). \tag{4.1}$$

This assumption has a biological interpretation. In a case of fixed amount of available global resources, a large system of individuals may only exist if the biomass of each interacting individual scales as $\frac{1}{N}$, which implies that the interaction effect between two individuals scales as $\frac{1}{N}$ as well. The parameter N can also be interpreted as scaling the resources available, so that the renormalization of μ reflects the decrease of competition for resources.

We assume that the sequence $\frac{\nu_0^N}{N}$ converges, as N tends to infinity. The size $\langle \nu_0^N, 1\rangle$ of the population is then of order N and will stay at this order (or at a smaller order) during finite time-intervals, since birth rates are bounded. Hence, our aim is to study the asymptotic behavior, as N tends to infinity, of the càdlàg process

$$\Lambda_t^N = \frac{1}{N}\sum_{i=1}^{N_t} \delta_{(X_t^i, U_t^i)} = \frac{1}{N}\nu_t^N, \tag{4.2}$$

taking values in $\mathcal{M}^N = \{\frac{1}{N}\nu, \nu \in \mathcal{M}\}$.

The process $(\Lambda_t^N)_{t\geq 0}$ is a Markov process with generator $L_N = L_{N,1} + L_{N,2}$. An easy computation, for $F \in C^2(\mathbb{R})$ and $f \in C_0^{2,0}$, gives that

$$L_{N,2}F_f(\nu) = \langle \nu, m(.)\Delta_x f + b(.).\nabla_x f\rangle F'(\langle \nu, f\rangle) + \langle \nu, \frac{m(.)}{N}|\nabla_x f|^2\rangle F''(\langle \nu, f\rangle) \tag{4.3}$$

and (using (4.1))

$$\begin{aligned} L_{N,1}F_f(\nu) = N\int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ & \lambda(x,u)\big(F(\langle \nu, f\rangle + \frac{1}{N}f(x,u)) - F(\langle \nu, f\rangle)\big) \\ & + \mu(x, u, I^\delta W \star \nu(x,u))\big(F(\langle \nu, f\rangle - \frac{1}{N}f(x,u)) - F(\langle \nu, f\rangle)\big) \\ & + \int_{\mathcal{U}} \big(F(\langle \nu, f\rangle + \frac{1}{N}f(x,v)) - F(\langle \nu, f\rangle)\big)M(x,u,v)dv\Big\}\nu(dx,du) \end{aligned} \tag{4.4}$$

We deduce from Theorem 3.3 the following martingale properties.

Lemma 4.1 *Let $N \geq 1$ be fixed and assume that for some $p \geq 2$, $E\left(\langle \Lambda_0^N, 1\rangle^p\right) < \infty$. For all $C_0^{2,0}$-function f, the process*

$$Z_t^{N,f} = \langle \Lambda_t^N, f\rangle - \langle \Lambda_0^N, f\rangle - \int_0^t \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ m(x,u)\Delta_x f(x,u) + b(x,u).\nabla_x f(x,u)$$
$$+ \big(\lambda(x,u) - \mu(x,u,I^\delta W\star\Lambda_s^N(x,u))\big) f(x,u) + \int_{\mathcal{U}} f(x,v)M(x,u,v)dv \Big\} \Lambda_s^N(dx,du)ds \tag{4.5}$$

is a càdlàg L^2 martingale starting from 0 with predictable quadratic variation

$$\langle Z^{N,f}\rangle_t = \frac{1}{N}\int_0^t \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ 2m(x,u)|\nabla_x f|^2 + \big(\lambda(x,u)+\mu(x,u,I^\delta W\star\Lambda_s^N(x,u))\big) f^2(x,u)$$
$$+ \int_{\mathcal{U}} f^2(x,v)M(x,u,v)dv \Big\} \Lambda_s^N(dx,du)ds \tag{4.6}$$

We assume

Assumption (H1):
1) The initial measures Λ_0^N converge in law and for the weak topology on $M_F(\bar{\mathcal{X}}\times\mathcal{U})$ to some deterministic finite measure $\xi_0 \in M_F(\bar{\mathcal{X}}\times\mathcal{U})$, and $\sup_N E(\langle \Lambda_0^N, 1\rangle^3) < +\infty$.
2) All the parameters of the model are assumed to be continuous, either on $\bar{\mathcal{X}}\times\mathcal{U}$, or on $\bar{\mathcal{X}}\times\mathcal{U}\times\mathbb{R}$.
3) There exists a constant k_μ such that

$$\forall x \in \mathcal{X},\ u \in \mathcal{U},\ r_1, r_2 \in \mathbb{R}, \quad |\mu(x,u,r_1) - \mu(x,u,r_2)| \leq k_\mu |r_1 - r_2|. \tag{4.7}$$

By the law of large numbers, Assumption (H1-1) is for example satisfied for $\Lambda_0^N = \frac{1}{N}\sum_{i=1}^N \delta_{(X_0^i, U_0^i)}$, with independent random variables $(X_0^i, U_0^i)_{\{1\leq i\leq N\}}$ distributed following the law ξ_0 with finite 3rd-order moment.

Let us recall that the parameters of diffusion, birth and mutation associated with Λ^N stay unchanged, whereas the parameter of selection μ_N is defined by (4.1).

Theorem 4.2 *Assume Hypotheses (H) and (H1), and consider the sequence of processes Λ^N defined by (4.2). Then for all $T > 0$, the sequence (Λ^N) converges in law, in $\mathbb{D}([0,T], M_F(\bar{\mathcal{X}}\times\mathcal{U}))$, to a deterministic continuous function ξ^δ belonging to $C([0,T], M_F(\bar{\mathcal{X}}\times\mathcal{U}))$.*

This measure-valued function ξ^δ is the unique weak solution satisfying $\sup_{t\in[0,T]}\langle \xi_t^\delta, 1\rangle < +\infty$ of the following nonlinear integro-differential equation. For all function $f \in C_0^{2,b}$,

$$\langle \xi_t^\delta, f\rangle = \langle \xi_0, f\rangle + \int_0^t \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ m(x,u)\Delta_x f(x,u) + b(x,u).\nabla_x f(x,u)$$
$$+ \big(\lambda(x,u) - \mu(x,u,I^\delta W\star\xi_s^\delta(x,u))\big) f(x,u) + \int_{\mathcal{U}} f(x,v)M(x,u,v)dv \Big\}\ \xi_s^\delta(dx,du)ds \tag{4.8}$$

Remark 4.3 *Applying (4.8) to the constant function equal to* 1*, the positivity of* μ *and Hypotheses (H) gives* $\langle \xi^\delta_t, 1\rangle \ \leq \ \langle \xi_0, 1\rangle + C\int_0^t \langle \xi^\delta_s, 1\rangle ds$*. We conclude by Gronwall's lemma that any solution* ξ^δ *of (4.8) is bounded on every finite time interval* $[0,T]$*:*

$$\sup_{t\in[0,T]} \langle \xi^\delta_t, 1\rangle \ \leq \ \langle \xi_0, 1\rangle e^{CT}.$$

As a first step in the proof of Theorem 4.2, we now give a mild formulation for solutions of (4.8). To this aim, and for each fixed trait $u\in\mathcal{U}$, we denote by P^u the semigroup of the diffusion process normally reflected at the boundary of $\mathcal{X}$, with diffusion matrix $m(\cdot,u)\mathrm{Id}$ and drift coefficient $b(\cdot,u)$.

Lemma 4.4 *Let us consider a solution* ξ^δ *of (4.8). Then, for each measurable and bounded function* φ *defined on* $\bar{\mathcal{X}}\times\mathcal{U}$*,*

$$\langle \xi^\delta_t, \varphi\rangle = \langle \xi_0, P^u_t\varphi\rangle + \int_0^t\int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ \big(\lambda(x,u) - \mu(x,u,I^\delta W\star\xi^\delta_s(x,u))\big)P^u_{t-s}\varphi(x,u) \\ + \int_{\mathcal{U}} P^v_{t-s}\varphi(x,v)M(x,u,v)dv \Big\}\, \xi^\delta_s(dx,du)ds. \quad (4.9)$$

Proof. We may classically derive from (4.8) a space-time weak equation for measurable functions $\psi_s(x,u)=\psi(s,x,u)$ which are of class $C^{1,2}$ on $[0,t]\times\bar{\mathcal{X}}$, measurable and bounded in u and such that $\partial_n\psi = 0$ on $[0,t]\times\partial\mathcal{X}\times\mathcal{U}$, given by

$$\langle \xi^\delta_t, \psi_t\rangle = \langle \xi_0, \psi_0\rangle + \int_0^t\int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ \partial_s\psi_s(x,u) + m(x,u)\Delta_x\psi_s(x,u) + b(x,u).\nabla_x\psi_s(x,u) \\ + \big(\lambda(x,u) - \mu(x,u,I^\delta W\star\xi^\delta_s(x,u))\big)\psi_s(x,u) + \int_{\mathcal{U}} \psi_s(x,v)M(x,u,v)dv \Big\}\, \xi^\delta_s(dx,du)ds \quad (4.10)$$

Let us now consider a continuous function φ on $\bar{\mathcal{X}}\times\mathcal{U}$ and fix a time $t\in[0,T]$. Let us define for $(s,x,u)\in[0,t]\times\bar{\mathcal{X}}\times\mathcal{U}$,

$$\psi_s(x,u) = P^u_{t-s}\varphi(x,u).$$

Then ψ is solution of the boundary value problem

$$\begin{aligned}
&\partial_s\psi_s(x,u) + m(x,u)\Delta_x\psi_s(x,u) + b(x,u).\nabla_x\psi_s(x,u) = 0 \quad \text{ on } [0,T]\times\mathcal{X}\times\mathcal{U}\\
&\partial_n\psi_s(x,u) = 0 \quad \text{ on } [0,T]\times\partial\mathcal{X}\times\mathcal{U}\\
&\psi_t(x,u) = \varphi(x,u) \quad \text{ on } \bar{\mathcal{X}}\times\mathcal{U}.
\end{aligned}$$

Equation (4.10) applied to this function ψ yields the evolution equation

$$\langle \xi^\delta_t, \varphi\rangle = \langle \xi_0, P^u_t\varphi\rangle + \int_0^t\int_{\bar{\mathcal{X}}\times V} \Big\{ \big(\lambda(x,u) - \mu(x,u,I^\delta W\star\xi^\delta_s(x,u))\big)P^u_{t-s}\varphi(x,u) \\ + \int_{\mathcal{U}} P^v_{t-s}\varphi(x,v)M(x,u,v)dv \Big\}\, \xi^\delta_s(dx,du)ds. \quad (4.11)$$

Equation (4.11) is true for each continuous (and then bounded) function φ, and characterizes the finite measure ξ^δ. Lemma 4.4 is proved. $\square$

Proof. (of Theorem 4.2). Let us fix $T > 0$.
Let us firstly prove the uniqueness of solutions ξ of (4.8). Using Remark 4.3 and Lemma 4.4, we prove the uniqueness of bounded solutions of (4.9). Let us consider two such solutions $(\xi_t)_{t\geq 0}$ and $(\bar{\xi}_t)_{t\geq 0}$ and compute the quantity $|\langle \xi_t - \bar{\xi}_t, \varphi\rangle|$, for each measurable and bounded function φ such that $\|\varphi\|_\infty \leq 1$.

Using (4.9), we obtain for $t \leq T$

$$\begin{aligned}
|\langle \xi_t - \bar{\xi}_t, \varphi\rangle| \leq \int_0^t \Bigg| \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Big\{ & \big(\lambda(x,u) - \mu(x,u,I^\delta W \star \xi_s(x,u))\big) P^u_{t-s}\varphi(x,u) \\
& + \int_{\mathcal{U}} P^v_{t-s}\varphi(x,v) M(x,u,v)dv \Big\} \big(\xi_s(dx,du) - \bar{\xi}_s(dx,du)\big) \Bigg| ds \\
+ \int_0^t \int_{\bar{\mathcal{X}}\times\mathcal{U}} \big| \big(\mu(x,u,I^\delta W \star \bar{\xi}_s(x,u)) & - \mu(x,u,I^\delta W \star \xi_s(x,u))\big) P^u_{t-s}\varphi(x,u) \big| \,\bar{\xi}_s(dx,du)ds
\end{aligned}$$

Now, using Hypotheses (H), applying Remark 4.3 to $\bar{\xi}$ and since $\|\varphi\|_\infty \leq 1$, there exists a positive constant C_1 such that for all $(x,u) \in \bar{\mathcal{X}} \times \mathcal{U}$ and all $0 < s \leq t \leq T$,

$$\begin{aligned}
|\lambda(x,u)P^u_{t-s}\varphi(x,u) + \int_{\mathcal{U}} P^v_{t-s}\varphi(x,v)M(x,u,v)dv| &\leq C_1, \\
|\mu(x,u,I^\delta W \star \bar{\xi}_s(x,u))P^u_{t-s}\varphi(x,u)| \leq \mu_0(1 + \|I^\delta W\|_\infty \langle \bar{\xi}_s, 1\rangle) &\leq C_1
\end{aligned}$$

while thanks to (H1-2),

$$|\mu(x,u,I^\delta W \star \bar{\xi}_s(x,u)) - \mu(x,u,I^\delta W \star \xi_s(x,u))| \leq k_\mu \|I^\delta W\|_\infty \sup_{\|\varphi\|_\infty \leq 1} |\langle \xi_s - \bar{\xi}_s, \varphi\rangle|,$$

and then

$$\begin{aligned}
\left| \int_{\bar{\mathcal{X}}\times\mathcal{U}} \big(\mu(x,u,I^\delta W \star \bar{\xi}_s(x,u)) - \mu(x,u,I^\delta W \star \xi_s(x,u))\big) P^u_{t-s}\varphi(x,u)\bar{\xi}_s(dx,du) \right| \\
\leq C_2 \sup_{\|\varphi\|_\infty \leq 1} |\langle \xi_s - \bar{\xi}_s, \varphi\rangle|
\end{aligned}$$

where C_2 is a positive constant. We deduce that there exists $C > 0$ such that

$$|\langle \xi_t - \bar{\xi}_t, \varphi\rangle| \leq C \int_0^t \sup_{\|\varphi\|_\infty \leq 1} |\langle \xi_s - \bar{\xi}_s, \varphi\rangle| ds$$

and by Gronwall's lemma, we conclude that for all $t \leq T$, $\sup_{\|\varphi\|_\infty \leq 1} |\langle \xi_t - \bar{\xi}_t, \varphi\rangle| = 0$. Thus, for all $t \leq T$, $\xi_t = \bar{\xi}_t$ and uniqueness holds.

Let us next prove that for all $T > 0$,

$$\sup_{N\in\mathbb{N}^*} E\left(\sup_{[0,T]} \langle \Lambda^N_t, 1\rangle^3 \right) < +\infty \tag{4.12}$$

Introducing $S_k^N = \inf\{t \geq 0, \langle \Lambda_t^N, 1 \rangle \geq k\}$ for $k \in \mathbb{N}^*$, a simple computation using the specific form of $L_{N,1}F_f$ and $L_{N,2}F_f$ with $f = 1$ and $F(y) = y^3$ and dropping the negative death term yields

$$E\left(\sup_{s \leq t \wedge S_k^N} \langle \Lambda_s^N, 1 \rangle^3\right) \leq E(\langle \Lambda_0^N, 1 \rangle^3) + CE\left(\int_0^{t \wedge S_k^N} (\langle \Lambda_s^N, 1 \rangle + \langle \Lambda_s^N, 1 \rangle^3) ds\right)$$

where C is a positive constant independent of k and N. Then Assumption (H1-1) and Gronwall's lemma imply that there exists a constant C_T independent of k and N such that $E\left(\sup_{s \leq T \wedge S_k^N} \langle \Lambda_s^N, 1 \rangle^3\right) \leq C_T$. We deduce that the sequence $(S_k^N)_k$ tends a.s. to infinity and finally obtain (4.12) by Fatou's lemma.

Using Remark 1.1, and following Roelly [37], one observes that the sequence of laws Q^N of Λ^N is uniformly tight in $\mathcal{P}(\mathbb{D}([0,T], M_F(\bar{\mathcal{X}} \times \mathcal{U})))$, where M_F is endowed with the vague topology, as soon as for any function $f \in C_0^{2,0}$, the sequence of the laws of the processes $\langle \Lambda^N, f \rangle$ is tight in $\mathcal{P}(\mathbb{D}([0,T], \mathbb{R}))$. Using Aldous' [1] and Rebolledo's [22] criteria, this tightness follows from

$$\sup_{N \in \mathbb{N}^*} E(\sup_{[0,T]} | \langle \Lambda_s^N, f \rangle |) < \infty, \tag{4.13}$$

and from the tightness of the laws of $(\langle Z^{N,f} \rangle)$ and of the drift part of the semi-martingales $\langle \Lambda^N, f \rangle$.

Clearly, since f is bounded, (4.13) is a consequence of (4.12). Let us now consider stopping times (S, S') satisfying a.s. $0 \leq S \leq S' \leq S + \delta \leq T$. Thanks to Doob's inequality, Lemma 4.1, and (4.12), we get

$$E\left(\langle Z^{N,f} \rangle_{S'} - \langle Z^{N,f} \rangle_S\right) \leq E\left(C \int_S^{S+\delta} \left(\langle \Lambda_s^N, 1 \rangle + \langle \Lambda_s^N, 1 \rangle^2\right) ds\right) \leq C\delta.$$

Similar arguments prove that the expectation of the finite variation part of $\langle \Lambda_{S'}^N, f \rangle - \langle \Lambda_S^N, f \rangle$ is bounded by $C\delta$. Finally it turns out that the sequence $(Q^N)_N$ is uniformly tight.

Let us now denote by Q the limiting law in $\mathcal{P}(\mathbb{D}([0,T], M_F(\bar{\mathcal{X}} \times \mathcal{U})))$ of a subsequence of Q^N, still denoted by Q^N for simplicity. By construction, almost surely,

$$\sup_{t \in [0,T]} \sup_{||f||_\infty \leq 1} |\langle \Lambda_s^N, f \rangle - \langle \Lambda_{s-}^N, f \rangle| \leq 1/N.$$

We deduce immediately that each process Λ with law Q is a.s. strongly continuous. Let us finally prove that it is the unique solution of (4.8) .

For $t \leq T$, $f \in C_0^{2,0}$ and $\nu \in \mathbb{D}([0,T], M_F(\bar{\mathcal{X}} \times \mathcal{U}))$, let us define

$$\Psi_{t,f}(\nu) = \langle \nu_t, f \rangle - \langle \nu_0, f \rangle - \int_0^t \int_{\bar{\mathcal{X}} \times \mathcal{U}} \Big\{ m(x,u) \Delta_x f(x,u) + b(x,u).\nabla_x f(x,u)$$
$$+ \big(\lambda(x,u) - \mu(x,u, I^\delta W \star \nu_s(x,u))\big) f(x,u) + \int_{\mathcal{U}} f(x,v) M(x,u,v) dv \Big\} \nu_s(dx) ds.$$

We want to show that for any $t \leq T$,

$$E\left(|\Psi_{t,f}(\Lambda)|\right) = 0, \tag{4.14}$$

knowing from Lemma 4.1 that

$$Z_t^{N,f} = \Psi_{t,f}(\Lambda^N). \tag{4.15}$$

A fair computation using Lemma 4.1, Hypotheses (H) and (H1), and (4.12) shows that

$$E\left(|Z_t^{N,f}|^2\right) = E\left(\langle Z^{N,f}\rangle_t\right) \leq \frac{C_f}{N} E\left(\int_0^t \left\{1 + \langle \Lambda_s^N, 1\rangle^2\right\} ds\right) \leq \frac{C_{f,t}}{N} \tag{4.16}$$

which goes to 0 as N tends to infinity. On another hand, since Λ is a.s. strongly continuous, since $f \in C_0^{2,0}$ and thanks to the assumption (H), the function $\Psi_{t,f}$ is a.s. continuous at Λ. Furthermore, for any $\nu \in \mathbb{D}([0,T], M_F(\bar{\mathcal{X}} \times \mathcal{U}))$,

$$|\Psi_{t,f}(\nu)| \leq C_{t,f} \sup_{[0,t]} \left(1 + \langle \nu_s, 1\rangle^2\right),$$

and (4.12) implies that the sequence $(\Psi_{t,f}(\Lambda^N))_N$ is uniformly integrable. Thus

$$\lim_N E\left(|\Psi_{t,f}(\Lambda^N)|\right) = E\left(|\Psi_{t,f}(\Lambda)|\right) \tag{4.17}$$

Combining (H1-1), (4.15), (4.16) and (4.17), we conclude that (4.14) holds and that (4.8) is satisfied for any $f \in C_0^{2,0}$.

Then Λ is uniquely identified to ξ^δ, and the sequence (Λ^N) converges to ξ^δ in $\mathbb{D}([0,T], M_F(\bar{\mathcal{X}} \times \mathcal{U}))$, where $M_F(\bar{\mathcal{X}} \times \mathcal{U})$ is endowed with the vague topology. To extend this result to the weak topology, we use a criterion proved in [28]. Since the limiting process is continuous, it suffices to prove that the sequence $(\langle \Lambda^N, 1\rangle)_N$ converges in law to $\langle \xi^\delta, 1\rangle$ in $\mathbb{D}([0,T], \mathbb{R})$. We may apply what has been done above with $f \equiv 1$. Theorem 4.2 is proved. □

In the next section, we will be interested in the limit of small spatial interaction range δ. An intermediate result consists in proving the existence of a density for each measure ξ_t^δ, $t \geq 0$. We make the additional

Assumption (H2):

1) The diffusion coefficient $m(x,u)$ is of class C^2 in x and the second derivative of m (in x) is α-Hölderian, uniformly in u, with $\alpha > 0$. Moreover, m is assumed to be positive. Hence, since $\bar{\mathcal{X}} \times \mathcal{U}$ is a compact set, there exists $m_* > 0$ such that for all $(x,u) \in \bar{\mathcal{X}} \times U$,

$$m(x,u) \geq m_* > 0.$$

2) The drift coefficient $b(x,u)$ is of class C^1 in x and the derivative of b (in x) is α-Hölderian, uniformly in u, with $\alpha > 0$.

Assumptions (H) and (H2) and the smoothness of $\partial\mathcal{X}$ allow us to adapt Sato-Ueno [40] (Theorem 2.1 and Appendix) to obtain the following lemma.

Lemma 4.5 *There exists a unique function* $p_t(x,u,y)$ *defined on* $\mathbb{R}_+ \times \bar{\mathcal{X}} \times \mathcal{U} \times \bar{\mathcal{X}}$, *continuous in* (t,x,y) *and which is a density function in* $y \in \bar{\mathcal{X}}$ *such that for each continuous function* φ *defined on* $\bar{\mathcal{X}} \times U$, *each* $(x,u) \in \bar{\mathcal{X}} \times \mathcal{U}$,

$$P_t^u \varphi(x,u) = \int_{\bar{\mathcal{X}}} p_t(x,u,y)\varphi(y,u)dy \tag{4.18}$$

Let us now prove the propagation in time of the absolute continuity property of the measure-valued solution ξ^δ.

Theorem 4.6 *Assume (H), (H1) and (H2) and that* $\xi_0(dx,du) = g_0(x,u)dxdu$. *Then for each time* t, *the measure* ξ_t^δ *has a density* $g^\delta \in L^\infty([0,T],L^1)$ *with respect to the Lebesgue measure on* $\bar{\mathcal{X}} \times \mathcal{U}$. *Moreover, for each* t *and* u, *the function* $g_t^\delta(.,u)$ *is continuous on* $\bar{\mathcal{X}}$.

Proof. Let us come back to the equation (4.9) satisfied by ξ^δ.

Using basic results on linear parabolic equations, we construct by induction a sequence of functions $(g_n)_n$ satisfying in a weak sense

$$\begin{aligned}
&\partial_t g_t^{n+1}(x,u) = \Delta_x(m(x,u)g_t^{n+1}(x,u)) - \nabla_x(b(x,u)g_t^{n+1}(x,u)) \\
&\qquad + \lambda(x,u)g_t^n(x,u) + \int_{\mathcal{U}} g_t^n(x,v)M(x,u,v)dv - \mu(x,u,I^\delta W \star g_t^n(x,u))g_t^{n+1}(x,u) \\
&g_0^{n+1}(x,u) = g_0(x,u) \\
&\nabla_x g^{n+1}(t,x,u).n(x) = 0 \quad \forall (t,x,u) \in \mathbb{R}_+ \times \partial\mathcal{X} \times \mathcal{U}.
\end{aligned} \tag{4.19}$$

Thanks to the nonnegativity of g_0, μ, λ and M, and applying the maximum principle, we can show that the functions g_n are nonnegative (see [6]). By symmetry of M, Equation (4.19) (understood in the weak sense) means that for all $C_0^{2,b}$-function φ from $\bar{\mathcal{X}} \times \mathcal{U}$ into $\mathbb{R}$,

$$\begin{aligned}
\langle g_t^{n+1}, \varphi\rangle = \langle g_0, \varphi\rangle + \int_0^t \int_{\bar{\mathcal{X}}\times\mathcal{U}} \Bigg\{ &\Big(m(x,u)\Delta_x\varphi(x,u) + b(x,u).\nabla_x\varphi(x,u)\Big) g_s^{n+1}(x,u) \\
&+ \Big(\lambda(x,u)\varphi(x,u) + \int_{\mathcal{U}} \varphi(x,v)M(x,u,v)dv\Big) g_s^n(x,u) \\
&- \mu(x,u,I^\delta W \star g_s^n(x,u))\varphi(x,u)g_s^{n+1}(x,u)\Bigg\} dx\,du\,ds.
\end{aligned} \tag{4.20}$$

The associated mild equation writes as before: for each continuous function φ,

$$\begin{aligned}\langle g_t^{n+1},\varphi\rangle = &\int_{\bar{\mathcal{X}}\times\mathcal{U}}\Big(\int_{\bar{\mathcal{X}}} p_t(x,u,y)\varphi(y,u)dy\Big)g_0(x,u)dxdu\\ &+\int_0^t\int_{\bar{\mathcal{X}}\times\mathcal{U}}\Big\{\Big[\lambda(x,u)\Big(\int_{\bar{\mathcal{X}}} p_{t-s}(x,u,y)\varphi(y,u)dy\Big)\\ &+\int_{\mathcal{U}}\Big(\int_{\bar{\mathcal{X}}} p_{t-s}(x,v,y)\varphi(y,v)dy\Big)M(x,u,v)dv\Big]g_s^n(x,u)\\ &-\mu(x,u,I^\delta W\star g_s^n(x,u))\Big(\int_{\bar{\mathcal{X}}} p_{t-s}(x,u,y)\varphi(y,u)dy\Big)g_s^{n+1}(x,u)\Big\}dxduds.\end{aligned} \tag{4.21}$$

Hypotheses on the coefficients allow us to apply Fubini's theorem and to obtain that for each $(y,u)\in\bar{\mathcal{X}}\times\mathcal{U}$,

$$\begin{aligned}g_t^{n+1}(y,u) = &\int_{\bar{\mathcal{X}}} p_t(x,u,y)g_0(x,u)dx\\ &+\int_0^t\int_{\bar{\mathcal{X}}}\Big\{(\lambda(x,u)p_{t-s}(x,u,y)g_s^n(x,u)+\int_{\mathcal{U}} p_{t-s}(x,u,y)g_s^n(x,v)M(x,u,v)dv\\ &-\mu(x,u,I^\delta W\star g_s^n(x,u))p_{t-s}(x,u,y)g_s^{n+1}(x,u)\Big\}dxds.\end{aligned} \tag{4.22}$$

Then, thanks to the nonnegativity of g^{n+1}, we get

$$\begin{aligned}0\le g_t^{n+1}(y,u)\le &\int_{\bar{\mathcal{X}}} p_t(x,u,y)g_0(x,u)dx+\int_0^t\int_{\bar{\mathcal{X}}}\Big\{(\lambda(x,u)p_{t-s}(x,u,y)g_s^n(x,u)\\ &+\int_{\mathcal{U}} p_{t-s}(x,u,y)g_s^n(x,v)M(x,u,v)dv\Big\}dxds,\end{aligned} \tag{4.23}$$

and deduce easily, integrating over $y\in\bar{\mathcal{X}}$, using Fubini's Theorem, the symmetry of M and Gronwall's Lemma that there exists a constant C independent of δ such that

$$\sup_{n\in\mathbb{N}}\sup_{t\le T}\|g_t^n\|_1\le\|g_0\|_1e^{CT}. \tag{4.24}$$

Let us now show the convergence of the sequence g^n in $L^\infty([0,T],L^1)$ to a function g^δ. A straightforward computation using (4.22), Hypotheses (H), (H1) and (H2), and similar arguments as above yields

$$\sup_{s\le t}\|g_s^{n+1}-g_s^n\|_1\le C\int_0^t\Big(\sup_{u\le s}\|g_u^{n+1}-g_u^n\|_1+\sup_{u\le s}\|g_u^n-g_u^{n-1}\|_1\Big)ds$$

where C is a positive constant. Thanks to Gronwall's Lemma, we deduce that for each $T>0$, each $t\le T$ and each n, $\sup_{s\le t}\|g_s^{n+1}-g_s^n\|_1\le C\int_0^t\sup_{u\le s}\|g_u^n-g_u^{n-1}\|_1ds$. Picard's Lemma allows us to conclude that for any $T>0$, $\sum_{n\in\mathbb{N}}\sup_{t\in[0,T]}\|g_t^{n+1}-$

$g_t^n\|_1 < +\infty$, and the sequence $(g^n)_n$ converges in $L^\infty([0,T],L^1)$ to a function g^δ. We deduce from (4.24) that

$$\sup_{\delta>0}\sup_{t\leq T}\|g_t^\delta\|_1 \leq \|g_0\|_1 e^{CT}. \tag{4.25}$$

Moreover, the function g^δ is solution of (4.8), and thus, the uniqueness result proved in Theorem 4.2 implies that $\xi^\delta(dx,du) = g^\delta(x,u)dxdu$. Then, the measure ξ^δ is absolutely continuous with respect to the Lebesgue measure, and the density g^δ is weak solution of the nonlocal nonlinear partial differential equation

$$\begin{aligned}
&\partial_t g^\delta = \Delta_x(m(x,u)g_t^\delta(x,u)) - \nabla_x(b(x,u)g_t^\delta(x,u))\\
&\qquad + \big(\lambda(x,u) - \mu(x,u,I^\delta W\star g_t^\delta(x,u))\big)g_t^\delta(x,u) + \int_{\mathcal{U}} g_t^\delta(x,v)M(x,u,v)dv\ ;\\
&g_0^\delta(x,u) = g_0(x,u)\ ;\\
&\nabla_x g^\delta(t,x,u).n(x) = 0 \quad \forall(t,x,u)\in\mathbb{R}_+\times\partial\mathcal{X}\times\mathcal{U}.
\end{aligned} \tag{4.26}$$

Lemma 4.4 implies that g^δ is also solution of the mild equation

$$\begin{aligned}
g_t^\delta(y,u) &= \int_{\mathcal{X}} p_t(x,u,y)g_0(x,u)dx\\
&\quad + \int_0^t\int_{\mathcal{X}}\Big\{\big(\lambda(x,u) - \mu(x,u,I^\delta W\star g_s^\delta(x,u))\big)p_{t-s}(x,u,y)g_s^\delta(x,u)\\
&\qquad\qquad + \int_{\mathcal{U}} p_{t-s}(x,u,y)g_s^\delta(x,v)M(x,u,v)dv\Big\}dxds.
\end{aligned} \tag{4.27}$$

Using (4.27), the continuity of $y\mapsto g_t^\delta(y,u)$ follows immediately from the continuity of $(t,x,y)\mapsto p_t(x,u,y)$, the nonnegativity and boundedness of g^δ and the boundedness of birth parameters. □

5 Convergence of the number density when the interaction range decreases

Our aim in this section is to prove that under suitable assumptions, the sequence (g^δ) converges, when δ tends to 0, to a function $g\in L^\infty([0,T],L^1)$ with initial condition g_0, which is weak solution of the locally nonlinear partial differential equation

$$\begin{aligned}
&\partial_t g_t(x,u) = \Delta_x(m(x,u)g_t(x,u)) - \nabla_x(b(x,u)g_t(x,u))\\
&\qquad + \big(\lambda(x,u) - \mu(x,u,\rho_g(t,x,u))\big)g_t(x,u) + \int_{\mathcal{U}} g_t(x,v)M(x,u,v)dv\ ;\\
&\nabla_x g(t,x,u).n(x) = 0 \quad \forall(t,x,u)\in\mathbb{R}_+\times\partial\mathcal{X}\times\mathcal{U}
\end{aligned} \tag{5.1}$$

where ρ_g describes the (local) interaction in x, defined for $(x,u)\in\bar{\mathcal{X}}\times\mathcal{U}$ by

$$\rho_g(t,x,u) = \int_{\mathcal{U}} W(u-v)g_t(x,v)dv.$$

In order to control the terms $I^\delta W * g^\delta$ uniformly in δ in the nonlinear term of (4.26), we need L^∞-estimates on g^δ and we make the following initial data assumption:

(H3) *The initial density $g_0(x,u)$ is bounded on $\mathcal{X}\times\mathcal{U}$.*

Proposition 5.1 *Assume (H), (H1), (H2), (H3). Then there exists a positive constant C_T, such that*

$$\sup_{\delta>0}\sup_{t\in[0,T]}\|g_t^\delta\|_\infty \le C_T\|g_0\|_\infty. \tag{5.2}$$

Proof. Let us again consider the sequence $(g^n)_n$ approximating g^δ introduced in the proof of Theorem 4.6. The maximum principle implies that

$$\sup_n\sup_{t\le T}\|g_t^n\|_\infty \le C\|g_0\|_\infty,$$

where $C>0$ is a constant only depending on T, λ^* and M^* (and independent of δ). This property propagates taking the limit in n, and (5.2) is proved. (For details on the maximum principle, see [6].) □

Let us now prove the following convergence theorem:

Theorem 5.2 *Assume hypotheses (H), (H1), (H2), (H3). Assume that the measure $I^\delta(y)dy$ weakly converges to the Dirac measure δ_0 as δ tends to 0. (To fix ideas we may assume that $I^\delta(x)=C_\delta\mathbf{1}_{\{|x|\le\delta\}}$.) Then the sequence $(g^\delta)_{\delta>0}$ converges in $L^\infty([0,T],L^1)$ as δ tends to 0, to the unique function $g\in L^\infty([0,T],L^1\cap L^\infty(\bar{\mathcal{X}}\times\mathcal{U}))$ satisfying for each $y,u\in\bar{\mathcal{X}}\times\mathcal{U}$ the evolution equation*

$$\begin{aligned} g_t(y,u) = {} & \int_{\mathcal{X}} p_t(x,u,y)g_0(x,u)dx \\ & + \int_0^t\int_{\mathcal{X}}\Big\{\big(\lambda(x,u)-\mu(x,u,\rho_g(s,x,u))\big)p_{t-s}(x,u,y)g_s(x,u) \\ & \qquad + \int_{\mathcal{U}} p_{t-s}(x,u,y)g_s(x,v)M(x,u,v)dv\Big\}dxds. \end{aligned} \tag{5.3}$$

Moreover, for each t and u, the function $g_t(.,u)$ is continuous on $\mathcal{X}$.

Proof. One can easily prove the existence and uniqueness of the integrable and bounded function g solution of (5.3) by adapting the proofs of Theorem 4.6 and Proposition 5.1, replacing $\mu(x,u,I^\delta W\star g)$ by $\mu(x,u,\rho_g)$. The continuity of $y\to g_t(y,u)$ is obtained as in the proof of Theorem 4.6, and we can show as in the proof of Proposition 5.1 that

$$\sup_{t\in[0,T]}\|g_t\|_\infty \le C_T\|g_0\|_\infty. \tag{5.4}$$

Let us write

$$\begin{aligned}g_t^\delta(y,u)-g_t(y,u)=&\int_0^t\int_{\mathcal{X}}\Big\{\big(\lambda(x,u)p_{t-s}(x,u,y)\big(g_s^\delta(x,u)-g_s(x,u)\big)\\&+\int_{\mathcal{U}}p_{t-s}(x,u,y)\big(g_s^\delta(x,v)-g_s(x,v)\big)M(x,u,v)dv\\&-\Big[\mu(x,u,I^\delta W\star g_s^\delta(x,u))g_s^\delta(x,u)-\mu(x,u,\rho_g(s,x,u))g_s(x,u)\Big]p_{t-s}(x,u,y)\Big\}dxds\end{aligned} \tag{5.5}$$

Using (5.2) and (5.4), the unique term which deserves attention is the term $\mu(x,u,\rho_g(x,u))-\mu(x,u,I^\delta W\star g^\delta(x,u))$. By (4.7), we have

$$\begin{aligned}&\int_{\mathcal{X}}|\mu(x,u,\rho_g(t,x,u))-\mu(x,u,I^\delta W\star g_t^\delta(x,u))|dx\\&\leq k_\mu\int_{\mathcal{X}}\left|\int_{\mathcal{U}}W(u-v)g_t(x,v)dv-\int_{\mathcal{X}\times\mathcal{U}}I^\delta(x-z)W(u-v)g_t^\delta(z,v)dzdv\right|dx\\&\leq k_\mu\int_{\mathcal{X}}\left(\left|\int_{\mathcal{U}}W(u-v)g_t(x,v)dv-\int_{\mathcal{X}\times\mathcal{U}}I^\delta(x-z)W(u-v)g_t(z,v)dzdv\right|\right.\\&\qquad\left.+\int_{\mathcal{X}\times\mathcal{U}}I^\delta(x-z)W(u-v)\left|g_t(z,v)-g_t^\delta(z,v)\right|dzdv\right)dx\end{aligned}$$

Let us fix our attention on the first term in the last right inequality, that we will call $A_\delta(t,u)$. Since $I^\delta(y)dy$ weakly converges to δ_0, $\int_{\mathcal{X}}I^\delta(x-z)g_t(z,v)dz$ converges to $g_t(x,v)$ as δ goes to 0. Because of (5.4), this convergence holds in a bounded pointwise sense with respect to $t\leq T$, $x\in\mathcal{X}$ and $v\in\mathcal{U}$. Then Lebesgue's theorem implies that $A_{\delta,T}:=\int_{\mathcal{U}}\int_0^T A_\delta(t,u)dtdu$ tends to 0 as δ tends to 0.

Now, integrating (5.5) with respect to $dy\,du$, a straightforward computation yields

$$\sup_{s\leq t}\|g_s^\delta-g_s\|_1\leq C_T A_{\delta,T}+C'_T\int_0^t\sup_{u\leq s}\|g_u^\delta-g_u\|_1ds.$$

We conclude using Gronwall's lemma. □

The zero interaction range equation (5.1) has been numerically studied in Prévost [34]. A lot of simulations based on finite element schemes are given, studying the simultaneous effects of the diffusion, mutation and selection on the invasion of the domain by the population. The simulations show that the coefficient which seems to affect the most the invasion aptitude is the mutation size coefficient. However, they restrict to local interactions.

In the next section, we wish additionally to illustrate, by simulations of the stochastic discrete model, the effect of the spatial interaction range on the interplay between invasion and evolution, and the emergence of spatial and phenotypic diversity (clustering and polymorphism). Our simulations focus on the qualitative differences between local and nonlocal interactions.

6 Simulations

We will give in this section simulations of several biologically realistic examples, based on the algorithm of Section 3. The Euler scheme to simulate reflected diffusions will be detailed in Section 6.1, as well as some simplifications in the algorithm of Section 3, in the case of linear death rates.

Next, we will give simulations of three biologically relevant examples. First (Section 6.2), we show that, when migrations and mutations are not too strong, a large interaction range induces a spatial organization of the population as a finite set of isolated clusters. Conversely, for sufficiently small interaction range, the clustering phenomenon is no more observed. Second (Section 6.3), we propose another example where a similar phase transition occurs for spatial clustering and in which the critical interaction range can be identified. In our last example (Section 6.4), we investigate a model describing the invasion of a species with evolving dispersal speed (the trait is proportional to the migration speed, as in [6]).

6.1 Euler scheme and algorithm for logistic interaction

As mentionned in Section 3, the reflected diffusion of our particles can be simulated with an Euler scheme. We will assume in this subsection and in the following examples that $\mathcal{X} = (\alpha, \beta) \subset \mathbb{R}$ and we will use the scheme of Lépingle [24] (see also [17]). Fix $x \in [\alpha, \beta]$ and $u \in \mathcal{U}$. On any time interval where its trait is constant, an indivual at (x, u) moves according to the reflected diffusion

$$\begin{aligned} X_t &= x + \int_0^t \sqrt{2m(X_s, u)}dB_s + \int_0^t b(X_s, u)ds - k_t \ , \\ |k|_t &= \int_0^t \mathbf{1}_{\{X_s \in \{\alpha,\beta\}\}} d|k|_s \ ; \ k_t = \int_0^t \left(\mathbf{1}_{\{X_s=\beta\}} - \mathbf{1}_{\{X_s=\alpha\}}\right) d|k|_s, \end{aligned} \tag{6.1}$$

where B is a one-dimensional Brownian motion.

If m and b are Lipschitz with respect to the first variable, then one can simulate this diffusion on $[0, T]$ as follows. Fix $h > 0$, $\bar{\alpha}$ and $\bar{\beta}$ such that $\alpha < \bar{\alpha} < \bar{\beta} < \beta$, and let n be the first integer greater than T/h. For $\rho \in \{0, 1, \dots, n-1\}$ and $\rho h < t \leq (\rho+1)h$, let

$$\begin{aligned} \tilde{X}_0 &= x, \\ \tilde{X}_t &= \max[\alpha, \min[\beta, \tilde{X}_{\rho h} + b(\tilde{X}_{\rho h}, u)(t - \rho h) + \sqrt{2m(\tilde{X}_{\rho h}, u)}(B_t - B_{\rho h}) \\ &\qquad + \mathbf{1}_{\{\tilde{X}_{\rho h} < \bar{\alpha}\}} \max(0, A_t^\rho - (\tilde{X}_{\rho h} - \alpha)) \\ &\qquad - \mathbf{1}_{\{\tilde{X}_{\rho h} > \bar{\beta}\}} \max(0, B_t^\rho + (\tilde{X}_{\rho h} - \beta))]], \end{aligned}$$

where

$$A_t^\rho = \sup_{\rho h \le s \le t} \left\{ -b(\tilde{X}_{\rho h}, u)(s - \rho h) - \sqrt{2m(\tilde{X}_{\rho h}, u)}(B_s - B_{\rho h}) \right\},$$
$$B_t^\rho = \sup_{\rho h \le s \le t} \left\{ b(\tilde{X}_{\rho h}, u)(s - \rho h) + \sqrt{2m(\tilde{X}_{\rho h}, u)}(B_s - B_{\rho h}) \right\}.$$

Then, there exists a constant C independent of h such that for any function f on $[\alpha, \beta]$ with finite variation bounded by 1, $\sup_{0 \le t \le T} |E(f(X_t) - f(\tilde{X}_t))| \le C\sqrt{h}$.

In each step of this scheme, one has to simulate simultaneously B_t and $S_t := \sup_{s \le t}(aB_s + bs)$ for fixed constants a, b. This can be done as follows (Shepp [41]). Let U be a Gaussian centered random variable with variance t, and let V be an exponential random variable with parameter $1/2t$ independent of U. Put

$$Y = \frac{1}{2}\left(aU + bt + \sqrt{a^2V + (aU + bt)^2}\right).$$

Then the vectors (B_t, S_t) and (U, Y) have the same distribution.

Note that this scheme can be easily generalized to state spaces of the form $(\alpha_1, \beta_1) \times \ldots \times (\alpha_d, \beta_d) \subset \mathbb{R}^d$, as explained in [24].

Next, we want to study a particular case in which we can considerably reduce the complexity of the algorithm. In Section 3, one needs to compute $I^\delta W * \nu(x, u)$ at some point $(x, u) \in \mathcal{X} \times \mathcal{U}$ at each time step, which involves a sum over all individuals in the population. In the case of logistic competition (linar death rate) where

$$\mu(x, u, r) = \mu_0(x, u) + \mu_1(x, u)r, \tag{6.2}$$

one can use the following algorithm.

Fix a constant C_δ in a similar way as in (2.6) such that $\mu_0(x, u) + \lambda^* + \|M^*\|_1 \le C_\delta$ and $\mu_1(x, u)\|I^\delta W\|_\infty \le C_\delta$. Take the Brownian motions $(B^{j,k})_{j,k \in \mathbb{N}}$ and the random variables $(\theta_k)_{k \in \mathbb{N}}$, $(V_k)_{k \in \mathbb{N}}$ and $(\tau_k)_{k \in \mathbb{N}}$ as in Section 3. Set $T_0 = 0$ and $N_0 = N$ (the initial number of individuals). Assume that $(T_{k-1}, N_{k-1}, X_{T_{k-1}}, U_{T_{k-1}})$ are given. N_{k-1} is the number of individuals at time T_{k-1}. At this time, their positions and traits are the coordinates of the vectors $X_{T_{k-1}} = (X^i_{T_{k-1}})_{1 \le i \le N_{k-1}}$ and $U_{T_{k-1}} = (U^i_{T_{k-1}})_{1 \le i \le N_{k-1}}$. The two first steps of the algorithm are the same: the new time step is given by $T_k = T_{k-1} + \tau_k / N_{k-1}(N_{k-1} + 1)$ and the motion of each particle is governed by the SDE with normal reflection (3.1).

The third step deals with the different events that may happen at time T_k. Choose at random one individual $I_k = i$ uniformly among the N_{k-1} individuals living during the time interval $[T_{k-1}, T_k)$. Its position and trait are $(X^i_{T_k}, U^i_{T_{k-1}})$. The event occurring at time T_k is decided by comparing θ_k with constants related to the rate of each kind of event. The only difference with the algorithm of Section 3 is in the first sub-step, that has to be divided in two steps as follows:

- If $0 \le \theta_k < \frac{N_{k-1}}{N_{k-1}+1} =: \theta_0^i(X_{T_k}, U_{T_{k-1}})$, then let $j \in \{1, \ldots, N_{k-1}\}$ be such that $\frac{j-1}{N_{k-1}+1} \le \theta_k < \frac{j}{N_{k-1}+1}$. If $\theta_k - \frac{j-1}{N_{k-1}+1} < \frac{\mu_1(X^i_{T_k}, U^i_{T_{k-1}}) I^\delta(X^i_{T_k} - X^j_{T_k}) W(U^i_{T_{k-1}} - U^j_{T_{k-1}})}{C_\delta}$, then the individual i dies from competition with individual j and $N_k = N_{k-1} - 1$. Otherwise, nothing happens and $N_k = N_{k-1}$.

- If $\theta_0^i(X_{T_k}, U_{T_{k-1}}) \leq \theta_k \leq \theta_0^i(X_{T_k}, U_{T_{k-1}}) + \frac{\mu_0(X^i_{T_k}, U^i_{T_{k-1}})}{C_\delta(N_{k-1}+1)} =: \theta_1^i(X_{T_k}, U_{T_{k-1}})$, then the individual i dies by natural death and $N_k = N_{k-1} - 1$.

The three other sub-steps are the same.

The main difference with the algorithm of Section 3 is that we no longer have to compute $\sum_{j=1}^{N_{k-1}} I^\delta(X^i_{T_k} - X^j_{T_k})W(U^i_{T_{k-1}} - U^j_{T_{k-1}})$ in the first sub-step, but it suffices to compute $I^\delta(X^i_{T_k} - X^j_{T_k})W(U^i_{T_{k-1}} - U^j_{T_{k-1}})$ for chosen i and j. Moreover, we do not need to compute the position of each individual in the population at each time step. The third step above only needs to compute the position of at most two particles at time T_k (the particles numbered i and j).

We assume in the following examples a logistic competition of the form (6.2) and a physical space of the form $\mathcal{X} = (\alpha, \beta)$. Our simulations are realized with the previous algorithm.

6.2 Example 1. Spatial clustering

We consider here a set of parameters similar to the one of [10] and [34], in which, for each spatial position x, the growth rate is maximal for the trait value $u = x$. This can represent the effect of a gradual spatial distribution of different resources, involving a gradual distribution of traits. For example, for some bird species, a linearly spatially varying seed size determines a linear variation of the beak sizes (Grant and Grant [18]).

$$\mathcal{X} = (0,1), \quad \mathcal{U} = [0,1], \quad m(x,u) \equiv m, \quad b(x,u) \equiv 0,$$
$$\lambda(x,u) = 2 - 20(x-u)^2 \text{ if } |x-u| \leq 1/\sqrt{10};\ 0 \text{ otherwise},$$
$$\mu_N(x,u,r) = 1 + \frac{r}{N}, \quad I^\delta(y) = C_\delta \mathbf{1}_{\{|y| \leq \delta\}}, \quad W(v) \equiv 1.$$

Moreover, $M(x,u,v) = 0.1 \times k_s(u,v)$ where 0.1 is the mutation rate and $k_s(u,v)$ is the probability density of a Gaussian random variable with mean u and standard deviation s conditioned on staying in $\mathcal{U} = [0,1]$. Therefore, we have four free parameters in this model, m, δ, s and the population size N. The initial population in our simulations is composed of N individuals at $(0.5, 0.5)$.

The simulations of this model show, as in [34], that the invasion of space occurs along the diagonal $x = u$, and, as in [10], that speciation (stable coexistence of several sub-populations with different typical traits) may occur in this model, accompanied with a spatial specialization. Several different population clusters may coexist at different position, with trait values located around the corresponding optimal traits. We have investigated in our simulations the effect of the different parameters on the clustering and polymorphism of the population. We give pictures of the seemingly stable state of the population (Fig. 1). Our first general observation is that the clusters are more concentrated at the boundary of the domain. Indeed, the reflected diffusion governing the motion of individuals is not isotropic close to this boundary, so that the population density is bigger.

On the one hand, we have investigated the effect of the interaction range δ. The main result is that the existence, the number of clusters and the distance between clusters strongly depend on the interaction range δ. As shown in Fig. 1(a–c), the number of clusters decreases with δ and the distance between two population peaks is roughly 2δ, which is exactly the width of the interaction interval. The emergence of population clusters is mainly a consequence of local births ([45]). Indeed, since the progeny of an individual is close to its original location, each individual's progeny can create a colony with stable position on short timescales. Once an individual is at a distance greater than δ from the main part of the population, it experiences very little competition and it can create a new colony. When several colonies appear, they organize in a way to minimize the competition between them and to maximize the growth rate.

If δ is sufficiently small, we observe a flat distribution of the population (Fig. 1(c)), and thus a qualitative difference with respect to cases (a–b). As an explanation, decreasing δ increases the number of clusters and the width of a cluster increases with the speed of dispersal m and the range of mutation s. Then no distinct colony can be observed for sufficiently small δ, and fixed m and s.

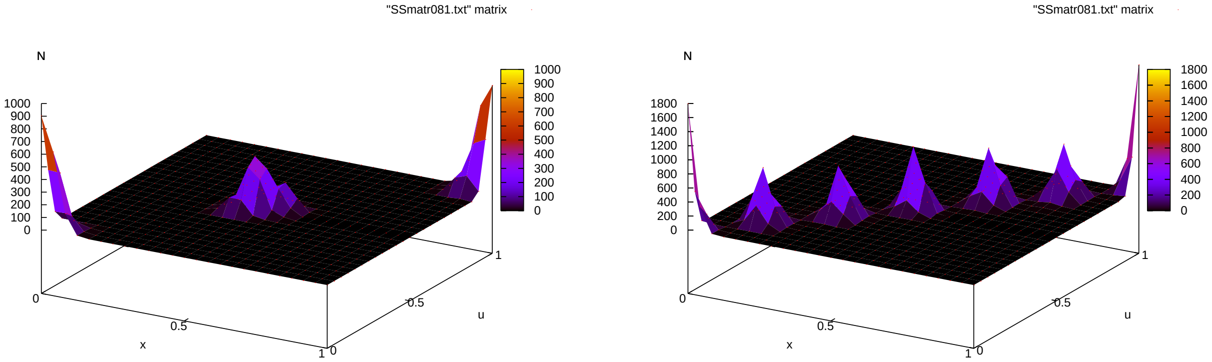
We also investigated the effect of the population size N. It appears that this parameter has very little qualitative effect on the clustering of the population, except for small N (Fig. 1(d)), where the width of each clusters is reduced, and we observe much more fluctuations in the population distribution. However, we still can observe a similar pattern of population clusters than in Fig. 1(b).

On the other hand, we also studied the effect of the diffusion coefficient m and the mutation range s. Comparing Fig. 1(b) and (f), we observe that too large s and m induce the same flat distribution as for small δ. This confirms that the clusters pattern depends mainly on the balance between m and s, and δ. In Fig. 1(f), quick movements mix the population so that no spatial structure can appear.

Finally, we also studied the relative effect of s and m in the appearance of spatial or phenotypic structure. As shown in Fig. 1(e), small s can induce a differentiation over the phenotype space $\mathcal{U}$ even when m is large enough to have a flat distribution over space $\mathcal{X}$ (compare with Fig. 1(f)). Fig. 1(e) can be seen as an intermediate state between Fig. 1(a) and Fig. 1(f). When m is reduced instead of s, a reversed pattern can be observed.

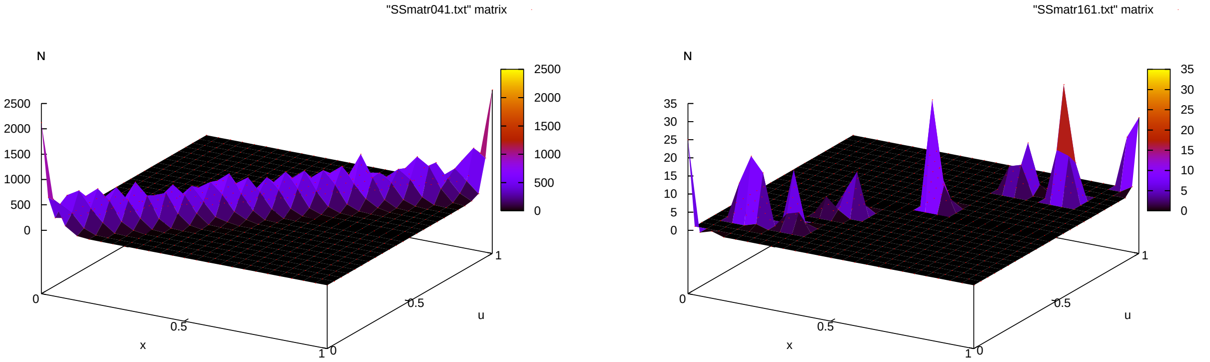
6.3 Example 2. The role of spatial competition for clustering

As we have seen above, the balance between the spatial competition range δ and the diffusion parameters s and m has an important effect on the clustering of the population. Here we want to address the balance between the range of competition and the growth rate. For this purpose, we consider the following model, inspired by



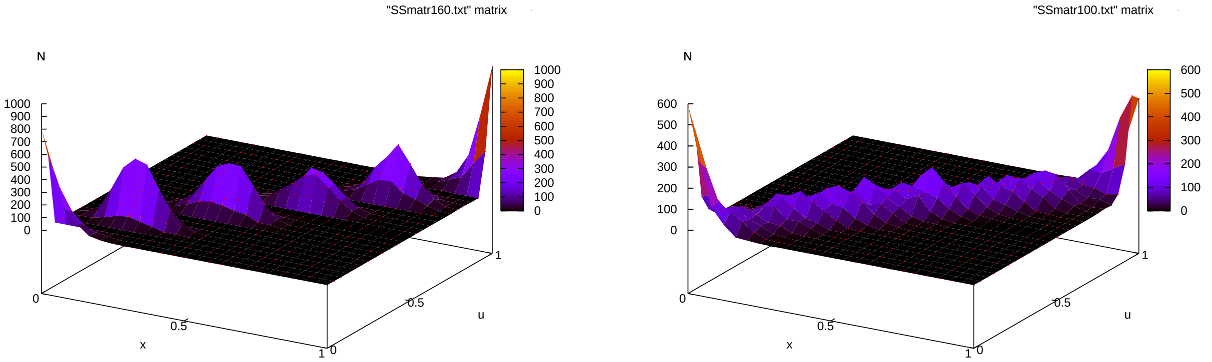
(a) $N = 3000, s = 0.01, m = 0.01, \delta = 0.3.$

(b) $N = 3000, s = 0.01, m = 0.01, \delta = 0.1.$



(c) $N = 3000, s = 0.01, m = 0.01, \delta = 0.03.$

(d) $N = 50, s = 0.01, m = 0.01, \delta = 0.1.$



(e) $N = 3000, s = 0.003, m = 0.03, \delta = 0.1.$

(f) $N = 3000, s = 0.03, m = 0.03, \delta = 0.1.$

Figure 1: Simulations of example 1 for various parameters. All of them are taken at time 4000.

the adaptive dynamics model of [7]:

$$\mathcal{X} = (-1,1), \quad \mathcal{U} = [0,2], \quad m(x,u) \equiv m, \quad b(x,u) \equiv 0,$$
$$\lambda(x,u) = \exp(-x^2/2\rho^2), \quad \mu_N(x,u,r) = 1 + \frac{r}{N},$$
$$I^\delta(y) = C_\delta \exp(-y^2/2\delta^2), \quad W(v) = \exp(-v^2/0.02).$$

and the same mutation kernel as above. This example has five free parameters m, δ, s, N, and ρ, which represents the width of the space region with significant growth rate (namely, a parameter describing the width of the space region with high concentration of resources). The initial population in our simulations is composed of N individuals at $(0,1)$. Observe that in this example, the trait has no effect on the growth rate, so that the trait structure is neutral (all individual's parameters are equal, independent of the trait, in absence of interaction).

Remark that if we consider the space $\mathcal{X}$ as a trait space, this model is similar to the one of [7]. In particular, the biological theory of adaptive dynamics ([16]) suggests that evolutionary branching, i.e. the split of the population into two subpopulations with different traits stably coexisting, translating in our model into spatial clustering, occurs when the range of interaction (δ in our case) is smaller than the range of the growth rate (ρ in our case). This is illustrated by Fig. 2(a) and (b), where, in (a), $\delta < \rho$ and the population stabilizes around two distinct positions (branching occurs) and in (b), $\delta > \rho$ and the population stabilizes around position 0 (there is no branching).

Figures (c) and (d) prove that other phase transitions occur for smaller δ, leading to the coexistence of three clusters or more. As in example 1, we notice in Figure (d) that very small δ leads to a distribution without distinct clusters.

It is possible to add some phenotypic structure to this example by assuming that the growth rate depends on the trait u, in a way such that spatial branching occurs for some traits but not for others, according to the above branching criterion. We take the same parameters, except for the birth rate, which has the following form.

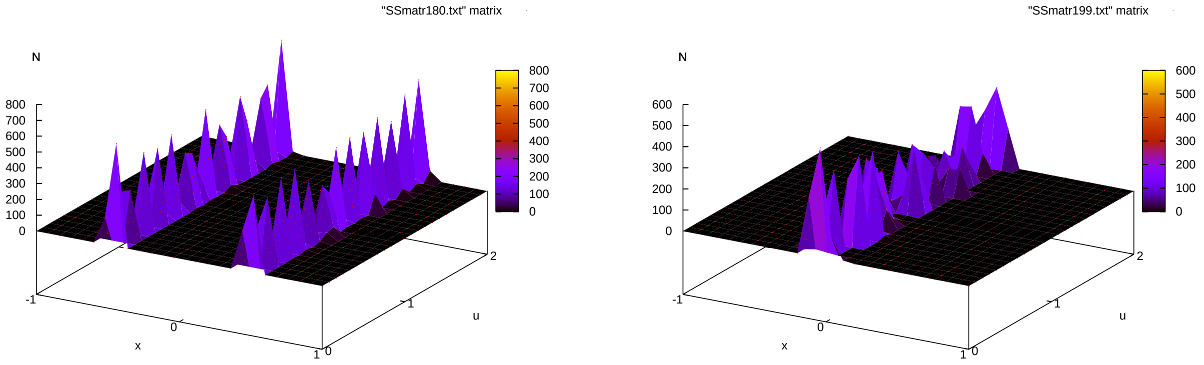
$$\lambda(x,u) = \exp(-x^2/2(u+0.1)).$$

The parameter ρ is then replaced by $\sqrt{u+0.1}$, so that branching occurs if $\sqrt{u+0.1} > \delta$.

This is what happens actually for small times (Fig. 3(a)), but after a longer time (Fig. 3(b,c)), the two clusters spread over the trait space because of the mutations. Eventually, if we let time go on, we actually observe the appearance and the spread of three spatial clusters, colonizing all the trait space (Fig. 3(d)).

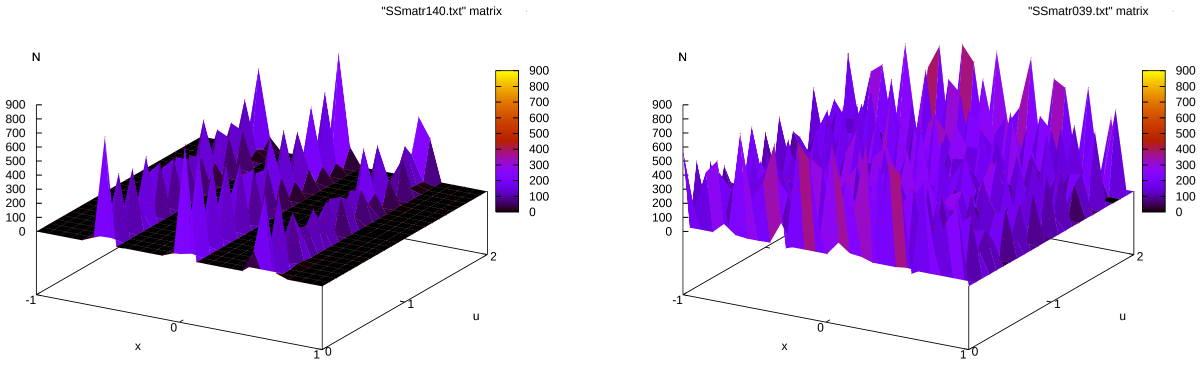
6.4 Example 3. Invasion and evolution of migration speed

Here, we investigate a model describing the invasion of a species with evolving dispersal speed (as in [6]). This can model phenomena such as the invasion of



(a) $\delta = 0.9$, $\rho = 1$.

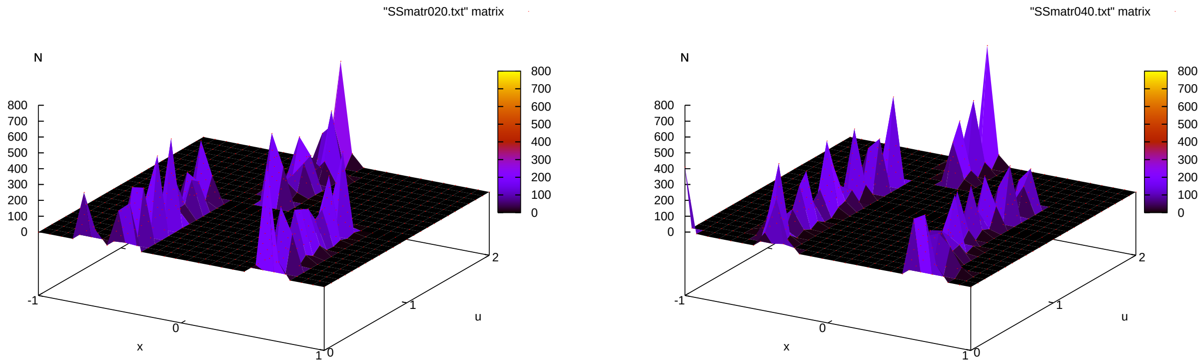
(b) $\delta = 1.1$, $\rho = 1$.



(c) $\delta = 0.5$, $\rho = 1$.

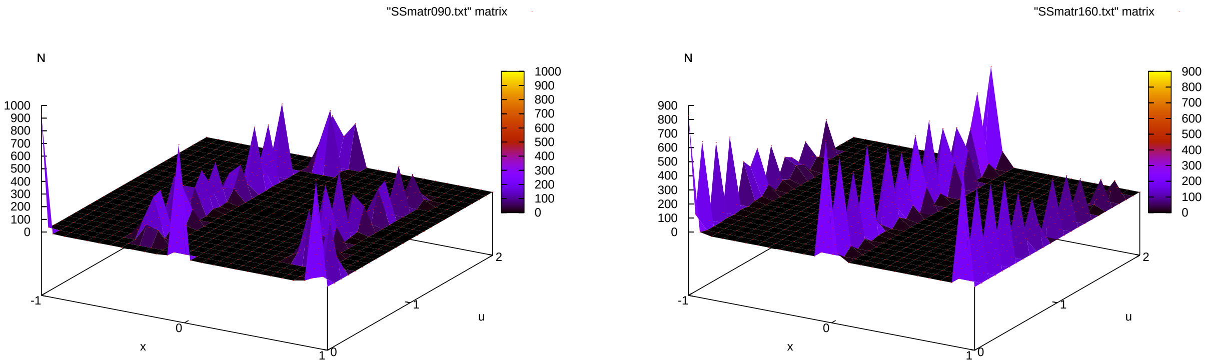
(d) $\delta = 0.1$, $\rho = 1$.

Figure 2: Simulations of example 2. Neutral case. All the figures are taken at time 5000, except the last one, taken at time 10000 (more time is needed to fill the whole space). In all the simulations, $N = 1000$, $s = 0.003$ and $m = 0.003$.



(a) $t = 10000$.

(b) $t = 20000$.



(c) $t = 45000$.

(d) $t = 80000$.

Figure 3: Simulations of example 2. Trait-dependent case. In this simulation, $N = 1000, s = 0.003, m = 0.003$ and $\delta = 1$.

Australia by cane toads, for which an adaptation to high invasion speeds has been recently detected (Phillips et al. [33]). The parameters are as follows.

$$\mathcal{X} = (-1, 1), \quad \mathcal{U} = [0, 3], \quad m(x, u) \equiv m(u + 0.1), \quad b(x, u) \equiv 0,$$
$$\lambda(x, u) = 1, \quad \mu_N(x, u, r) = 1 + \frac{r}{N},$$
$$I^\delta(y) = C_\delta \mathbf{1}_{\{|y| \leq \delta\}}, \quad W(v) = \exp(-10v^2).$$

and the same mutation kernel as above. Here we study invasion into an homogeneous space (λ is constant). The diffusion rate m is proportional (up to a constant) to the trait u. Thus, individuals with large u move fast. The trait u can be a morphological trait responsible for the speed of dispersal (e.g. the length of legs for toads, [33]). Space competition occurs between individuals within a distance δ, and the kernel W models competition between close traits. This example has four free parameters, the diffusion coefficient m, the interaction range δ, the standard deviation of mutations s and the population size N.

In Fig. 4 and 5, we present two extreme cases with respect to the initial trait distribution, but with identical parameters. In the first one, all individuals are at (physical) position 0, and with traits regularly distributed in $\mathcal{U} = [0, 3]$. In the second one, all individuals are initially located at a single point $(0, 0)$.

In both figures, we observe a triangular invasion pattern indicating that the invasion front is composed of faster individuals. In Fig. 5, we also observe a simultaneous invasion in physical and trait spaces, and a slower spread of the population. This can be explained by the fact that the population, initially composed of slow individuals, has first to colonize the trait space before invading the physical space. Because of the progressive appearance of larger traits, the invasion speed increases over time (compare the different time values in Fig. 5).

When parameters vary, the simulations of this microscopic model can show different ways of colonization. As an illustration, we give an example (Fig. 6) where the interaction range δ is bigger. The parameters N and m are chosen such that two clusters appear for large traits and spread over the trait space in a short time. The initial condition is the same as in Fig. 4. We can observe two branches linking the initial cluster with the two extreme valued clusters (Fig. 6(c,d)).

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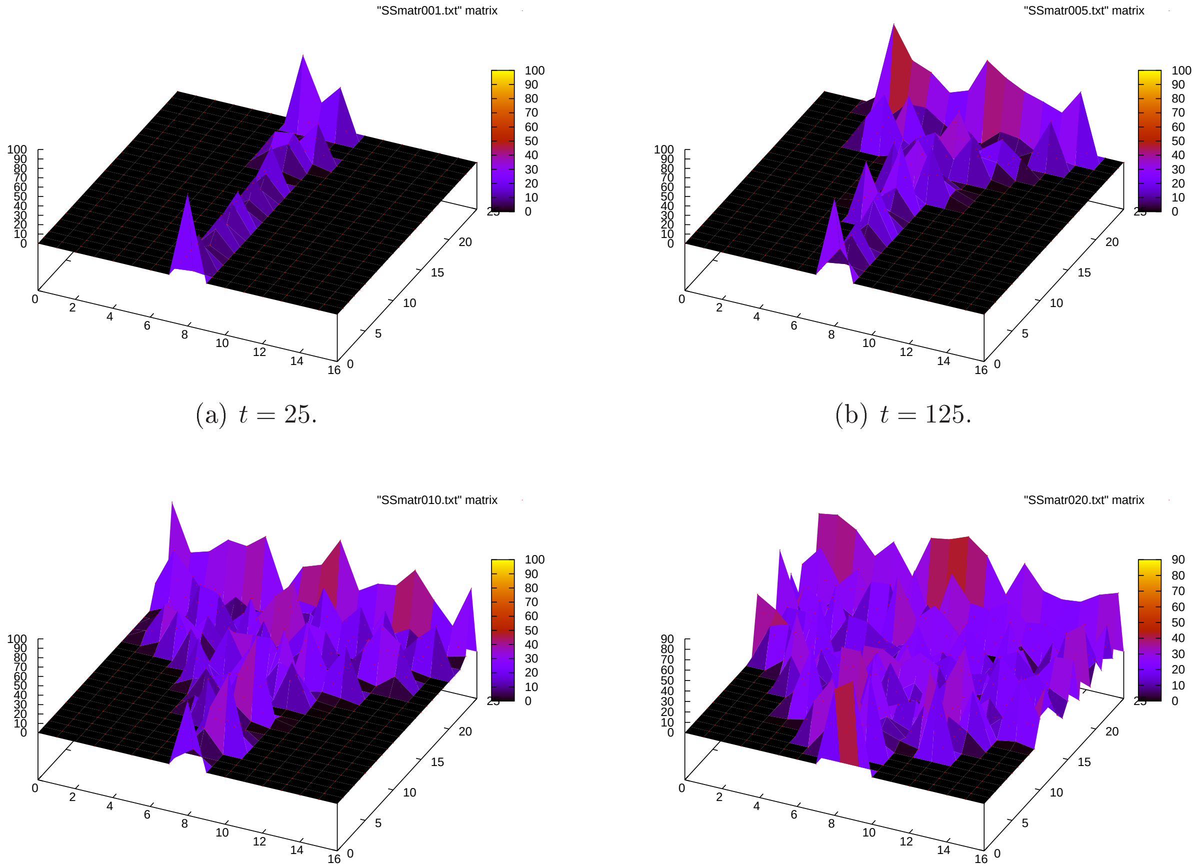


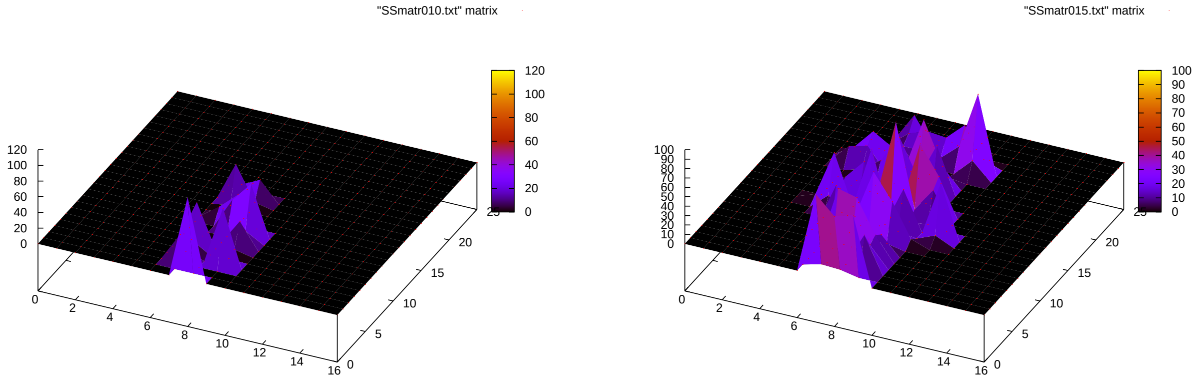
(a) $t = 25$.

(b) $t = 125$.

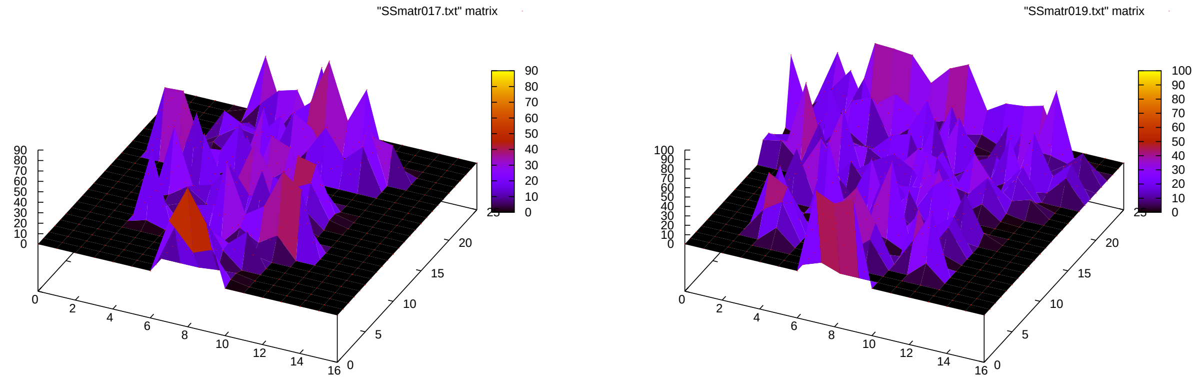
(c) $t = 250$.

(d) $t = 500$.

Figure 4: Simulations of example 3. The parameters are $N = 100, s = 0.03, m = 0.003$ and $\delta = 0.1$. The initial condition is composed of N individuals located at 0 and with trait values $3i/N$ for $1 \leq i \leq N$.

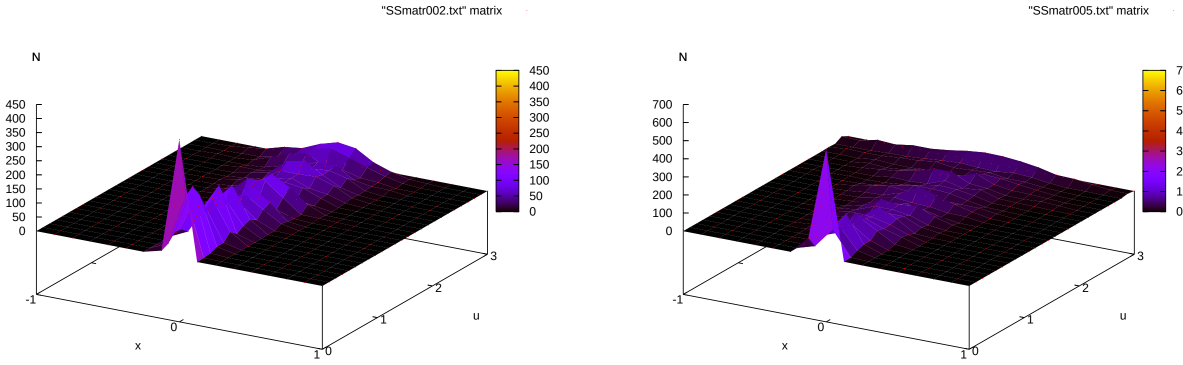


(a) $t = 500$. (b) $t = 750$.

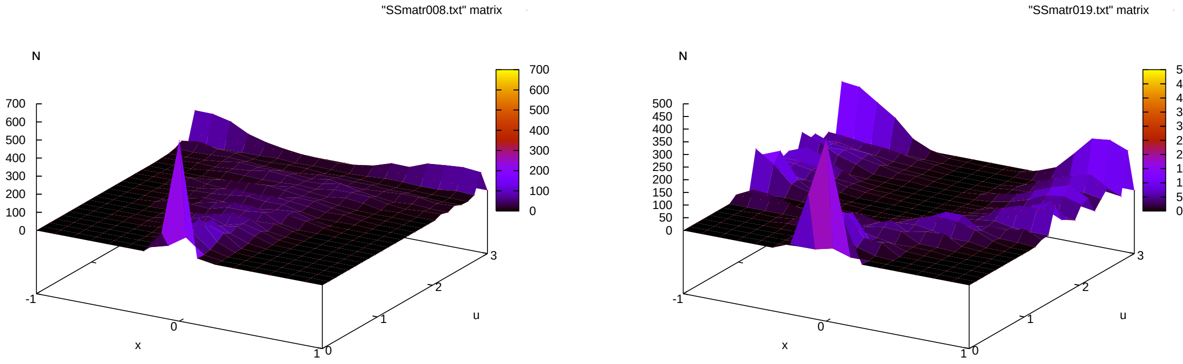


(c) $t = 850$. (d) $t = 1000$.

Figure 5: Simulations of example 3. The parameters are $N = 100, s = 0.03, m = 0.003$ and $\delta = 0.1$. The initial condition is composed of N individuals located at $(0, 0)$.



(a) $t = 5$. (b) $t = 10$.



(c) $t = 20$. (d) $t = 50$.

Figure 6: Simulations of example 3. The parameters are $N = 1000, s = 0.03, m = 0.03$ and $\delta = 1$. The initial condition is composed of N individuals located at 0 and with trait values $3i/N$ for $1 \leq i \leq N$.

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