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Non local Lotka-Volterra system with cross-diffusion in an heterogeneous medium

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Abstract We introduce a stochastic individual model for the spatial behavior of an animal population of dispersive and competitive species, considering various kinds of biological effects, such as heterogeneity of environmental conditions, mutual attractive or repulsive interactions between individuals or competition between them for resources. As a consequence of the study of the large population limit, global existence of a nonnegative weak solution to a multidimensional parabolic strongly coupled model of competing species is proved. The main new feature of the corresponding integro-differential equation is the nonlocal nonlinearity appearing in the diffusion terms, which may depend on the spatial densities of all population types. Moreover, the diffusion matrix is generally not strictly positive definite and the cross-diffusion effect allows for influences growing linearly with the subpopulations' sizes. We prove uniqueness of the finite measure-valued solution and give conditions under which the solution takes values in a functional space. We then make the competition kernels converge to a Dirac measure and obtain the existence of a solution to a locally competitive version of the previous equation. The techniques are essentially based on the underlying stochastic flow related to the dispersive part of the dynamics, and the use of suitable dual distances in the space of finite measures.

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1 Introduction

The spatial structure of a biological community is a fundamental subject in mathematical ecology and in particular the spatial distribution formed by dispersive motions of populations with intra- and inter- specific interactions (see e.g. Keller and Segel 1970; Nisbet and Gurney 1975a,b; Mimura and Murray 1978; Mimura and Yamaguti 1982; Shigesada et al. 1979). In the present work, the spatial behavior of a population of competitive species is studied. The dispersive motion of an individual in its environment is modeled as the result of various kinds of biological effects, such as heterogeneity of environmental conditions, mutual attractive or repulsive interactions with other individuals and competition for resources. These different effects will be modeled by local interaction kernels depending on the type of the individual and acting either on its spatial parameters or on its ecological parameters.

The population is composed of M sub-populations (species) characterized by different phenotypes. Each species has its own spatial and ecological dynamics depending on the spatial and genetic characteristics of the whole population. We assume that the motion of each individual (of a given type) is driven by a diffusion process on $\mathbb{R}^d$ whose coefficients depend on the spatial repartition of the different species around. Moreover, the individuals may reproduce and die, either from their natural death or because of the competition pressure for sharing resources. Each species has its own growth rate. The competition pressure of an individual of type j on an individual of type i depends both on the location of these individuals and on their type. It is called intra-specific competition if $i = j$, and inter-specific in case $i \neq j$. It is not assumed to be symmetric in (i, j).

We describe the stochastic dynamics of such a population by an individual-based model. Each individual is characterized by its type and its spatial location. Because of the births and deaths of individuals, the population doesn't live in a vector space of positions and we model its dynamics as a Markov process with values in the M-dimensional vector space of $\mathbb{R}^d$-point measures. We introduce the charge capacity parameter K describing the order of the population size. To be consistent, the individuals are weighted by $\frac{1}{K}$. The existence of the population process is obtained by standard arguments. Then, large population asymptotics is studied. We show that when K tends to infinity, the population process converges to a weak solution of the following nonlocal (in trait and space) nonlinear parabolic cross-diffusion-reaction system: for all $i \in \{1, \dots, M\}$,

$$\partial_t u^i = \sum_{k,l=1}^{d} \partial^2_{x_k x_l} \left(a^i_{k,l}(., G^{i1} * u^1, \dots, G^{iM} * u^M)\, u^i \right)$$
$$- \sum_{k=1}^{d} \partial_{x_k} \left(b^i_k(., H^{i1} * u^1, \cdots, H^{iM} * u^M)\, u^i \right) + \left(r_i - \sum_{j=1}^{M} C^{ij} * u^j \right) u^i. \quad (1)$$

Here, $u^i(t, .)$ denotes in general a finite measure on $\mathbb{R}^d$ for any $t \geq 0$, and $(G^{ij}, H^{ij}, C^{ij})_{1 \leq i,j \leq M}$ are $3M^2$ nonnegative and smooth L^1-functions defined from $\mathbb{R}^d$ to $\mathbb{R}_+$ that model the spatial interactions between individuals of type i and j.

By means of this convergence result, we get a theorem of existence of a weak solution to Eq. (1). Next we prove the uniqueness of such a solution and we give two sets of assumptions under which the measure solution has a density with respect to the Lebesgue measure, thus establishing the existence of a function solution to (1). The tools we use to establish this and the forthcoming results are probabilistic ones. They mainly rely on the stochastic flow related to the dispersive part of the equation and its inverse flow (as function of the initial position).

In the model leading to Eq. (1), the competition between two individuals is described as a function of the distance between them. This biological assumption is clear: the closer the animals are, the stronger is the fight to share resources. An extreme situation is the local case, when individuals only compete if they stay at the same place. Mathematically speaking, it means that for $i, j \in \{1, \dots, M\}$ and for $x \in \mathbb{R}^d$, the competition kernel has the form

$$C^{ij}(x) = c_{ij} C_\varepsilon(x),$$

where c_{ij} are positive constant numbers and the measures $C_\epsilon(x-y)dy$ weakly converge to the Dirac measure at x when the range of interaction ε tends to 0 (for instance, C_ε may be the centered Gaussian density with variance ε). We study the convergence of the solution u^ε of (1) when ε tends to zero. We show that u^ε converges to the unique solution u of the spatially nonlocal nonlinear cross-diffusion equation: for all $i \in \{1, \dots, M\}$,

$$\begin{aligned} \partial_t u^i = & \sum_{k,l=1}^{d} \partial^2_{x_k x_l} \left(a^i_{k,l}(., G^{i1} * u^1, \dots, G^{iM} * u^M)\, u^i \right) \\ & - \sum_{k=1}^{d} \partial_{x_k} \left(b^i_k(., H^{i1} * u^1, \dots, H^{iM} * u^M)\, u^i \right) + \left(r_i - \sum_{j=1}^{M} c_{ij}\, u^j \right) u^i. \end{aligned} \tag{2}$$

Ecological models featuring space displacements have been studied by Champagnat and Méléard (2007), Arnold et al. (2012) and Bouin et al. (2012), but the diffusion coefficients therein only depend on the type of each individual, and not on the spatial distribution of the other animals alive. To our knowledge, the nonlocal nonlinear Eq. (1) and (2) have never been studied in such generality, despite the fact that they naturally arise from the biological motivation. A recent paper on conservative relaxed cross-diffusion Lepoutre et al. (2012) addresses well posedness issues in a model with nonlocal interaction in the diffusion terms. Nonlocal reaction terms have otherwise been considered by Coville and Dupaigne (2005), Berestycki et al. (2009), Genieys et al. (2006) and in references therein. Our model incorporates those two features simultaneously.

The dependance of the diffusion coefficient on the individual density is indeed the main new difficulty we deal with in this paper. It is the reason why the introduction of different techniques from those developed in the aforementioned works is needed.

Cross-diffusion models with local spatial interaction and local competition have excited the scientific community, see for example the works of Mimura and Murray

(1978), Mimura and Kawasaki (1980), Lou et al. (2000), Chen and Jüngel (2004), Chen and Jüngel (2004, 2006) and more recently in a work by Desvillettes et al. (2013). The prototypical equation in this situation has the form

$$\partial_t u^1 = d_1 \Delta \left((a_1 + b_{12} u^2) u^1 \right) + (r_1 - c_{11} u^1 - c_{12} u^2) u^1,$$
$$\partial_t u^2 = d_2 \Delta \left((a_2 + b_{21} u^2) u^1 \right) + (r_2 - c_{21} u^1 - c_{22} u^2) u^2, \tag{3}$$

with boundary conditions on a given bounded smooth domain of $\mathbb{R}^d$. Although global existence results were obtained by Chen and Jüngel (2004, 2006) for such equation, their techniques do not seem to be useful in more general situations. In that direction, an interesting but highly difficult open challenge is to establish the convergence of the system (2) to systems of the type of (3) when the kernels G and H tend to Dirac measures.

2 The individual-based model

2.1 Assumptions

Let us denote by $\mathcal{S}_+(\mathbb{R}^d)$ the space of symmetric nonnegative diffusion matrices and define for $i = 1, \ldots, M$ the measurable functions

$$a^i : \mathbb{R}^d \times \mathbb{R}^M \mapsto \mathcal{S}_+(\mathbb{R}^d),$$
$$b^i : \mathbb{R}^d \times \mathbb{R}^M \mapsto \mathbb{R}^d,$$
$$r_i : \mathbb{R}^d \mapsto \mathbb{R}_+.$$

We denote by σ^i the $d \times d-$matrix such that $a^i = \sigma^i (\sigma^i)^*$. We will assume throughout this work the following hypotheses:

(**H**):

1. There is a positive constant L such that for any $x, x' \in \mathbb{R}^d$ and any $v_j, v'_j \in \mathbb{R}_+ (j \in \{1, \ldots, M\})$,

$$|\sigma^i(x, v_1, \ldots, v_M) - \sigma^i(x', v'_1, \ldots, v'_M)| + |b^i(x, v_1, \ldots, v_M) - b^i(x', v'_1, \ldots, v'_M)| \leq L \left(|x - x'| + \sum_{j=1}^M |v_j - v'_j| \right).$$

2. The functions $(G^{ij}, H^{ij}, C^{ij})_{1 \leq i,j \leq M}$ defined from $\mathbb{R}^d$ to $\mathbb{R}_+$ are assumed to be nonnegative, bounded and Lipschitz continuous.
3. The nonnegative functions r_i are assumed to be bounded. We fix an upper bound denoted by $\bar{r}_i$.

For later use, we also introduce some notation:

- For $k \geq 1$ and $\alpha \in (0, 1)$, we denote by $\mathcal{C}^{k,\alpha}(E)$ the space of k times differentiable functions on $E = \mathbb{R}^d$ or $E = \mathbb{R}^d \times \mathbb{R}_+^M$ which have bounded derivatives up to the $k-$th order and a globally α-Holder derivative of order k. Notice that functions in $\mathcal{C}^{k,\alpha}(E)$ are not required to be bounded.
- The subspace of bounded functions in $\mathcal{C}^{k,\alpha}(E)$ is denoted by $\mathcal{C}_b^{k,\alpha}(E)$.
- The notation $\mathcal{C}^k(E)$ and $\mathcal{C}_b^k(E)$ is defined analogously, without the Holder continuity requirement.

2.2 The diffusive M-type stochastic population dynamics

Let us now describe the dynamics of the population we are interested in. We take into account the births and deaths of all individuals and their motion during their life. The population dynamics will be modeled by a point measure-valued Markov processes. Let us fix the charge capacity $K \in \mathbb{N}^*$ and define

$$\mathcal{M}_K = \left\{ \frac{1}{K} \sum_{n=1}^{N} \delta_{x^n}, \, x^n \in \mathbb{R}^d, \, N \in \mathbb{N} \right\}$$

as the space of weighted finite point measures on $\mathbb{R}^d$. The stochastic population process $(\nu_t^K)_{t \geq 0}$ will take values in $(\mathcal{M}_K)^M$. The ith coordinate of this process describes the spatial configuration of the subpopulation of type i. Thus,

$$\nu_t^K = (\nu_t^{1,K}, \ldots, \nu_t^{M,K}) = (\nu_t^{i,K})_{1 \leq i \leq M}$$

with

$$\nu_t^{1,K} = \frac{1}{K} \sum_{n=1}^{N_t^1} \delta_{X_t^{n,1}} \;\; ; \cdots ; \;\; \nu_t^{M,K} = \frac{1}{K} \sum_{n=1}^{N_t^M} \delta_{X_t^{n,M}}.$$

where for any $i \in \{1, \ldots, M\}$, $N_t^i \in \mathbb{N}$ stands for the number of living individuals of type i at time t and $X_t^{1,i}, \ldots, X_t^{N_t^i,i}$ describe their positions (in $\mathbb{R}^d$).

The dynamics of the population can be roughly summarized as follows:

The initial population is characterized by the measures $(\nu_0^i)_{1 \leq i \leq M} \in (\mathcal{M}_K)^M$ at time $t = 0$. Any individual of type i located at $x \in \mathbb{R}^d$ at time t has two independent exponential clocks: a "clonal reproduction" clock with parameter $r_i(x)$ and a "mortality" clock with parameter $\sum_{j=1}^M C^{ij} * \nu_t^{j,K}(x)$. If the reproduction clock of an individual rings, then it produces at the same location an individual of same type as itself. If its mortality clock rings, then the individual disappears. The death rate of an ith type individual depends on the positions of the other individuals through the kernel C^{ij}, which describes how species j acts on i in the competition for resources.

During its life, an individual will move as a diffusion process whose coefficients depend on all individual positions. The motion of an individual with type i is a diffusion process with diffusion matrix $a^i(., G^{i1} * \nu^{1,K}, \ldots, G^{iM} * \nu^{M,K})$ and drift vector

$b^i(., H^{i1} * \nu^{1,K}, \ldots, H^{iM} * \nu^{M,K})$. The coefficients take into account the effects due to the nonhomogeneous spatial densities of the different species. Indeed, a species can be attracted or repulsed by the other ones and the concentration of species may increase or decrease the fluctuations in the dynamics.

The vector-measure valued process $(\nu_t)_{t\geq 0}$ is a Markov process which can be rigorously expressed as solution of a stochastic differential equation driven by d-dimensional Brownian motions $(B^{n,i})_{1\leq i\leq M, n\in\mathbb{N}^*}$ and Poisson point measures $(Q^i(dt, dn, d\theta))_{1\leq i\leq M}$ on $\mathbb{R}_+ \times \mathbb{N}^* \times \mathbb{R}_+$ with intensity $dt \sum_{n\in\mathbb{N}^*} \delta_n \, d\theta$, all independent and independent of the initial condition $(\nu_0^1, \ldots, \nu_0^M)$. The measure Q^i stochastically dominates the jump process which describes the births and deaths in the $i-$th population. The Brownian motions drive the spatial behavior of the individuals alive. By using Itô's formula, for $\mathcal{C}^2(\mathbb{R}^d)$-functions f_i, $i = 1, \ldots, M$, we get

$$
\begin{aligned}
\langle \nu_t^{i,K}, f_i\rangle &= \frac{1}{K} \sum_{n=1}^{K\langle \nu_t^i, 1\rangle} f_i(X_t^{n,i}) \\
&= \langle \nu_0^i, f_i\rangle + \frac{\sqrt{2}}{K} \int_0^t \sum_{n=1}^{K\langle \nu_s^i, 1\rangle} \sum_{k,l} \sigma_{k,l}^i(X_s^{n,i}, G^{i1} * \nu_s^{1,K}(X_s^{n,i}), \cdots, G^{iM} \\
&\quad * \nu_s^{M,K}(X_s^{n,i}))\partial_{x_k} f_i(X_s^{n,i})\, dB_l^{n,i}(s) \\
&\quad + \int_0^t \Big\langle \nu_s^{i,K}, \sum_{k,l} a_{k,l}^i(\cdot, G^{i1} * \nu_s^{1,K}, \ldots, G^{iM} * \nu_s^{M,K}))\, \partial^2_{x_k x_l} f_i \\
&\quad + \sum_k b_k^i(\cdot, H^{i1} * \nu_s^{1,K}, \ldots, H^{iM} * \nu_s^{M,K})\, \partial_{x_k} f_i \Big\rangle ds \\
&\quad + \frac{1}{K} \int_{[0,t]\times\mathbb{N}\times\mathbb{R}_+} f_i(X_{s-}^{n,i}) \Big(\mathbf{1}_{0<\theta\leq r_i(X_{s-}^{n,i})} - \mathbf{1}_{r_i(X_{s-}^{n,i})<\theta\leq r_i(X_{s-}^{n,i}) + \sum_{j=1}^M C^{ij} * \nu^{j,K}(X_{s-}^{n,i})} \Big) \\
&\quad \times \mathbf{1}_{n\leq K\,\langle \nu_{s-}^i, 1\rangle}\, Q^i(ds, dn, d\theta).
\end{aligned}
$$

The law of $(\nu_t)_t$ is characterized by its infinitesimal generator L which captures the dynamics described above. L is the sum of a birth and death (ecological) part L_e and a diffusion part L_d. The generator L_e is defined for bounded and measurable functions ϕ from $(\mathcal{M}_K)^M$ into $\mathbb{R}$. Let us denote by ϵ_i the ith unit vector of $\mathbb{R}^M$. For $\nu = (\nu^i)_{1\leq i\leq M} = (\frac{1}{K}\sum_{n=1}^{N^i} \delta_{x^{n,i}})_{1\leq i\leq M}$, we define

$$
\begin{aligned}
L_e\phi(\nu) &= \sum_{i=1}^M r_i(x^{n,i}) \sum_{n=1}^{N^i} \phi\left(\left(\nu + \frac{1}{K}\delta_{x^{n,i}}\,.\epsilon_i\right) - \phi(\nu)\right) \\
&\quad + \sum_{i=1}^M \sum_{n=1}^{N^i} \left(\sum_{j=1}^M Cij * \nu^j(x^{n,i})\right)\left(\phi\left(\nu - \frac{1}{K}\delta_{x^{n,i}}\,.\epsilon_i\right) - \phi(\nu)\right).
\end{aligned} \tag{4}
$$

In order to define the diffusion part of the generator we need to introduce a standard class of cylindrical functions generating the set of bounded and measurable functions from $(\mathcal{M}_K)^M$ into $\mathbb{R}$. Let us consider $F \in \mathcal{C}_b^2(\mathbb{R}^M)$ and for $i \in \{1, \ldots, M\}$, we introduce $f_i \in \mathcal{C}^2(\mathbb{R}^d)$ and define

$$F_f(\nu) = F(\langle \nu^1, f_1 \rangle, \ldots, \langle \nu^M, f_M \rangle). \tag{5}$$

The diffusive part L_d 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 Dawson (1993) and is given by

$$\begin{aligned} L_d F_f(\nu) = \sum_{i=1}^{M} \Bigg(& \sum_{k,l=1}^{d} \Bigg\langle \nu^i, \Bigg\{ a^i_{kl}(\cdot, G^{i1} * \nu^i, \ldots, G^{iM} * \nu^M)\, \partial^2_{x_k x_l} f_i \\ & + \sum_{k=1}^{d} b^i_k(\cdot, H^{i1} * \nu^i, \ldots, H^{iM} * \nu^M)\, \partial_{x_k} f_i \Bigg\} \Bigg\rangle F'_i(\langle \nu^1, f_1 \rangle, \ldots, \langle \nu^M, f_M \rangle) \\ & + \sum_{k,l=1}^{d} \Big\langle \nu^i,\ a^i_{kl}(\cdot, G^{i1} * \nu^i, \ldots, G^{iM} * \nu^M)\, \partial_{x_l} f_i\, \partial_{x_k} f_i \Big\rangle \\ & \times F''_{ii}(\langle \nu^1, f_1 \rangle, \ldots, \langle \nu^M, f_M \rangle) \Bigg). \end{aligned} \tag{6}$$

Hence, we have

$$L F_f(\nu) = L_e F_f(\nu) + L_d F_f(\nu). \tag{7}$$

3 Large population approximation and non local Lotka-Volterra cross diffusion system

3.1 Existence and uniqueness of weak measure solutions

We now state a large population approximation for the previous M species model by making the charge capacity K tend to infinity. This result in particular implies the existence of weak solutions to a non local cross-diffusion system of nonlinear partial differential equations.

We denote by $\mathcal{M}$ the space of finite measures in $\mathbb{R}^d$ endowed the weak topology.

Theorem 3.1 *Assume that for some $p \geq 2$, $\sup_K \mathbb{E}(\langle \nu_0^{i,K}, 1 \rangle^p) < +\infty$ for any $i = 1, \ldots, M$. Assume also* (**H**) *and moreover that the sequence of finite measures $(\nu_0^{1,K}, \ldots, \nu_0^{M,K})$ converges in law as K goes to infinity to the deterministic finite measures $(\xi_0^1, \ldots, \xi_0^M)$. Then, when K tends to infinity, the sequence $(\nu_\cdot^{1,K}, \ldots, \nu_\cdot^{M,K})$ converges in law in $\mathbb{D}([0, T], \mathcal{M}^M)$ to the unique deterministic continuous finite measure-valued function $\xi = (\xi^1, \ldots, \xi^M)$ weak solution of the following cross-diffusion system: for all $i = 1, \ldots, M$,*

$$\langle \xi_t^i, f_t^i \rangle = \langle \xi_0^i, f_0^i \rangle + \int_0^t \int \Bigg\{ \sum_{k,l} a_{kl}^i(\cdot, G^{i1} * \xi_t^1, \ldots, G^{iM} * \xi_t^M)\, \partial^2_{x_k x_l} f_s^i$$
$$+ \sum_k b_k^i(\cdot, H^{i1} * \xi_t^1, \ldots, H^{iM} * \xi_t^M)\, \partial_{x_k} f_s^i$$
$$+ \left(r_i - \sum_{j=1}^M C^{ij} * \xi_s^j \right) f_s^i + \partial_s f_s^i \Bigg\} (x)\, \xi_s^i(dx) ds \tag{8}$$

for every bounded continuous function $(t,x) \mapsto f_t^i(x)$ *with continuous bounded derivatives up to the first order in* $t \in [0,T]$ *and up to second order in* $x \in \mathbb{R}^d$.

Remark 3.2 Observe that in contrast to the models of cross-diffusion introduced by Shigesada et al. (1979) or Mimura and Kawasaki (1980), Eq. (8) allows for long range interaction in the coefficients of spatial diffusion. For example, taking $G^{ij} = H^{ij} = 1$, the spatial behavior of individuals of type i depend on the total mass of the subspecies j. It also covers some cases where the diffusion matrix might vanish , e.g. $a^i(x, v_1, \ldots, v_M) = I_d \Psi_i^2(\sum_{j=1}^M v_j)$ with $\Psi_i : [0,\infty] \to \mathbb{R}_+$ a Lipschitz continuous function vanishing at 0 and I_d the identity matrix.

Remark 3.3 Notice that a solution to (8) satisfies $\sup_{t\in[0,T]} \|\xi_t^i\|_{TV} < e^{\bar{r}_i T} \|\xi_0^i\|_{TV}$ for $i = 1, \ldots, M$, as is readily seen by taking $f^i = 1$ and using the non negativity of the functions C^{ij} and Gronwall's lemma.

The proof is decomposed in several steps: propagation of moments of the total mass, uniform tightness of the laws of $(\nu_\cdot^{1,K}, \ldots, \nu_\cdot^{M,K})$, identification of the limit as solution of (8) and uniqueness of solutions to that equation. The first three steps are standard and can be adapted from the arguments of Fournier and Méléard (2004) and of Champagnat and Méléard (2007), with some modifications owed to the unbounded diffusion coefficients in the expression (6), which can be dealt with in a similar way as with the competition terms in those works, thanks to the uniform control of moments of the total mass.

The proof of uniqueness of weak measure solutions to (8) requires new techniques and arguments in order to deal with the interaction in the diffusion terms. It is established in next proposition where, for notational simplicity, we will deal only with the case $M = 2$. All arguments easily extend to the general case.

Proposition 3.4 *Let* $\xi = (\xi^1, \xi^2)$ *and* $\tilde{\xi} = (\tilde{\xi}^1, \tilde{\xi}^2)$ *be two solutions of the system* (8) *in* $[0,T]$ *with* $M = 2$. *Then* $(\xi_t^1, \xi_t^2) = (\tilde{\xi}_t^1, \tilde{\xi}_t^2)$ *for all* $t \in [0,T]$.

We will need to use a distance that is weaker than to total variation one but better adapted to perturbations in the diffusion coefficients. Denote by $\mathcal{LB}(\mathbb{R}^d)$ the space of Lipschitz continuous and bounded functions on $\mathbb{R}^d$, and by $\|\cdot\|_{\mathcal{LB}}$ or simply $\|\cdot\|$ the corresponding norm,

$$\|\varphi\|_{\mathcal{LB}} := \sup_{x\neq y} \frac{|\varphi(x) - \varphi(y)|}{|x-y|} + \sup_x |\varphi(x)|.$$

We endow $\mathcal{M}(\mathbb{R}^d)$ with the dual norm with respect to $\mathcal{LB}(\mathbb{R}^d)$,

$$\|\eta\|_{\mathcal{LB}^*} := \sup_{\|\varphi\|_{\mathcal{LB}}\leq 1} \langle \eta, \varphi \rangle, \quad \eta \in \mathcal{M}(\mathbb{R}^d).$$

Given a solution $(\xi_t^1, \ldots, \xi_t^M)_{t\in[0,T]}$ to (8), we set for $i = 1, \ldots, M$,

$$\begin{aligned} \sigma(i,t,x) &= \sigma^i(x, G^{i1} * \xi_t^1(x), \ldots, G^{iM} * \xi_t^M(x)), \\ b(i,t,x) &= b^i(x, H^{i1} * \xi_t^1(x), \ldots, H^{iM} * \xi_t^M(x)). \end{aligned} \tag{9}$$

Remark 3.5 From assumption (**H**) i),ii) and Remark 3.3, the functions in (9) are Lipschitz functions of $x \in \mathbb{R}^d$, uniformly in $[0, T]$.

We introduce next the family of SDEs associated with the coefficients (9), and the corresponding transition semigroups. For each $x \in \mathbb{R}^d$ and $s \in [0, T]$ consider the unique (strong) solution

$$X_{s,t}^i(x) = (X_{s,t}^{i,1}(x), \ldots, X_{s,t}^{i,d}(x)) \quad t \in [s, T]$$

of the stochastic differential equation in $\mathbb{R}^d$,

$$X_{s,t}^i(x) = x + \int_s^t \sigma(i, r, X_{s,r}^i(x)) dB_r^i + \int_s^t b(i, r, X_{s,r}^i(x)) dr, \quad t \in [s, T] \tag{10}$$

where $B^i = (B^{i,q})_{q=1}^d$ is a standard d-dimensional Brownian motion in a given probability space. The fact that for each s the mapping $(t, x) \mapsto X_{s,t}^i(x)$ is measurable can be classically deduced from the properties of functions $\sigma(i, t, x)$ and $b(i, t, x)$ noted in Remark 3.5. The three parameter process $(s, t, x) \mapsto X_{s,t}^i(x)$ is called the *stochastic flow* associated with the coefficients $\sigma(i, t, x)$ and $b(i, t, x)$. Finer properties of this processes will be recalled and used later.

Given a second solution $(\tilde{\xi}_t^1, \tilde{\xi}_t^2)_{t\in[0,T]}$ of (8), define analogously coefficients $\tilde{\sigma}(i, t, x)$ and $\tilde{b}(i, t, x)$ in terms of $(\tilde{\xi}^1, \tilde{\xi}^2)$, and the processes $\tilde{X}_{s,t}^i(x)$ given for $i = 1, 2$ by the solution to the SDEs

$$\tilde{X}_{s,t}^i(x) = x + \int_s^t \tilde{\sigma}(i, r, \tilde{X}^i{}_{s,r}(x)) dB_r^i + \int_s^t \tilde{b}(i, r, \tilde{X}^i{}_{s,r}(x)) dr,$$

driven by *the same* Brownian motions B^i as the processes $X_{s,t}^i(x)$ in (10).

The proof of Proposition 3.4 will rely on stability properties of the non homogenous transition semigroups of $X_{s,t}^i(x)$ and $\tilde{X}_{s,t}^i(x)$, which we respectively denote by $P_{s,t}^i(x, dy)$ and $\tilde{P}_{s,t}^i(x, dy)$. Below and in all the sequel, $C > 0$ denotes a constant that may change from line to line.

Lemma 3.6 *For all* $T > 0$, $\varphi \in \mathcal{LB}(\mathbb{R}^d)$, $0 \le s \le t \le T$, $i = 1, 2$,

a) $\|P^i_{s,t}\varphi\|^2_{\mathcal{LB}} \le C(\xi^1, \xi^2, T)\|\varphi\|^2_{\mathcal{LB}}$ *and* $\|\tilde{P}^i_{s,t}\varphi\|^2 \le C(\tilde{\xi^1}, \tilde{\xi^2}, T)\|\varphi\|^2_{\mathcal{LB}}$.
b) For all $x \in \mathbb{R}^d$,

$$
\begin{aligned}
&|P^i_{s,t}\varphi(x) - \tilde{P}^i_{s,t}\varphi(x)|^2 \\
&\quad \le C'(\xi^1, \xi^2, \tilde{\xi}^1, \tilde{\xi}^2, T)\|\varphi\|^2_{\mathcal{LB}} \int_s^t \|\xi^1_r - \tilde{\xi}^1_r\|^2_{\mathcal{LB}^*} + \|\xi^2_r - \tilde{\xi}^2_r\|^2_{\mathcal{LB}^*} dr
\end{aligned}
$$

The constants depend on ξ^i *or* $\tilde{\xi}^i$ *only through* $\sup_{t\in[0,T]} \|\xi^i_t\|_{TV}$ *and* $\sup_{t\in[0,T]} \|\tilde{\xi}^i_t\|_{TV}$*, and can be chosen to depend only on* $e^{\bar{r}_i T}\|\xi^i_0\|_{TV}$.

Proof a) Is enough to control the Lipschitz constants of the function $P^i_{s,t}\varphi$ or $\tilde{P}^i_{s,t}\varphi$. We have, by Burkholder-Davis-Gundy inequality

$$
\begin{aligned}
E|X^i_{s,t}(x) - X^i_{s,t}(y)|^2 &\le C|x-y|^2 + C\int_s^t \mathbb{E}|\sigma(i, r, X^i_{s,r}(x)) - \sigma(i, r, X^i_{s,r}(y))|^2 dr \\
&\quad + C\int_s^t \mathbb{E}|b(i, r, X^i_{s,r}(x)) - b(i, r, X^i_{s,r}(y))|^2 dr \\
&\le C|x-y|^2 + C\int_s^t \mathbb{E}|X^i_{s,r}(x) - X^i_{s,r}(y)|^2 dr
\end{aligned}
$$

for all $s \le t$. The above constants depend on bounds for the Lipschitz constants of the coefficients σ^i, b^i (as functions of the position), on Lipschitz constants of the Kernels G^{1j} and H^{1j} and on $\sup_{t\in[0,T]} \|\xi^i_t\|_{TV}$ and $\sup_{t\in[0,T]} \|\tilde{\xi}^i_t\|_{TV}$. The latter suprema are in turn controlled by $e^{\bar{r}_i T}\|\xi^i_0\|_{TV}$ by Remark 3.3. By Gronwall's lemma, $\mathbb{E}|X^i_{s,t}(x) - X^i_{s,t}(y)|^2 \le C|x-y|^2$ which easily yields

$$
|P^i_{s,t}\varphi(x) - P^i_{s,t}\varphi(y)|^2 \le C\|\varphi\|^2_{\mathcal{LB}}|x-y|^2
$$

as required. *b)* For notational simplicity we consider first the case $b = 0$. Using similar types of inequalities as before, we have for all $s \le t \le T$,

$$
\begin{aligned}
\mathbb{E}|X^i_{s,t}(x) - \tilde{X}^i_{s,t}(x)|^2 \le\ & C'\Bigg(\int_s^t \mathbb{E}|X^i_{s,r}(x) - \tilde{X}^i_{s,r}(x)|^2 + \mathbb{E}|G^{i1} * \xi_1(X^i_{s,r}(x)) \\
& - G^{i1} * \tilde{\xi}_1(\tilde{X}^i_{s,r}(x))|^2 + \mathbb{E}|G^{i2} * \xi_2(X^i_{s,r}(x)) - G^{i2} * \tilde{\xi}_2(\tilde{X}^i_{s,r}(x))|^2\, dr\Bigg)
\end{aligned}
$$

$$\leq C''\left(\int_s^t \mathbb{E}|X^i_{s,r}(x)-\tilde{X}^i_{s,r}(x)|^2+\mathbb{E}\left|\int G^{i1}(X^i_{s,r}(x)-y)(\xi^1_s(dy)-\tilde{\xi}^1(dy))\right|^2\right.$$
$$\left.+\mathbb{E}\left|\int G^{i2}(X^i_{s,r}(x)-y)(\xi^2_s(dy)-\tilde{\xi}^2(dy))\right|^2 dr\right)$$

Since the functions $y\mapsto G^{ij}(X^i_s(x)-y)$ are uniformly Lipschitz continuous, we deduce with Gronwall's lemma that

$$\mathbb{E}(|X^i_{s,t}(x)-\tilde{X}^i_{s,t}(x)|^2)\leq C\int_s^t \|\xi^1_r-\tilde{\xi}^1_r\|^2_{\mathcal{LB}^*}+\|\xi^2_r-\tilde{\xi}^2_r\|^2_{\mathcal{LB}^*}dr$$

which allows us to easily conclude. The case $b\neq 0$ is similar with additional terms involving the kernels H^{ij}. □

Proof of Proposition 3.4 Take $\varphi\in\mathcal{LB}(\mathbb{R}^d)$ with $\|\varphi\|\leq 1$. By the Feynmann-Kac formula (e.g. Karatzas and Shreve 1991), the function $f^{(t)}(s,x)=\mathbb{E}(\varphi(X^i_{s,t}(x)))=P^i_{s,t}\varphi(x)$ is the unique classic (bounded) solution of the linear parabolic problem

$$\begin{aligned}\partial_s f^{(t)}(s,x)&+a^1_{kl}(\cdot,G^{i1}*\xi^1_t,G^{i2}*\xi^2_t)\partial_{x_kx_l}f^{(t)}(s,x)\\&+b^1_k(\cdot,H^{i1}*\xi^1_t,H^{i2}*\xi^2_t)\partial_{x_k}f^{(t)}(s,x)=0\end{aligned}$$

with final condition at time $s=t$ equal to $\varphi(x)$. Replacing $f^{(t)}$ in the first equation in (8), we see that ξ^1 satisfies

$$\begin{aligned}\langle\xi^1_t,\varphi\rangle&=\langle\xi^1_0,P^1_{0,t}\varphi\rangle\\&+\int_0^t\int\big(r_1(x)-C^{11}*\xi^1_s(x)-C^{12}*\xi^2_s(x)\big)P^1_{s,t}\varphi(x)\xi^1_s(dx)ds,\end{aligned}\tag{11}$$

and, similarly,

$$\begin{aligned}\langle\tilde{\xi}^1_t,\varphi\rangle&=\langle\xi^1_0,\tilde{P}^1_{0,t}\varphi\rangle\\&+\int_0^t\int\big(r_1(x)-C^{11}*\tilde{\xi}^1_s(x)-C^{12}*\tilde{\xi}^2_s(x)\big)\tilde{P}^1_{s,t}\varphi(x)\tilde{\xi}^1_s(dx)ds.\end{aligned}$$

Consequently,

$$\langle\xi^1_t-\tilde{\xi}^1_t,\varphi\rangle^2\leq\langle\xi^1_0,(P^1_{0,t}-\tilde{P}^1_{0,t})\varphi\rangle^2$$
$$+C\int_0^t\left\{\left[\int(P^1_{s,t}-\tilde{P}^1_{s,t})\varphi(x)\xi^1_s(dx)\right]^2+\left[\int\tilde{P}^1_{s,t}\varphi(x)(\xi^1_s(dx)-\tilde{\xi}^1_s(dx))\right]^2\right.$$

$$
\begin{aligned}
&+\left[\int C^{11} * (\xi_s^1 - \tilde{\xi}_s^1)(x) P_{s,t}^1 \varphi(x) \xi_s^1(dx)\right]^2 \\
&+\left[\int C^{11} * \tilde{\xi}_s^1(x) (P_{s,t}^1 \varphi(x) - \tilde{P}_{s,t}^1 \varphi(x)) \xi_s^1(dx)\right]^2 \\
&+\left[\int C^{11} * \tilde{\xi}_s^1(x) \tilde{P}_{s,t}^1 \varphi(x) (\xi_s^1(dx) - \tilde{\xi}_s^1(dx))\right]^2 \\
&+\left[\int C^{12} * (\xi_s^2 - \tilde{\xi}_s^2)(x) P_{s,t}^1 \varphi(x) \xi_s^1(dx)\right]^2 \\
&+\left[\int C^{12} * \tilde{\xi}_s^2(x) (P_{s,t}^1 \varphi(x) - \tilde{P}_{s,t}^1 \varphi(x)) \xi_s^1(dx)\right]^2 \\
&+\left[\int C^{12} * \tilde{\xi}_s^2(x) \tilde{P}_{s,t}^1 \varphi(x) (\xi_s^1(dx) - \tilde{\xi}_s^1(dx))\right]^2 \Bigg\} ds \\
&\leq C \sup_y |(P_{0,t}^1 - \tilde{P}_{0,t}^1)\varphi(y)|^2 + C \int_0^t \Bigg\{ \sup_y |(P_{s,t}^1 - \tilde{P}_{s,t}^1)\varphi(y)|^2 + \langle \xi_s^1 - \tilde{\xi}_s^1, \tilde{P}_{s,t}^1 \varphi \rangle^2 \\
&+\sup_y |C^{11} * (\xi_s^1 - \tilde{\xi}_s^1)(y)|^2 + \left[\int C^{11} * \tilde{\xi}_s^1(x) \tilde{P}_{s,t}^1 \varphi(x) (\xi_s^1(dx) - \tilde{\xi}_s^1(dx))\right]^2 \\
&+\sup_y |C^{12} * (\xi_s^2 - \tilde{\xi}_s^2)(y)|^2 + \left[\int C^{12} * \tilde{\xi}_s^2(x) \tilde{P}_{s,t}^1 \varphi(x) (\xi_s^1(dx) - \tilde{\xi}_s^1(dx))\right]^2 \Bigg\} ds,
\end{aligned}
$$

for constants depending on $\sup_{t\in[0,T]} \|\xi_t^i\|_{TV}^2$, $\sup_{t\in[0,T]} \|\tilde{\xi}_t^i\|_{TV}^2$ and T. The functions $x \mapsto C^{1j}(x-y)$ are Lipschitz continuous uniformly in y and, by Lemma 3.6 *a)*, $C^{1j} * \tilde{\xi}_s^j(x) \tilde{P}_{s,t}^1 \varphi(x)$ are Lipschitz continuous bounded functions, uniformly in $s, t \in [0, T]$. Together with Lemma 3.6 *b)*, this entails

$$
\langle \xi_t^1 - \tilde{\xi}_t^1, \varphi \rangle^2 \leq C \int_0^t \sum_{i=1,2} \|\xi_s^i - \tilde{\xi}_s^i\|_{\mathcal{LB}^*}^2 ds,
$$

and we can analogously obtain a similar bound for $\langle \xi_t^2 - \tilde{\xi}_t^2, \varphi \rangle^2$. Taking $\sup_{\|\varphi\|\leq 1}$, summing the two obtained inequalities and using Gronwall's lemma we conclude that

$$
\|\xi_t^i - \tilde{\xi}_t^i\|_{\mathcal{LB}^*}^2 = 0
$$

for all $t \in [0, T]$ and $i = 1, 2$ and thus uniqueness for System (8). □

3.2 Regularity of the stochastic flow and function solutions

We next show under two types of suitable assumptions on the coefficients and the initial condition that the solution $\xi_t^i(dx)$ has a density $\xi_t^i(x)$ with respect to Lebesgue measure for $i = 1, \ldots, M$.

Lemma 3.7 *Let* $(\xi_t^1, \ldots, \xi_t^M)_{t\in[0,T]}$ *be the measure solution of* (8). *Then, for all* $t \in [0, T]$,

$$\xi_t^i \le e^{\bar{r}_i T} m_t^i,$$

where m_t^i *is the finite measure defined by*

$$\langle m_t^i, \varphi \rangle := \mathbb{E}\left(\int_{\mathbb{R}^d} \varphi(X_{0,t}^i(x)) \xi_0^i(dx) \right) \tag{12}$$

for any bounded function φ.

Proof We write the proof for $M = 2$ and $i = 1$, and omit for notational simplicity the superscript 1 in the flow $X_{s,t}^1(x)$. Taking in the first equation in (8) the function

$$f^{(t)}(s, x) := \mathbb{E}\left(\varphi(X_{s,t}(x)) \exp\left\{ \int_s^t r_1(X_{s,r}(x)) - C^{11} * \xi_r^1(X_{s,r}(x)) \right.\right.$$
$$\left.\left. - C^{12} * \xi_r^2(X_{s,r}(x)) dr \right\} \right),$$

which is by the Feynman-Kac formula (see Karatzas and Shreve 1991) the unique classic (bounded) solution of the parabolic problem

$$\begin{aligned} 0 &= \partial_s f^{(t)}(s, x) + a_{kl}^1(\cdot, G^{i1} * \xi_t^1, G^{i2} * \xi_t^2) \partial_{x_k x_l} f^{(t)}(s, x) \\ &\quad + b_k^1(\cdot, H^{i1} * \xi_t^1, H^{i2} * \xi_t^2) \partial_{x_k} f^{(t)}(s, x) \\ &\quad + \left(r_1(x) - C^{11} * \xi_s^1 - C^{12} * \xi_s^2\right) f^{(t)}(s, x) \end{aligned}$$

with final condition at time $s = t$ equal to $\varphi(x)$, we get that

$$\langle \xi_t^1, \varphi \rangle = \mathbb{E}\left(\int_{\mathbb{R}^d} \varphi(X_{0,t}(x)) \exp\left\{ \int_0^t r_1(X_{0,r}(x)) \right.\right.$$
$$\left.\left. - C^{11} * \xi_r^1(X_{0,r}(x)) - C^{12} * \xi_r^2(X_{0,r}(x)) dr \right\} \xi_0^1(dx) \right) \tag{13}$$

for each continuous bounded function $\varphi \ge 0$. This yields $\langle \xi_t^1, \varphi \rangle \le e^{\bar{r}_1 T} \langle m_t^1, \varphi \rangle$ for all bounded continuous φ. The measure $\xi_t^1 + e^{\bar{r}_1 T} m_t^1$ being regular, for each Borel set A and $\epsilon > 0$ we can find a closed set $B \subseteq A$ s.t. $\langle \xi_t^1 - e^{\bar{r}_1 T} m_t^1, A \backslash B \rangle \le \epsilon$. Since the sequence of bounded continuous functions $f_k(x) = (1 - kd(x, B)) \vee 0$ pointwise converges to $\mathbf{1}_B$ as $k \to \infty$, we have $\langle \xi_t^1 - e^{\bar{r}_1 T} m_t^1, \mathbf{1}_B - f_k \rangle \to 0$ by dominated convergence w.r.t. the positive finite measure $|\xi_t^1 - e^{\bar{r}_1 T} m_t^1|$. It follows that for k sufficiently large

$$\langle \xi_t^1 - e^{\bar{r}_1 T} m_t^1, A \rangle \leq \langle \xi_t^1 + m_t^1, A \backslash B \rangle + \langle \xi_t^1 - e^{\bar{r}_1 T} m_t^1, \mathbf{1}_B - f_k \rangle + \langle \xi_t^1 - e^{\bar{r}_1 T} m_t^1, f_k \rangle \leq 2\varepsilon,$$

that is, $\langle \xi_t^1, A \rangle \leq e^{\bar{r}_1 T} \langle m_t^1, A \rangle$. □

We immediately deduce from (12) the following

Corollary 3.8 *For any initial finite measure $(\xi_0^1, \ldots, \xi_0^M)$ and in the uniform elliptic case: $\exists \lambda_i > 0$ such that $y^* a^i(x, v) y \geq \lambda_i |y|^2$ $\forall x, y \in \mathbb{R}^d$, $v \in \mathbb{R}_+^M$, the measure $\xi_t^i(dx)$ has a density $\xi_t^i(x)$ with respect to Lebesgue measure for all $t \in (0, T]$.*

Indeed, in that case, the law of the random variable $X_{0,t}^i(x)$ has a density with respect to Lebesgue measure. Lemma 3.7 allows us to conclude.

As pointed out in Remark 3.2, some natural biological examples are not covered by this ellipticity assumption. We will next provide a finer result covering some non elliptic cases under additional regularity assumptions. In all the sequel, we assume

$(\mathbf{H})'$: Hypothesis $(\mathbf{H})$ holds and moreover

1. $\sigma^i(x, v_1, \ldots, v_M)$ and $b^i(x, v_1, \ldots, v_M)$ are respectively $\mathcal{C}^{2,\alpha}(\mathbb{R}^d \times [0, \infty)^M)$ and $\mathcal{C}^{1,\alpha}(\mathbb{R}^d \times [0, \infty)^M)$ for some $\alpha \in (0, 1)$.
2. The functions $(G^{ij})_{1 \leq i,j \leq M}$ and $(H^{ij})_{1 \leq i,j \leq M}$ are respectively of class $\mathcal{C}_b^{2,\alpha}(\mathbb{R}^d)$ and $\mathcal{C}_b^{1,\alpha}(\mathbb{R}^d)$ for some $\alpha \in (0, 1)$.

Remark 3.9 Under assumptions $(\mathbf{H})'$ and by Remark 3.3, $\sigma(i, t, x)$ and $b(i, t, x)$ in (9) are respectively $\mathcal{C}^{2,\alpha}(\mathbb{R}^d)$ and $\mathcal{C}^{1,\alpha}(\mathbb{R}^d)$ for some $\alpha \in (0, 1)$, uniformly in $[0, T]$.

Proposition 3.10 *Assume hypothesis $(\mathbf{H})'$. If for some type i the measure ξ_0^i has a density, then ξ_t^i has a density for all $t \in [0, T]$.*

The proof will require classical regularity properties of stochastic flows stated by Kunita (1984) and summarized in the next Lemma.

Lemma 3.11 *Under assumptions $(\mathbf{H})'$, the process $(s, t, x) \mapsto X_{s,t}^i(x)$ has a continuous version such that, a.s. for each $s < t$ the function $(s, t, x) \mapsto X_{s,t}^i(x)$ is a global diffeomorphism of class $\mathcal{C}^{1,\beta}$ for all $\beta \in (0, \alpha)$.*

Moreover, for each $(t, y) \in [0, T] \times \mathbb{R}^d$ the inverse mappings $\eta_{s,t}^i(y) := (X_{s,t}^i)^{-1}(y)$, $0 \leq s < t \leq T$, satisfy the stochastic differential equation

$$\eta_{s,t}^i(y) = y - \int_s^t \sigma(i, r, \eta_{r,t}^i(y)) \widehat{d} B_r^i - \int_s^t \hat{b}(i, r, \eta_{r,t}^i(y)) dr \tag{14}$$

where for $k \in \{1, \ldots, d\}$, $\hat{b}_k(i, r, y) = b_k(i, r, y) - \sum_{q,l=1}^d \sigma_{lq}(i, r, y) \partial_{y_l} \sigma_{kq}(i, r, y)$ and $\widehat{d} B^i$ refers to the backward Itô integral with respect to the Brownian motion B^i (see p. 194 in Kunita 1984).

Finally, for each $(t, y) \in [0, T] \times \mathbb{R}^d$ *the (invertible) Jacobian matrix* $\nabla_y \eta^i_{s,t}(y) = \left(\partial_{y_l} \eta^{i,k}_{s,t}(y)\right)_{k,l=1}^{d}$ *of* $\eta^i_{s,t}(y)$ *satisfies the system of backward linear stochastic differential equations:*

$$\partial_{y_l} \eta^{i,k}_{s,t}(y) = \delta_{kl} - \sum_{p,q=1}^{d} \int_s^t \partial_{x_p} \sigma_{kq}(i, r, \eta^i_{r,t}(y)) \partial_{y_l} \eta^{i,p}_{r,t}(y) \widehat{d} B^{i,q}_r$$
$$- \sum_{p=1}^{d} \int_s^t \partial_{x_p} \hat{b}_k(i, r, \eta^i_{r,t}(y)) \partial_{y_l} \eta^{i,p}_{r,t}(y) dr. \tag{15}$$

Proof Thanks to assumption $(\mathbf{H})'$ and Remark 3.9 we can apply Theorems 3.1 and 6.1 in Ch. II of Kunita (1984). □

Proof of Proposition 3.10 Let $\varphi \geq 0$ be a bounded measurable function in $\mathbb{R}^d$. By the previous lemma, we can do the change of variable $X_{0,t}(x) = y$ in the integral inside the expectation in (12), to get

$$\langle m_t, \varphi \rangle = \mathbb{E} \left(\int_{\mathbb{R}^d} \varphi(y) \xi^1_0(\eta_{0,t}(y)) |det \nabla \eta_{0,t}(y)| dy \right) < +\infty.$$

Everything being positive in the above expression, Fubini's theorem yields that m_t has the (integrable) density $y \mapsto \mathbb{E}\left[\xi^1_0(\eta_{0,t}(y)) |det \nabla \eta_{0,t}(y)|\right]$ with respect to Lebesgue measure, and we conclude by Lemma 3.7. □

4 Convergence to local competition

Our aim in this section is to describe some situations where the interaction range of the competition is much smaller than the one of spatial diffusion. For example one may assume that animals interact for sharing resources as they are on the same place but diffuse depending on the densities of the different species staying around them in a larger neighbourhood. To model such situation, we suppose now that $C^{ij} = c^{ij} \gamma_\varepsilon$ for $c^{ij} \geq 0$ some fixed constant and γ_ε a suitable smooth approximation of the Dirac mass as $\varepsilon \to 0$. Our goal is to show that, under additional regularity assumptions, the (unique) solution $\xi = (\xi^1, \ldots, \xi^M)$ of Eq. (8) given by Theorem 3.1 for such competition coefficients converges, as $\varepsilon \to 0$, to a weak function solution of the system of Eq. (2).

In what follows, stronger conditions on the coefficients will be enforced, namely:

$(\mathbf{H})''$: Hypothesis $(\mathbf{H})$ holds and moreover

1. $\sigma^i(x, v_1, \ldots, v_M)$ and $b^i(x, v_1, \ldots, v_M)$ are respectively $\mathcal{C}^{3,\alpha}(\mathbb{R}^d \times [0, \infty)^M)$ and $\mathcal{C}^{2,\alpha}(\mathbb{R}^d \times [0, \infty)^M)$ for some $\alpha \in (0, 1)$. Moreover, there exists a constant $C_M > 0$ such that for all $x \in \mathbb{R}^d$ and $v = (v_1, \ldots, v_M) \in \mathbb{R}^M_+$,

$$|\sigma^i(x, v_1, \ldots, v_M)| \leq C_M(1 + |v|).$$

2. Functions $(G^{ij})_{1\le i,j\le M}$ and $(H^{ij})_{1\le i,j\le M}$ are respectively $\mathcal{C}^{3,\alpha}(\mathbb{R}^d)$ and $\mathcal{C}^{2,\alpha}(\mathbb{R}^d)$ for some $\alpha \in (0,1)$. Moreover, functions $(C^{ij})_{1\le i,j\le M}$ are integrable in $\mathbb{R}^d$ and have bounded derivatives.
3. Functions r_i have bounded derivatives.

Remark 4.1 Under assumptions $(\mathbf{H})''$, functions $\sigma(i,t,x)$ and $b(i,t,x)$ in (9) are respectively $C_b^{3,\alpha}(\mathbb{R}^d)$ and $C^{2,\alpha}(\mathbb{R}^d)$ for some $\alpha \in (0,1)$, uniformly in $[0,T]$, and with bounds that do not depend on the kernels C^{ij} (cf. Remark 3.3). The uniform in x growth condition in the v variable in $(\mathbf{H})''$ i) is needed in the sequel in order that the coefficients driving the reverse flow (14) be of class $\mathcal{C}^{2,\alpha}(\mathbb{R}^d)$. Notice nevertheless that $\sigma^i(x,v_1,\ldots,v_M)$ might still allow for an unbounded influence of the population densities $(v_1,\ldots,v_M)$ on the diffusion terms.

We will next establish

Theorem 4.2 *Assume that hypothesis* $(\mathbf{H})''$ *hold, and that the initial measures* $(\xi_0^1,\ldots,\xi_0^M)$ *have densities in* $L^1\cap L^\infty$ *and distributional derivatives in* L^∞.

Furthermore, assume that $C^{ij} = c^{ij}\gamma_\varepsilon$ *for* $c^{ij}\ge 0$ *some fixed constant and* $\gamma_\varepsilon = \gamma(x/\varepsilon)\varepsilon^{-d}$ *for some regular function* $\gamma\ge 0$ *satisfying* $\int_{\mathbb{R}^d}\gamma(x)dx = 1$ *and* $\int_{\mathbb{R}^d}|x|\gamma(x)dx<\infty$.

Then, for each $T>0$ *the unique weak function-solution* ξ^ε *to Eq.* (8) *converges in the space* $C([0,T],\mathcal{M}^M)$ *(endowed with the uniform topology) at speed* ε *with respect to the dual Lipschitz norm, to a solution* $u=(u^1,\ldots,u^M)$ *of the non local cross-diffusion system with local competition:*

$$\begin{aligned}\langle u_t^i, f_t^i\rangle = \langle \xi_0^i, f_0^i\rangle + \int_0^t\int \Bigg\{ &\sum_{k,l} a_{kl}^i(\cdot, G^{i1}*u_t^1,\ldots,G^{iM}*u_t^M)\,\partial_{x_kx_l} f_s^i\\ &+\sum_k b_k^i(\cdot, H^{i1}*u_t^1,\ldots,H^{iM}*u_t^M)\,\partial_{x_k} f_s^i\\ &+\left(r_i-\sum_{j=1}^M c^{ij}u_s^j\right) f_s^i + \partial_s f_s^i\Bigg\}(x)\, u_s^i(x)dxds. \end{aligned} \tag{16}$$

Moreover the function u *is the unique function solution of* (16) *such that*

$$\sup_{t\in[0,T]} \|u_t\|_1 + \|u_t\|_\infty + \|\nabla u_t\|_\infty < +\infty. \tag{17}$$

To prove Theorem 4.2, we will extend to a convergence argument some of the techniques previously used in the uniqueness result. The same dual norm will be used, along with some additional estimates and technical results:

Lemma 4.3 *Under the assumptions of Theorem* 4.2*, for each* $t\in[0,T]$ *the functions* $(\xi_t^\varepsilon)^i$, $i=1,\ldots,M$ *have bounded first order derivatives. Moreover, there exists for each* i *a constant* $K_i>0$ *depending on the functions* C^{ij}, $j=1,\ldots,M$ *only through their* L^1 *norms* c^{ij} *(and not on* ε*), such that*

$$\max\{\sup_{t\in[0,T]}\|(\xi_t^\varepsilon)^i\|_\infty, \sup_{t\in[0,T]}\|\nabla(\xi_t^\varepsilon)^i\|_\infty\} < K_i, \quad \forall i = 1, \dots M.$$

This result relies on an enhancement of Lemma 3.11 needing finer properties of stochastic flows established by Kunita (1990).

Lemma 4.4 *Under assumption* $(\mathbf{H})''$ *for each* $i = 1, \dots, M$ *and* $p \geq 2$*, there exist finite constants* $K_{i1}(p) > 0$ *and* $K_{i2}(p) > 0$ *not depending on the kernels* C^{ij} *such that for all* $t \in [0, T]$*,*

$$\sup_{y\in\mathbb{R}^d}\mathbb{E}\left(\sup_{s\in[0,t]}|\nabla_y\eta^i_{s,t}(y)|^p\right) < K_{i1}(p) \text{ and } \sup_{y\in\mathbb{R}^d}\mathbb{E}\left(\sup_{s\in[0,t]}|det\nabla_y\eta^i_{s,t}(y)|^p\right) < K_{i2}(p).$$

Moreover, for each $s < t$ *with* $s, t \in [0, T]$ *the function* $y \mapsto det\nabla_y\eta^i_{s,t}(y)$ *is a.s. differentiable and there exists* $K_{i3}(p) > 0$ *not depending on the kernels* C^{ij} *such that for all* $t \in [0, T]$*,*

$$\sup_{y\in\mathbb{R}^d}\mathbb{E}\left(\sup_{s\in[0,t]}|\nabla_y\left[det\nabla_y\eta^i_{s,t}(y)\right]|^p\right) < K_{i3}(p).$$

Proof of Lemma 4.4 For fixed $i \in \{1, \dots, M\}$ and $t \in [0, T]$ we define coefficients $\beta : [0, t] \times \mathbb{R}^d \to \mathbb{R}^d$ and $A^q : [0, t] \times \mathbb{R}^d \to \mathbb{R}^d$, $q = 1, \dots, d$ with components β_k and A^q_k, $k = 1, \dots, d$ by

$$\beta_k(s, y) := -\hat{b}_k(i, t-s, y), \quad A^q_k(s, y) := \sigma_{kq}(i, t-s, y)$$

(see Lemma 3.11 for the notation) and the process $(Z_s(y); s \in [0, t], y \in \mathbb{R}^d)$ by $Z_s(y) = \eta^i_{t-s,t}(y)$. Then, denoting by $W = (W^1, \dots, W^d)$ the standard $d-$ dimensional Brownian motion $W_s := B^i_{t-s} - B^i_t$, it easily follows from Lemma 3.11 that $Z_s(y)$ satisfies the classic Itô stochastic differential equation

$$Z_s(y) = y + \int_0^s A(r, Z_r(y))dW_r + \int_0^s \beta(r, Z_r(y))dr\,, \tag{18}$$

whereas the associated Jacobian matrix satisfies the linear system:

$$\begin{aligned}\partial_{y_l}Z^k_s(y) = I_d &+ \sum_{p,q=1}^d\int_0^s \partial_{x_p}A^q_k(r, Z_r(y))\partial_{y_l}Z^p_r(y)dW^q_r\\ &+\sum_{p=1}^d\int_0^s \partial_{x_p}\beta_k(r, Z_r(y))\partial_{y_l}Z^p_r(y)dr.\end{aligned} \tag{19}$$

Notice that the (non-homogenous) coefficients of this linear SDE are uniformly bounded (cf. Remark 4.1) independently of kernels C^{ij}. Using the Burkholder-Davis-Gundy inequality, the boundedness of the derivatives of A^q and β and Gronwall's lemma, we deduce that

$$\mathbb{E}\left(\sup_{s\in[0,t]} |\nabla_y Z_s(y)|^p\right) < K_{i1}(p) \tag{20}$$

for some constant $K_{i1}(p)$ which depends on bounds for those derivatives and on $\sup_{t\in[0,T]} \|\xi_t^i\|_{TV}$ (cf. Remark 3.9) but does not depend on $y \in \mathbb{R}^d$. This yields the first asserted estimate.

In order to get the estimates for the determinant and its gradient, we rewrite (18) in Stratonovich form

$$Z_s(y) = y + \int_0^s A(r, Z_r(y)) \circ dW_r + \int_0^s \beta^\circ(r, Z_r(y))dr$$

where $\beta^\circ(r,x) = \beta(r,x) - \frac{1}{2}\sum_{l,q} A_l^q(r,x)\partial_{x_l} A^q(r,x)$. By the proof of Lemma 4.3.1 of Kunita (1990), $det\nabla_y Z_s(y)$ satisfies the linear Stratonovich stochastic differential equation

$$\begin{aligned} &det\nabla_y Z_s(y) = 1 \\ &\quad + \int_0^s det\nabla_y Z_r(y) \sum_{k=1}^d \left[\sum_{q=1}^d \partial_{y_k} A_k^q(r, Z_r(y)) \circ dW_r^q + \partial_{y_k}\beta_k^\circ(r, Z_r(y))dr\right]. \end{aligned} \tag{21}$$

Again, the coefficients of this scalar linear SDE are uniformly bounded independently of the kernels C^{ij}. Using Burkholder-Davis-Gundy inequality in the Itô's form of the previous equation, we deduce using also Gronwall's lemma that

$$\mathbb{E}\left(\sup_{s\in[0,t]} |det\nabla_y Z_s(y)|^p\right) < K_{i2}(p) \tag{22}$$

for some constant $K_{i2}(p)$ depending on bounds on the (up to second order) derivatives of σ^i and (up to first order derivatives) of b, on $\sup_{t\in[0,T]} \|\xi_t^i\|_{TV}$ and on the constant C_M in assumption $(\mathbf{H})''$ i). This yields the second required estimate. Remark 3.3 ensures that the constants $K_{i1}(p)$ and $K_{i2}(p)$ do not depend on the kernels C^{ij} nor on ε.

Finally, under assumptions $(\mathbf{H})''$ we deduce from Eq. (21) and Theorem 3.3.3 of Kunita (1990) (see also Exercise 3.1.5 therein) the a.s. differentiability of the mapping $y \mapsto det\nabla_y \eta_{s,t}^i(y)$, and the fact that its derivative with respect to y_l satisfies

$$\begin{aligned} &\partial_{y_l}[det\nabla_y Z_s(y)] \\ &\quad = \int_0^s \partial_{y_l}[det\nabla_y Z_r(y)] \sum_{k=1}^d \left[\sum_{q=1}^d \partial_{y_k} A_k^q(r, Z_r(y)) \circ dW_r^q + \partial_{y_k}\beta_k^\circ(r, Z_r(y))dr\right] \\ &\qquad + \int_0^s det\nabla_y Z_r(y) \sum_{m,k=1}^d \partial_{y_l} Z_s^m(y) \left[\sum_{q=1}^d \partial^2_{y_m y_k} A_k^q(r, Z_r(y)) \circ dW_r^q \right. \\ &\qquad \left. + \partial_{y_m y_k}\beta_k^\circ(r, Z_r(y))dr\right]. \end{aligned}$$

Note that all coefficients inside the square brackets are uniformly bounded functions (independently of kernels C^{ij}). Writing this equation in Itô's form, we now deduce with the Burkholder-Davis-Gundy inequality that $\phi(s) := \mathbb{E}\left(\sup_{r\in[0,s]} |\nabla_y \left[det \nabla_y Z_r(y)\right]|^p\right)$ satisfies the inequality

$$\phi(s) \le C' \int_0^s \phi(r)dr + C'' \int_0^s \mathbb{E}\left(\sup_{\theta\in[0,r]} |det\nabla_y Z_\theta(y)|^p \sup_{\theta\in[0,r]} |\nabla_y Z_\theta(y)|^p \right) dr.$$

By Cauchy-Schwarz inequality and the estimates (20) and (22) with $2p$ instead of p, the above expectation is seen to be bounded uniformly in $r \in [0, t]$, $y \in \mathbb{R}^d$. We deduce by Gronwall's lemma that

$$\mathbb{E}\left(\sup_{s\in[0,t]} |\nabla_y \left[det\nabla_y Z_s(y)\right]|^p \right) < K_{i3}(p)$$

for some constant $K_{i3}(p)$ as required, and conclude the third asserted estimate. □

Proof of Lemma 4.3 We again consider $M = 2$, $i = 1$ and omit the superscript 1 in the process $X^1_{s,t}(x)$, the inverse flow and its derivative. By Lemma 3.11 we can do the change of variables $X_{0,t}(x) = y$ in the integral with respect to dx inside the expectation in (13). Using the semigroup property of the flow and its inverse stated by Kunita (1984, 1990) together with Fubini's theorem (thanks to Lemma 4.4), we deduce that for a.e. $y \in \mathbb{R}^d$,

$$\xi^1_t(y) = \mathbb{E}\left[\Psi(t, y)\right] \tag{23}$$

where $\Psi(t, y)$ is the random function

$$\Psi(t, y) := \exp\left\{ \int_0^t (r_1(\eta_{r,t}(y)) - C^{11} * \xi^1_r(\eta_{r,t}(y)) - C^{12} * \xi^2_r(\eta_{r,t}(y)))dr \right\}$$
$$\xi^1_0(\eta_{0,t}(y))det\nabla_y\eta_{0,t}(y).$$

Notice that we have used the fact that $det\nabla_y\eta_{0,t}(y) > 0$, which follows from $det\nabla_y\eta_{r,t}(y) \neq 0$ for all $r \in [0, t]$ and $r \mapsto \nabla_y\eta_{r,t}(y)$ being continuous with value I_d at $r = t$. The bound on $\sup_{t\in[0,T]} \|\xi^i_t\|_\infty$ readily follows from the previous identity, the assumptions on ξ^i_0 and the second estimate in Lemma 4.4.

The function $y \mapsto \Psi(t, y)$ is moreover continuously differentiable, by Lemmas 3.11 and 4.4. Since the kernels C^{11} and C^{12} have bounded derivatives we deduce that, a.s.

$$\nabla\Psi(t, y) = \exp\left\{ \int_0^t r_1(\eta_{r,t}(y)) - C^{11} * \xi^1_r(\eta_{r,t}(y)) - C^{12} * \xi^2_r(\eta_{r,t}(y))dr \right\}$$
$$\times \left[\xi^1_0(\eta_{0,t}(y))det\nabla\eta_{0,t}(y) \int_0^t \nabla^*\eta_{r,t}(y) \right.$$

$$\times \left[\nabla r_1 - (\nabla C^{11}) * \xi_r^1 - (\nabla C^{12}) * \xi_r^2\right](\eta_{r,t}(y))dr$$
$$+\nabla^* \eta_{0,t}(y)\nabla\left[\xi_0^1\right](\eta_{0,t}(y))det\nabla\eta_{0,t}(y)$$
$$\left. +\xi_0^1(\eta_{0,t}(y))\nabla\left[det\nabla\eta_{0,t}(y)\right]\right] \tag{24}$$

for all $y \in \mathbb{R}^d$. From Lemma 4.4, thanks to Cauchy-Schwarz inequality we get that

$$\mathbb{E}\left(|det\nabla\eta_{0,t}(y)|\int_0^t |\nabla\eta_{r,t}(y)|dr + |\nabla\eta_{0,t}(y)|\,|det\nabla\eta_{0,t}(y)| + |\nabla\left[det\nabla\eta_{0,t}(y)\right]|\right) < \infty.$$

Thus, we can take derivatives inside the expectation (23) and deduce the existence of

$$\nabla\xi_t^1(y) = \mathbb{E}\left[\nabla\Psi(t,y)\right],$$

and moreover that $\sup_{t\in[0,T]}\|\nabla\xi_t^1\|_\infty < \infty$. Similarly, $\sup_{t\in[0,T]}\|\nabla\xi_t^2\|_\infty < \infty$. We can now rewrite (24) as

$$\nabla\Psi(t,y) = \exp\left\{\int_0^t r_1(\eta_{r,t}(y)) - C^{11} * \xi_r^1(\eta_{r,t}(y)) - C^{12} * \xi_r^2(\eta_{r,t}(y))dr\right\}$$
$$\times \left[\xi_0^1(\eta_{0,t}(y))det\nabla\eta_{0,t}(y)\int_0^t \nabla^*\eta_{r,t}(y)\right.$$
$$\times\left[\nabla r_1 - C^{11} * \nabla\xi_r^1 - C^{12} * \nabla\xi_r^2\right](\eta_{r,t}(y))dr$$
$$+\nabla^*\eta_{0,t}(y)\nabla\left[\xi_0^1\right](\eta_{0,t}(y))det\nabla\eta_{0,t}(y)$$
$$\left.+\xi_0^1(\eta_{0,t}(y))\nabla\left[det\nabla\eta_{0,t}(y)\right]\right]. \tag{25}$$

Since $\|C^{1j}\|_1 = c^{1j}$, we have $\|C^{1j} * \nabla\xi_s^j\|_\infty \le c^{1j}\|\nabla\xi_s^j\|_\infty$ for all $s \in [0,T]$. Taking expectation in (25) and using the estimates in Lemma 4.4, we deduce that for all $t \in [0,T]$,

$$\|\nabla\xi_t^1\|_\infty \le C''\int_0^t (\|\nabla\xi_r^1\|_\infty + \|\nabla\xi_r^2\|_\infty)dr + C'''$$

for constants $C''', C'' > 0$ depending on the functions C^{1j} only through their L^1 norms c^{1j} (in particular not depending on ε). Summing the later estimate with the analogous one for $\|\nabla\xi_t^2\|_\infty$, we conclude thanks to Gronwall's lemma. □

We are now ready for the

Proof of Theorem 4.2 Again, we write the proof in the case $M = 2$. Let $\varepsilon > \bar{\varepsilon} > 0$. To lighten notation, we denote simply by $\xi = (\xi^1, \xi^2)$ and $\bar{\xi} = (\bar{\xi}^1, \bar{\xi}^2)$ two solutions of system (8) in $[0, T]$ respectively with $C^{ij} = c^{ij}\varphi_\varepsilon$ and $\bar{C}^{ij} := c^{ij}\varphi_{\bar{\varepsilon}}$. Proceeding as in the proof of Proposition 3.4, we deduce that for all function φ with $\|\varphi\|_{\mathcal{LB}} \leq 1$,

$$\begin{aligned}
\langle \xi^1_t - \bar{\xi}^1_t, \varphi\rangle^2 &\leq \langle \xi^1_0, (P^1_{0,t} - \bar{P}^1_{0,t})\varphi\rangle^2 + C\int_0^t \left\{ \left[\int (P^1_{s,t} - \bar{P}^1_{s,t})\varphi(x)\xi^1_s(x)dx\right]^2 \right.\\
&+ \left[\int \bar{P}^1_{s,t}\varphi(x)(\xi^1_s(x) - \bar{\xi}^1_s(x))dx\right]^2 + \left[\int C^{11} * (\xi^1_s - \bar{\xi}^1_s)(x) P^1_{s,t}\varphi(x)\xi^1_s(x)dx\right]^2\\
&+ \left[\int C^{11} * \bar{\xi}^1_s(x)(P^1_{s,t}\varphi(x) - \bar{P}^1_{s,t}\varphi(x))\xi^1_s(x)dx\right]^2\\
&+ \left[\int C^{11} * \bar{\xi}^1_s(x)\bar{P}^1_{s,t}\varphi(x)(\xi^1_s(x) - \bar{\xi}^1_s(x))dx\right]^2\\
&+ \left[\int [C^{11} - \bar{C}^{11}] * \bar{\xi}^1_s(x)\bar{P}^1_{s,t}\varphi(x)\bar{\xi}^1_s(x)dx\right]^2\\
&+ \left[\int C^{12} * (\xi^2_s - \bar{\xi}^2_s)(x) P^1_{s,t}\varphi(x)\xi^1_s(x)dx\right]^2\\
&+ \left[\int C^{12} * \bar{\xi}^2_s(x)(P^1_{s,t}\varphi(x) - \bar{P}^1_{s,t}\varphi(x))\xi^1_s(x)dx\right]^2\\
&+ \left[\int C^{12} * \bar{\xi}^2_s(x)\bar{P}^1_{s,t}\varphi(x)(\xi^1_s(x) - \bar{\xi}^1_s(x))dx\right]^2\\
&+ \left.\left[\int [C^{12} - \bar{C}^{12}] * \bar{\xi}^2_s(x)\bar{P}^1_{s,t}\varphi(x)\bar{\xi}^1_s(x)dx\right]^2 \right\} ds. \qquad (26)
\end{aligned}$$

Thanks to Lemma 4.3, $P^1_{s,t}\varphi\xi^1_s$ is a bounded Lipschitz function with Lipschitz norm bounded independently of ε, $\bar{\varepsilon}$ and $s, t \in [0, T]$. We thus can rewrite and bound the first term in the third line of (26) as follows:

$$\left[\int (\xi^1_s - \bar{\xi}^1_s)(y) C^{11} * (P^1_{s,t}\varphi\xi^1_s)(y)\, dy\right]^2 \leq C\|\xi^1_s - \bar{\xi}^1_s\|^2_{\mathcal{LB}^*}$$

for some $C > 0$ not depending on $\varepsilon, \bar{\varepsilon}$. The second term in the third line is controlled by

$$\begin{aligned}
&C\|\bar{\xi}^1_s\|^2_\infty \|\xi^1_s\|^2_{TV} \sup_{x\in\mathbb{R}^d} \Big| P^1_{s,t}\varphi(x)\\
&\quad - \bar{P}^1_{s,t}\varphi(x)\Big|^2 \leq C\|\bar{\xi}^1_s\|^2_\infty \|\xi^1_s\|^2_{TV} \int_s^t \|\xi^1_r - \bar{\xi}^1_r\|^2_{\mathcal{LB}^*} + \|\xi^2_r - \bar{\xi}^2_r\|^2_{\mathcal{LB}^*} dr
\end{aligned}$$

thanks to Lemma 3.6 b). The term in the fourth line is easily controlled by $C\|\xi_s^1 - \bar{\xi}_s^1\|^2_{\mathcal{LB}^*}$. Using the fact that, by Lemma 4.3, $\bar{\xi}_s^1$ has derivatives uniformly bounded independently of $\bar{\varepsilon} > 0$ and $s \in [0, T]$, we deduce by the assumption on γ that

$$\sup_{x\in\mathbb{R}^d} |[C^{11} - \bar{C}^{11}] * \bar{\xi}_s^1(x)|^2 \le C|\varepsilon - \bar{\varepsilon}|^2.$$

A similar upper bound then follows for the term in the fifth line of (26). The last three lines can be bounded in a similar way, and the first line on the right hand side is bounded in terms of dual Lipschitz distances by similar arguments as in Proposition 3.4. Proceeding in a similar way as therein, we now obtain the estimate

$$\langle \xi_t^1 - \bar{\xi}_t^1, \varphi\rangle^2 \le C\int_0^t \sum_{i=1,2} \|\xi_s^i - \bar{\xi}_s^i\|^2_{\mathcal{LB}^*} ds + C|\varepsilon - \bar{\varepsilon}|^2,$$

where the constants do not depend on $t \in [0, T]$ nor on ε or $\bar{\varepsilon}$. Taking suitable suprema, the latter estimate can thus be strengthened to

$$\sup_{r\in[0,t]} \|\xi_r^1 - \bar{\xi}_r^1\|^2_{\mathcal{LB}^*} \le C\int_0^t \sum_{i=1,2} \sup_{r\in[0,s]} \|\xi_r^i - \bar{\xi}_r^i\|^2_{\mathcal{LB}^*} ds + C|\varepsilon - \bar{\varepsilon}|^2,$$

which when summed with the corresponding estimate for $i = 2$ yields

$$\sum_{i=1,2} \sup_{r\in[0,T]} \|\xi_r^i - \bar{\xi}_r^i\|^2_{\mathcal{LB}^*} \le C|\varepsilon - \bar{\varepsilon}|^2, \tag{27}$$

after applying Gronwall's lemma. Therefore, as ε goes to 0, the sequence $(\xi^\varepsilon)_{\varepsilon>0}$ is Cauchy in the Polish space $C([0, T], \mathcal{M}^M)$ and thus converges to some element in that space. Dunford-Pettis criterion for weak compactness in L^1, together with the uniform bounds both in L^1 and L^∞ for $(\xi_t^\varepsilon)_{\varepsilon>0}$, imply that the components of the previous limit have densities for each $t \in [0, T]$, which we denote by $u_t^i(x)$, and which satisfy the same L^1 and L^∞ bounds.

Weak L^1-convergence is however not enough to identify u as a solution of (16) and some regularity of the limit will be needed to do so. We denote by $\hat{P}^i_{s,t}(x, dy)$ the semigroup associated with the SDE with coefficients defined in terms of the measures $(u_t^i(x)dx)_{t\in[0,T]}$ as previously. For φ such that $\|\varphi\|_{\mathcal{LB}} \le 1$, we set

$$\begin{aligned}\Psi^1(t, \varphi) &:= \langle u_t^1, \varphi\rangle \\ &\quad -\langle \xi_0^1, \hat{P}^1_{0,t}\varphi\rangle - \int_0^t \int \big(r_1(x) - c^{11}u_s^1(x) - c^{12}u_s^2(x)\big)\hat{P}^1_{s,t}\varphi(x)u_s^1(x)dxds.\end{aligned}$$

Since $\xi = \xi^{\varepsilon}$ satisfies

$$\langle \xi_t^1, \varphi\rangle - \langle \xi_0^1, P_{0,t}^1\varphi\rangle - \int_0^t \int \left(r_1(x) - C^{11} * \xi_s^1(x) - C^{12} * \xi_s^2(x)\right) P_{s,t}^1\varphi(x)\xi_s^1(x)dxds = 0,$$

proceeding in a similar way as done to obtain the estimate (26), we deduce that

$$|\Psi^1(t,\varphi)|^2 \leq \sum_{i=1,2} \sup_{r\in[0,t]} \|\xi_r^i - u_r^i\|_{\mathcal{LB}^*}^2 + \int_0^t \left[\int [C^{1i} * u_s^i(x) - c^{1i}u_s^i(x)]\hat{P}_{s,t}^1\varphi(x)u_s^1(x)dx\right]^2 ds \tag{28}$$

(the last term corresponding to the sum of the fifth and last lines in (26) when $\bar{\varepsilon} = 0$). Now, by Lemma 4.3, there exists a constant $K > 0$ (independent of $\varepsilon > 0$ ad $s \in [0,T]$) such that for any $\varepsilon > 0$ one has $|\langle(\xi_s^{\varepsilon})^i, \partial_{x_l}\varphi\rangle| \leq K\|\varphi\|_1$ for any $\mathcal{C}^{\infty}$ compactly supported function φ. By letting $\varepsilon \to 0$, the same bound is satisfied by u_s^i. By standard results on Sobolev spaces (see e.g. Proposition IX.3 of Brezis 1983) we get that u_s^i has distributional derivatives in L^{∞} and that u_s^i is Lipschitz continuous with Lipschitz constant less than or equal to K. Since $C^{1i} * u_s^i(x) - c^{1i}u_s^i(x) = c^{1i}\int \gamma(z)[u_s^i(x + \varepsilon z) - u_s^i(x)]dz$ and $\int \gamma(z)|z|dz < \infty$, we deduce that $\|C^{1i} * u_s^i - c^{1i}u_s^i\|_{\infty} \leq C\varepsilon$, which combined with the bound

$$\sum_{i=1,2} \sup_{r\in[0,t]} \|\xi_r^i - u_r^i\|_{\mathcal{LB}^*}^2 \leq C\varepsilon^2,$$

following from (27), yields $|\Psi(t,\varphi)| \leq C\varepsilon$ for all $\varepsilon > 0$. That is, u solves (16).

Let us finally prove the uniqueness of the solution u. Recall that $\hat{P}_{s,t}^i(x,dy)$ denotes the associated diffusion semigroup. Consider a second function solution v in $C([0,T],\mathcal{M}^M)$ satisfying (17) and with associated semigroups denoted $\check{P}_{s,t}^i(x,dy)$. Then,

$$\begin{aligned}
&\langle u_t^1 - v_t^1, \varphi\rangle^2 \\
&\quad\leq \langle u_0^1, (\hat{P}_{0,t}^1 - \check{P}_{0,t}^1)\varphi\rangle^2 \\
&\qquad + C\int_0^t \left\{ \left[\int (\hat{P}_{s,t}^1 - \check{P}_{s,t}^1)\varphi(x)u_s^1(x)dx\right]^2 + \left[\int \check{P}_{s,t}^1\varphi(x)(u_s^1(x) - v_s^1(x))dx\right]^2 \right.\\
&\qquad + \left[\int c^{11}(u_s^1 - v_s^1)(x)\hat{P}_{s,t}^1\varphi(x)u_s^1(x)dx\right]^2 \\
&\qquad + \left[\int c^{11}v_s^1(x)(\hat{P}_{s,t}^1\varphi(x) - \check{P}_{s,t}^1\varphi(x))u_s^1(x)dx\right]^2
\end{aligned}$$

$$
\begin{aligned}
&+\left[\int c^{11} v_s^1(x)\check{P}^1_{s,t}\varphi(x)(u_s^1(x)-v_s^1(x))dx\right]^2\\
&+\left[\int c^{12}(u_s^2-v_s^2)(x)\hat{P}^1_{s,t}\varphi(x)u_s^1(x)dx\right]^2\\
&+\left[\int c^{12}v_s^2(x)(\hat{P}^1_{s,t}\varphi(x)-\check{P}^1_{s,t}\varphi(x))u_s^1(x)dx\right]^2\\
&+\left[\int c^{12}v_s^2(x)\check{P}^1_{s,t}\varphi(x)(u_s^1(x)-v_s^1(x))dx\right]^2\Bigg\}ds. \qquad (29)
\end{aligned}
$$

The functions $\hat{P}^1_{s,t}\varphi u_s^1$ and $\check{P}^1_{s,t}\varphi v_s^1$ having Lipschitz norm bounded independently of $s,t\in[0,T]$, the first term in the third line and the term in the forth line above are bounded by $C\|u_s^1-v_s^1\|^2_{\mathcal{LB}^*}$. The second term in the third line is bounded by

$$
\begin{aligned}
&C\|v_s^1\|^2_\infty\|u_s^1\|_1^2\sup_{x\in\mathbb{R}^d}\Big|\hat{P}^1_{s,t}\varphi(x)\\
&\quad-\check{P}^1_{s,t}\varphi(x)\Big|^2 \le C\|v_s^1\|^2_\infty\|u_s^1\|_1^2\int_s^t \|u_r^1-v_r^1\|^2_{\mathcal{LB}^*}+\|u_r^2-v_r^2\|^2_{\mathcal{LB}^*}dr
\end{aligned}
$$

by Lemma 3.6 b). The last threes lines are similarly dealt with and we can easily conclude as in Proposition 3.4. □

5 Concluding remarks

We have developed models for dispersive and competitive multi species population dynamics permitting nonlocal nonlinearity in the diffusive behavior of individuals. Depending on the value of the spatial competition range, the continuum (macro) limits of the individual (micro) dynamics turned out to be described by deterministic solutions of nonlocal cross-diffusion systems with nonlocal or local competition terms. These systems generalize usual diffusion-reaction systems with nonlocal or local spatial nonlinearity in the diffusive coefficients, and nonlocal or local nonlinearity in the reaction terms. These limiting objects can now be used as approximate objects for numerical simulation of spatial and ecological dynamics, when the individual behaviors depend on the non homogeneous spatial densities of the different species. Of course, estimators of the relevant parameters of the phenomena under study have to be obtained first.

In the future it may also be worthwhile to elucidate the situation where the spatial interaction range would be very small. This could thus justify by an individual-based approach the cross-diffusion models with local spatial interaction and local competition extensively studied by the scientific community.

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References

Arnold A, Desvillettes L, Prévost C (2012) Existence of nontrivial steady states for populations structured with respect to space and a continuous trait. Commun Pure Appl Anal 11(1):83–96

Berestycki H, Nadin G, Perthame B, Ryzhik L (2009) The non-local Fisher-KPP equation: travelling waves and steady states. Nonlinearity 22(12):2813–2844

Bouin E, Calvez V, Meunier N, Mirrahimi S, Perthame B, Raoul G, Voituriez R (2012) Invasion fronts with variable motility: phenotype selection, spatial sorting and wave acceleration. C R Math Acad Sci Paris 350(15–16):761–766

Brezis H (1983) Analyse fonctionnelle. In: Collection Mathématiques Appliquées pour la Maîtrise. [Collection of Applied Mathematics for the Master's Degree], Masson, Paris. Théorie et applications. [Theory and applications]

Champagnat N, Méléard S (2007) Invasion and adaptive evolution for individual-based spatially structured populations. J Math Biol 55(2):147–188

Chen L, Jüngel A (2004) Analysis of a multidimensional parabolic population model with strong cross-diffusion. SIAM J Math Anal 36(1):301–322 (electronic)

Chen L, Jüngel A (2006) Analysis of a parabolic cross-diffusion population model without self-diffusion. J Differ Equ 224(1):39–59

Coville J, Dupaigne L (2005) Propagation speed of travelling fronts in non local reaction-diffusion equations. Nonlinear Anal 60(5):797–819

Dawson DA (1993) Measure-valued Markov processes. In: École d'Été de Probabilités de Saint-Flour XXI–1991, vol 1541. Lecture notes in mathematics. Springer, Berlin, pp 1–260

Desvillettes L, Lepoutre T, Moussa A (2013) Entropy, duality and cross diffusion. http://arxiv.org/abs/1302.1028

Fournier N, Méléard S (2004) A microscopic probabilistic description of a locally regulated population and macroscopic approximations. Ann Appl Probab 14(4):1880–1919

Genieys S, Volpert V, Auger P (2006) Pattern and waves for a model in population dynamics with nonlocal consumption of resources. Math Model Nat Phenom 1(1):65–82

Karatzas I, Shreve SE (1991) Brownian motion and stochastic calculus. In: Graduate texts in mathematics, 2nd edn, vol 113. Springer, New York

Keller E, Segel L (1970) Initiation of slime mold aggregation viewed as an instability. J Theor Biol 26(3):399–415

Kunita H (1984) Stochastic differential equations and stochastic flows of diffeomorphisms. In: École d'été de probabilités de Saint-Flour, XII–1982. Lecture notes in mathematics, vol 1097. Springer, Berlin, pp 143–303

Kunita H (1990) Stochastic flows and stochastic differential equations. In: Cambridge studies in advanced mathematics, vol 24. Cambridge University Press, Cambridge

Lepoutre T, Pierre M, Rolland G (2012) Global well-posedness of a conservative relaxed cross diffusion system. SIAM J Math Anal 44(3):1674–1693

Lou Y, Martínez S, Ni W-M (2000) On 3×3 Lotka-Volterra competition systems with cross-diffusion. Discrete Contin Dyn Syst 6(1):175–190

Mimura M, Kawasaki K (1980) Spatial segregation in competitive interaction-diffusion equations. J Math Biol 9(1):49–64

Mimura M, Murray JD (1978) On a diffusive prey-predator model which exhibits patchiness. J Theor Biol 75(3):249–262

Mimura M, Yamaguti M (1982) Pattern formation in interacting and diffusing systems in population biology. Adv Biophys 15:19–65

Nisbet RM, Gurney W (1975a) A note on non-linear population transport. J Theor Biol 56(1):441–457
Nisbet RM, Gurney W (1975b) The regulation of inhomogeneous populations. J Theor Biol 52:249–251
Shigesada N, Kawasaki K, Teramoto E (1979) Spatial segregation of interacting species. J Theor Biol 79(1):83–99