# MEASURE SOLUTIONS FOR SOME MODELS IN POPULATION DYNAMICS

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ABSTRACT. We give a direct proof of well-posedness of solutions to general selection-mutation and structured population models with measures as initial data. This is motivated by the fact that some stationary states of these models are measures and not  $L^1$  functions, so the measures are a more natural space to study their dynamics. Our techniques are based on distances between measures appearing in optimal transport and common arguments involving Picard iterations. These tools provide a simplification of previous approaches and are applicable or adaptable to a wide variety of models in population dynamics.

## 1. INTRODUCTION

Selection-mutation equations are models for structured populations with respect to continuous phenotypical evolutionary traits. They are usually written as equations for densities on the parameter space of phenotypes [3, 5, 19, 6], that is, they are usually formulated in  $L^1$  spaces. However, for some of these models a more natural space to study the time evolution is the space of positive measures, since it has been proven in some cases [5, 13] that for a small mutation rate the steady states tend to concentrate in a Dirac mass at the evolutionarily stable strategy value. More generally, the need for a theory of well-posedness in measures for structured population models was mentioned in [15, 14, 28].

Some efforts in this direction have been directed at particular models in population dynamics: pure selection models for phenotypic traits in the space of measures were recently studied in [1, 11], while in [4] a particular case of a selection-mutation equation for a genetic trait in the space of measures is analyzed. More recently in [10] the author shows well-posedness and studies asymptotic behavior of a selection-mutation equation.

Our aim here is to give a simple and general proof of well-posedness in the space of measures for a class of models that will include a wide range of selection-mutation models as well as many classical nonlinear structured population models [3, 14, 15, 22, 28, 27]. The basic model we consider is an

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abstract Cauchy problem of the form

$$\partial_t u + \nabla \cdot (F(x)u) = N(t, u), \tag{1a}$$

$$u(0,x) = u_0(x)$$
  $(x \in \mathbb{R}^d).$  (1b)

where u = u(t, x) is the unknown, which depends on  $t \ge 0$  and  $x \in \mathbb{R}^d$ (in any dimension  $d \ge 1$ ). Any differential terms in the equation should be included in the term  $\nabla \cdot (F(x)u)$  (e.g., growth or aging terms), and the term N(t, u) may include nonlinear birth and death rates and selection-mutation interactions. Several examples in population dynamics are given in Section 3, where it is also shown how the abstract result may be applied to equations whose domain is not the whole space  $\mathbb{R}^d$ .

Our proof of well-posedness in the space of measures to (1) will be based on techniques stemming from mass transportation and semigroup theory. Similar ideas were already used for studying the mean-field limit of kinetic equations such as the classical Vlasov equation [16] and more recently in swarming models [8]. The main advantage of our approach is its simplicity, coming from the use of techniques already well developed in other fields, and its flexibility, which allows it to be adapted to a wide range of models in population dynamics.

The well-posedness of measure solutions to some equations of the form (1) has recently been analysed by different although related techniques in [18, 17]. selection-mutation models were not included in their formulation but Sharpe-Lotka-McKendrick-type models (age-structured models) in which the boundary condition is introduced as a measure-valued right-hand side of the equation are treated, see subsection 3.3 for related results.

A nonlinear semigroup approach using the splitting method for the transport  $\nabla \cdot (F(x)u)$  and the right-hand side N(t, u) terms was introduced in the more recent paper [9] to treat equations of the form (1). Here, we give a direct and simpler proof based on Picard iterations in the right metric space to conclude existence, uniqueness, and continuous dependence without resorting to the splitting method or nonlinear semigroup techniques.

The organization of the paper is as follows: in Section 2 we show that the abstract Cauchy problem (1) is well posed for measures as initial data in the so-called bounded Lipschitz distance under reasonable Lipschitz conditions on F and N similar to the ones needed in [9]. Then, Section 3 is devoted to the application of these results to more explicit examples, mainly some non-linear selection-mutation models in subsections 3.1 and 3.2 where F = 0, but also some mixed nonlinear structured population/selection-mutation models in subsection 3.4 where  $F \neq 0$ . These applications highlight the wide applicability of the abstract theorem in Section 2 for this type of models, setting a possible functional framework for stability and asymptotic convergence towards measure solutions [1, 5].

## 2. Well-posedness theory

2.1. The bounded Lipschitz norm. Let us start with a quick summary of the definition and properties of the bounded Lipschitz norm, also called flat metric [23, 25]. We denote by  $\mathcal{M}(\mathbb{R}^d)$  the set of Radon measures in  $\mathbb{R}^d$ ,

and consider the space of Lipschitz functions  $W^{1,\infty}(\mathbb{R}^d)$  endowed with the norm  $\|\psi\|_{1,\infty} := \|\psi\|_{\infty} + \operatorname{Lip}(\psi)$ , with  $\operatorname{Lip}(\psi)$  the Lipschitz constant of  $\psi$ .

**Definition 2.1.** Given a Radon measure  $\mu \in \mathcal{M}(\mathbb{R}^d)$  we define its *bounded* Lipschitz norm  $\|\mu\|_{\mathcal{M}(\mathbb{R}^d)}, \|\mu\|$  when there is no ambiguity, by

$$\|\mu\| := \sup_{\psi \in \mathcal{L}} \left| \int_{\mathbb{R}^d} \psi \, d\mu \right|,$$

where  $\mathcal{L}$  is the set of bounded functions  $\psi : \mathbb{R}^d \to \mathbb{R}$  with  $\operatorname{Lip}(\psi) \leq 1$ , i.e.,  $\mathcal{L} := \{ \psi \in W^{1,\infty}(\mathbb{R}^d) \mid \|\psi\|_{1,\infty} \leq 1 \}.$ 

One sees from the definition that this is just the dual norm of  $W^{1,\infty}(\mathbb{R}^d)$ , and that by duality for any  $\psi \in W^{1,\infty}(\mathbb{R}^d)$ ,

$$\int_{\mathbb{R}^d} \psi \, d\mu \le \|\psi\|_{1,\infty} \|\mu\|$$

We remark that on positive measures this can also be defined as a distance of Kantorovich-Rubinstein, or Wasserstein, type: when  $\mu$ ,  $\nu$  are positive measures it holds that

$$\|\mu - \nu\| = \inf_{\sigma \in \Sigma} \int_{\mathbb{R}^d \times \mathbb{R}^d} \min\{|x - y|, 1\} \, d\sigma(x, y) \,,$$

where  $\Sigma$  is the set of *transference plans* between  $\mu$  and  $\nu$ , that is, positive Borel measures on  $\mathbb{R}^d \times \mathbb{R}^d$  with marginals  $\mu$  and  $\nu$  [25].

We will need to use the following simple result on this distance:

**Lemma 2.2.** If  $b \in W^{1,\infty}(\mathbb{R}^d)$  and  $\mu \in \mathcal{M}(\mathbb{R}^d)$ , then  $b\mu \in \mathcal{M}(\mathbb{R}^d)$  and  $\|b\mu\| \leq \|b\|_{1,\infty} \|\mu\|.$ 

*Proof.* It is clear that  $b\mu \in \mathcal{M}(\mathbb{R}^d)$ , since b is a bounded continuous function. We integrate against  $\psi \in W^{1,\infty}$  with  $\|\psi\|_{1,\infty} \leq 1$  to find

$$\left| \int_{\mathbb{R}^d} b\psi \, d\mu \right| \le \|b\psi\|_{1,\infty} \|\mu\| \tag{2}$$

On the other hand, we have

$$\begin{aligned} \|b\psi\|_{\infty} &\leq \|b\|_{\infty} \|\psi\|_{\infty}, \\ \operatorname{Lip}(b\psi) &\leq \operatorname{Lip}(b) \|\psi\|_{\infty} + \|b\|_{\infty} \operatorname{Lip}(\psi), \end{aligned}$$

 $\mathbf{SO}$ 

$$\begin{aligned} \|b\psi\|_{1,\infty} &= \|b\psi\|_{\infty} + \operatorname{Lip}(b\psi) \leq \|b\|_{\infty} \big(\|\psi\|_{\infty} + \operatorname{Lip}(\psi)\big) + \operatorname{Lip}(b)\|\psi\|_{\infty} \\ &\leq \|b\|_{\infty} + \operatorname{Lip}(b) = \|b\|_{1,\infty}. \end{aligned}$$

Plugging this into eq. (2) finishes the proof.

In the rest of this paper, we will work with measure solutions to some evolution partial differential equations and therefore, we will work with the space of bounded continuous curves on the set of measures  $BC(I; \mathcal{M}(\mathbb{R}^d))$ depending on  $t \in I$  denoting the time variable, with I = [0, T] for some T > 0 or  $I = [0, \infty)$ . The continuity of the curves of measures  $t \mapsto \mu(t)$  is always understood to be with respect to the bounded Lipschitz norm. We warn the reader that elements in  $BC(I; \mathcal{M}(\mathbb{R}^d))$  will often be denoted as if

they were absolutely continuous densities with respect to Lebesgue with the form  $d\mu(t) = u(t, x) dx$  for the sake of simplicity.

The standard total variation norm for measures will be denoted by  $|| ||_{TV}$ . We remark the natural necessity of the bounded Lipschitz distance (or similar distances between measures) to work with transport evolution equations, as opposed to the total variation norm. In fact, take any injective continuous path  $x : [0,T] \longrightarrow \mathbb{R}^d$  and take the curve of measures  $\mu$  defined by  $t \longrightarrow \delta_{x(t)}$ . It is easy to check that  $\mu$  belongs to  $BC([0,T]; \mathcal{M}(\mathbb{R}^d))$  while  $||\mu(t) - \mu(s)||_{TV} = 2$  for all  $0 \le t < s \le T$ .

Although all models in population dynamics study the evolution of positive measures (number density of individuals with respect to some variables), let us mention that we need to use the bounded Lipschitz norm and not other optimal transport distances since the total mass (total variation) of measure solutions will typically not be preserved in time. We will denote by  $B_{BL}(R)$ , resp.  $B_{TV}(R)$ , the ball of radius R centered at 0 in the Bounded Lipschitz norm and in the total variation norm resp. Finally, let us point out that balls  $B_{TV}(R)$  in  $\mathcal{M}(\mathbb{R}^d)$  with respect to the total variation norm are closed in the bounded Lipschitz norm by simple weak convergence arguments.

2.2. An abstract result. We consider the abstract evolution equation for measures given in (1), which we recall here:

$$\begin{aligned} \partial_t u + \nabla_x \cdot (F(x)u) &= N(t, u), \\ u(0, x) &= u_0(x) \qquad (x \in \mathbb{R}^d). \end{aligned}$$

Here u = u(t, x) is the unknown, which depends on  $t \ge 0$  and  $x \in \mathbb{R}^d$ , under the following hypotheses on F, N and  $u_0$ :

- (H1)  $u_0 \in \mathcal{M}(\mathbb{R}^d)$ .
- (H2)  $F : \mathbb{R}^d \to \mathbb{R}^d$  is a bounded Lipschitz map.
- (H3)  $N: [0, +\infty) \times \mathcal{M}(\mathbb{R}^d) \to \mathcal{M}(\mathbb{R}^d)$  is a continuous function both in t and u.
- (H4) N is locally Lipschitz in its second variable, i.e., for every bounded set  $K \subseteq [0, +\infty) \times \mathcal{M}(\mathbb{R}^d)$  there exists  $L_N = L_N(K) > 0$  such that

$$||N(t, u_1) - N(t, u_2)|| \le L_N ||u_1 - u_2|| \quad \forall \ (t, u_1), (t, u_2) \in K.$$

(H5) N carries bounded sets in the total variation norm to bounded sets in the total variation norm: for each R > 0 there exists  $C_R \ge 0$ such that  $||N(t, u)||_{\text{TV}} \le C_R$  for all  $t \ge 0$  and  $u \in \mathcal{M}(\mathbb{R}^d)$  with  $||u||_{TV} \le R$ .

**Definition 2.3.** Assume Hypotheses (H1)-(H5), and take  $T \in (0, +\infty]$ . We say  $u \in BC([0,T); \mathcal{M}(\mathbb{R}^d))$  is a solution of equation (1) on [0,T) with initial condition  $u_0$  when, for every  $\phi \in \mathcal{C}_0^{\infty}([0,T) \times \mathbb{R}^d)$ ,

$$-\int_0^T \int_{\mathbb{R}^d} \partial_t \phi(t,x) u(t,x) \, dx - \int_{\mathbb{R}^d} \phi(0,x) u_0(x) \, dx$$
$$-\int_0^T \int_{\mathbb{R}^d} F(x) \nabla \phi(t,x) u(t,x) \, dx \, dt = \int_0^T \int_{\mathbb{R}^d} \phi(t,x) N(t,u)(x) \, dx \, dt.$$

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**Theorem 2.4** (Well-posedness of the abstract equation). Assume Hypotheses (H1)-(H5). There exists a maximal time T > 0 such that there is a unique solution  $u \in B([0,T); \mathcal{M}(\mathbb{R}^d))$  of equation (1). In addition:

- (i) Either  $T = +\infty$  or  $\lim_{t \to T} ||u(t)||_{TV} = +\infty$ .
- (ii) This solution depends continuously on the initial condition u<sup>0</sup> in the bounded Lipschitz norm: take two solutions u<sub>1</sub>, u<sub>2</sub> of equation (1) on [0,T) with initial conditions u<sub>1</sub><sup>0</sup>, u<sub>2</sub><sup>0</sup>, respectively. Assume also that

$$||u_1(t)||, ||u_2(t)|| \le R \qquad (t \in [0, T)),$$

and take  $L_N$  to be the Lipschitz constant of N with respect to the second variable on the set  $[0,T) \times B_{BL}(R) \subseteq [0,+\infty) \times \mathcal{M}(\mathbb{R}^d)$ . Then,

$$||u_1(t) - u_2(t)|| \le e^{(L_F + L_N)t} ||u_1^0 - u_2^0|| \qquad (t \in [0, T)).$$

Remark 2.5. If there is no drift term present in equation (1) (this is, F = 0) and  $\Omega \subseteq \mathbb{R}^d$  is an open set, then the result holds if one changes  $\mathcal{M}(\mathbb{R}^d)$ by  $\mathcal{M}(\Omega)$ . The modifications needed in the proof below are straightforward and we omit them.

Proof of Theorem 2.4. Define  $X_t : \mathbb{R}^d \to \mathbb{R}^d$  as the flow at time t of the characteristic equations

$$\frac{dX}{dt} = F(X).$$

By standard arguments in the theory of ordinary differential equations we have that  $L_{X_t}$ , the Lipschitz constant of the flow  $X_t$  at time t, satisfies

$$L_{X_t} \le e^{L_F t} \qquad (t \ge 0),$$

where  $L_F$  is the Lipschitz constant of F.

We will prove existence by a fixed point argument in the set

$$\mathcal{M}_T := \{ u \in BC([0,T]; B_{TV}(R)) \mid u(0) = u^0 \},\$$

of radius  $R := 2 \|u_0\|_{TV}$ . We choose

$$T := \min\{\|u^0\|_{TV}/C_R, 1/L_F, 1/(3L_N)\},\tag{3}$$

where  $C_R$  and  $L_N$  are given in Hypotheses (H1)-(H5) with  $K = [0, T) \times B_{BL}(R)$ . We endow  $\mathcal{M}_T$  with the standard norm

$$|||u||| := \sup_{t \in [0,T]} ||u(t)||$$
.

As noticed before  $\mathcal{M}_T$  is a closed subset of the space  $BC([0, T]; B_{TV}(R))$ . Hence  $\mathcal{M}_T$  is complete and we may apply the Banach fixed point theorem in it. Define the map  $\Gamma : \mathcal{M}_T \to \mathcal{M}_T$  as

$$\Gamma(u)(t) := X_t \# u^0 + \int_0^t X_{t-s} \# N(s, u(s)) \, ds \,, \tag{4}$$

with # denoting the push-forward of a measure through a map. It is easy to check that a fixed point of this map is in fact a solution to equation (1).

Step 1:  $\Gamma$  is well-defined.- Let us first show that  $t \mapsto X_t \# u^0$  and  $s \mapsto X_{t-s} \# N(s, u(s))$  (for  $t \in [0, T]$  fixed) are continuous maps. For the first one, taking any test function  $\phi \in \mathcal{L}$  and any  $t, \tau \in [0, T]$ ,

$$\int_{\mathbb{R}^d} \phi \left( X_t \# u^0 - X_\tau \# u^0 \right) dx = \int_{\mathbb{R}^d} (\phi(X_t(x)) - \phi(X_\tau(x))) u^0(x) dx$$
  
$$\leq \int_{\mathbb{R}^d} |X_t(x) - X_\tau(x)| |u^0|(x) dx$$
  
$$\leq |t - \tau| \|F\|_{\infty} \|u^0\|_{TV},$$

which shows continuity. As for the second one, we take  $\phi$  as before, fix  $t \in [0,T]$  and take any  $\tau, s \in [0,t]$ . Denoting N(s, u(s)) as  $N_s$  for short, we have

$$\begin{split} &\int_{\mathbb{R}^d} \phi \left( X_{t-s} \# N_s - X_{t-\tau} \# N_\tau \right) dx \\ &= \int_{\mathbb{R}^d} \phi \left( X_{t-s} \# N_s - X_{t-s} \# N_\tau \right) dx + \int_{\mathbb{R}^d} \phi \left( X_{t-s} \# N_\tau - X_{t-\tau} \# N_\tau \right) dx \\ &= \int_{\mathbb{R}^d} (\phi \circ X_{t-s}) \left( N_s - N_\tau \right) dx + \int_{\mathbb{R}^d} (\phi (X_{t-s}(x)) - \phi (X_{t-\tau}(x))) \right) N_\tau(x) dx \\ &\leq L_{X_{t-s}} \| N_s - N_\tau \| + |\tau - s| \| F \|_\infty \| N_\tau(x) \|_{TV} \\ &\leq e^{(t-s)L_F} \| N_s - N_\tau \| + C_R \| F \|_\infty |\tau - s| \,. \end{split}$$

This proves continuity, as  $s \mapsto N(s, u(s))$  is continuous due to (H3). Hence, the integral in (4) makes sense,  $\Gamma(u)$  is continuous from [0, T] to  $\mathcal{M}(\mathbb{R}^d)$  in the bounded Lipschitz norm, and we only need to see that its image is inside  $B_{TV}(R)$ :

$$\|\Gamma(u)(t)\|_{TV} \le \|X_t \# u^0\|_{TV} + \int_0^t \|X_{t-s} \# N(u(s))\|_{TV} \, ds$$
  
$$\le \|u^0\|_{TV} + \int_0^t \|N(u(s))\|_{TV} \, ds$$
  
$$\le \|u^0\|_{TV} + C_R T \le 2 \|u^0\|_{TV} = R.$$

Step 2:  $\Gamma$  is contractive.- Take  $u, v \in \mathcal{M}_T$ . Using similar arguments we estimate

$$\begin{aligned} \|\Gamma(u)(t) - \Gamma(v)(t)\| &\leq \int_0^t \|X_{t-s} \# N(s, u(s)) - X_{t-s} \# N(s, v(s))\| \, ds \\ &\leq \int_0^t L_{X_{t-s}} \|N(s, u(s)) - N(s, v(s))\| \, ds \\ &\leq e^{L_F T} L_N \int_0^t \|u(s) - v(s)\| \, ds. \end{aligned}$$

By taking the maximum over  $t \in [0, T]$  this implies

$$|||\Gamma(u) - \Gamma(v)||| \le e^{L_F T} L_N T |||u - v||| < L |||u - v|||,$$

for some L < 1, due to the choice of T made in (3). An application of the Banach fixed point theorem together with usual arguments on the extension of solutions finishes the proof of point i) of the theorem.

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Step 3: Continuous dependence.- We estimate the difference of the two solutions as follows:

$$\begin{aligned} \|u(t) - v(t)\| \\ &\leq \|X_t \# u^0 - X_t \# v^0\| + \int_0^t \|X_{t-s} \# N(s, u(s)) - X_{t-s} \# N(s, v(s))\| \, ds \\ &\leq L_{X_t} \|u^0 - v^0\| + \int_0^t L_{X_{t-s}} \|N(s, u(s)) - N(s, v(s))\| \, ds \\ &\leq e^{L_F t} \|u^0 - v^0\| + L_N \int_0^t e^{L_F (t-s)} \|u(s) - v(s)\| \, ds. \end{aligned}$$
  
Gronwall's Lemma then implies the result.

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*Remark* 2.6. Theorem 2.4 is a generalization of ideas in the theory of linear evolution semigroups [21, 2], since equation (1) is the sum of a linear term. and a locally Lipschitz perturbation. However, a small modification of the argument is needed: this comes from the fact that one cannot work in the dual space  $[W^{1,\infty}(\mathbb{R}^d)]^*$ . Actually, the proof above shows that by restricting to measures in  $B_{TV}(R)$  we are able to prove the continuity of the transport semigroup. This continuity is not evident in  $B_{BL}(R)$ .

Finally, we point out that we are usually interested in positive measures as initial condition, even if Theorem 2.4 does not require positivity.

#### 3. Application to particular models

In this section we will apply Theorem 2.4 to show well-posedness of four particular models in population dynamics. The first one is a simple selectionmutation equation for a phenotypic variable inspired by the "continuum of alleles model" introduced by Crow and Kimura (see [12] and also [4]) in the field of population genetics in order to explain the maintenance of genetic variation due to the balance effect of selection and mutation. The second one, introduced in [6], is a modification of the first one in which it is assumed that the nonlinear term modelling the competition between individuals for resources is infinite-dimensional. The third model we consider was studied in [7] and it is a selection-mutation model for an age-structured population. The last model we present is an age- and size-structured model that was introduced in [26].

3.1. A simple selection-mutation equation. Let us consider the following selection-mutation equation:

$$\frac{\partial u}{\partial t}(t,x) = (1-\varepsilon)b(x)u(t,x) - m(x,P(t))u(t,x) 
+ \varepsilon \int_{\Omega} b(y)\gamma(x,y)u(t,y)\,dy := N(u(t,\cdot))(x) \quad (5)$$

for the density u(t,x) of individuals at time  $t \ge 0$  with respect to an (abstract) evolutionary variable x in an open set  $\Omega \subseteq \mathbb{R}^d$ . P(t) denotes the total population at time t

$$P(t) := \int_{\Omega} u(t, x) \, dx$$

and *m* is the trait-specific death rate which depends in an increasing way on the total population P(t) at time *t*. The inflow of non-mutant newborns will be given by  $(1-\varepsilon)b(x)u(t,x)$  where b(x) is the trait-specific fertility and  $\varepsilon$  stands for the probability of mutation. The inflow of mutant newborns will be given by the integral operator  $\varepsilon \int_{\Omega} b(y)\gamma(x,y)u(t,y) dy$  where  $\gamma(x,y)$ is the density of probability that the trait of the mutant offspring of an individual with trait *y* is *x*.

We may apply Theorem 2.4 to equation (5) under the following conditions:

**Theorem 3.1.** Assume (H1) and also that b, m and  $\gamma$  satisfy the following: (i)  $b: \Omega \to \mathbb{R}$  is in  $W^{1,\infty}$  (i.e., it is bounded and Lipschitz).

(ii)  $m: \Omega \times \mathbb{R} \to \mathbb{R}$  satisfies that for each  $p \in \mathbb{R}$ ,  $m(\cdot, p) \in W^{1,\infty}$ , and for each R > 0 there exists L > 0 such that

$$\|m(\cdot, p_1) - m(\cdot, p_2)\|_{1,\infty} \le L|p_1 - p_2| \quad \text{for all } p_1, p_2 \in [-R, R].$$
(6)

(iii) For each  $y \in \Omega$ ,  $\gamma(\cdot, y)$  is a positive probability measure on  $\Omega$  and there exists L > 0 such that

$$\|\gamma(\cdot, y) - \gamma(\cdot, z)\| \le L|y - z| \quad \text{for all } y, z \in \Omega.$$
(7)

Then the operator N in equation (5) satisfies the hypotheses of Theorem 2.4. Consequently, equation (5) is well-posed in the sense of Theorem 2.4.

*Proof.* We need to check that assumptions (H4) and (H5) are satisfied, as (H1) is included in the statement, (H2) is trivial here since F = 0, and (H3) is a consequence of (H4) since the operator N in equation (5) does not depend on time. We point out that due to Remark 2.5 we may use Theorem 2.4 in  $\mathcal{M}(\Omega)$ , as we have no drift term here (F = 0).

For (H4) we need to prove that given R > 0 there exists a constant L > 0 such that

$$||N(\mu) - N(\nu)|| \le L ||\mu - \nu||$$

for all  $\mu, \nu \in \mathcal{M}$  with  $\|\mu\|, \|\nu\| \leq R$ . For the first term in (5),

$$\|b\mu - b\nu\| = \|b(\nu - \mu)\| \le \|b\|_{1,\infty} \|\nu - \mu\|.$$
(8)

For the second,

$$|m(\cdot, P(\mu))\mu - m(\cdot, P(\nu))\nu|| = \|(m(\cdot, P(\mu)) - m(\cdot, P(\nu)))\mu\| + \|m(\cdot, P(\nu))(\mu - \nu)\| \le \|m(\cdot, P(\mu)) - m(\cdot, P(\nu))\|_{1,\infty}\|\mu\| + \|m(\cdot, P(\nu))\|_{1,\infty}\|\mu - \nu\| \le \|P(\mu) - P(\nu)\|\|\mu\| + C\|\mu - \nu\| \le \|\mu - \nu\|(C + \|\mu\|), \quad (9)$$

where C is a constant such that  $||m(\cdot, p)||_{1,\infty} \leq C$  for all  $p \in [-R, R]$  finite due to (6). Finally, in order to estimate the third term we notice that, for all  $\psi \in \mathcal{L}$ ,

$$\left\| \int \gamma(x, \cdot)\psi(x) \, dx \right\|_{1,\infty} \le C,\tag{10}$$

for some C > 0. Indeed,  $\int \gamma(x, y)\psi(x) dx$  is uniformly bounded for  $y \in \Omega$  due to the fact that  $\gamma(\cdot, y)$  is a probability measure, and it is also Lipschitz in y since

$$\left| \int (\gamma(x,y) - \gamma(x,z))\psi(x) \, dx \right| \le \|\gamma(\cdot,y) - \gamma(\cdot,z)\| \le L|y-z|$$

for all  $y, z \in \Omega$ , due to (7). Hence, (10) holds and we can estimate the third term in (5) by integrating against a function  $\psi \in \mathcal{L}$ :

$$\left| \int \int b(y)\gamma(x,y)(\mu(y) - \nu(y))\psi(x) \, dy \, dx \right|$$

$$= \left| \int (\mu(y) - \nu(y))b(y) \int \gamma(x,y)\psi(x) \, dx \, dy \right|$$

$$\leq \|\mu - \nu\| \|b\|_{1,\infty} \left\| \int \gamma(x,\cdot)\psi(x) \, dx \right\|_{1,\infty} \leq C \|\mu - \nu\| \|b\|_{1,\infty} \,.$$

$$(11)$$

Putting together (8), (9), and (11) we conclude that (H4) holds. Finally, (H5) is easily seen to hold using that b is bounded and  $\gamma(\cdot, y)$  is a probability measure.

In the general abstract theorem we do not show conservation of positivity for solutions. Since  $L^1(\Omega)$  is dense in  $\mathcal{M}(\Omega)$  in the bounded Lipschitz distance, this is a straightforward consequence of the result of conservation of positivity of  $L^1$  solutions, which is already available for all of the models mentioned here. We show positivity of solutions for this model for the sake of completeness, but this will be skipped for the rest of the models of the paper, to which analogous arguments are applicable.

**Lemma 3.2.** Every solution of (5) with positive initial condition  $u_0$  is positive.

*Proof.* We begin by showing positivity of local solutions of (5) in  $L^1(\mathbb{R}^d)$ . The initial value problem can be written as

$$\begin{cases} \frac{\partial u}{\partial t} = Au + f(u) \\ u(0) = u_0 \end{cases}$$
(12)

where

$$Au(t,x) := (1-\varepsilon)b(x)u(t,x) + \varepsilon \int_{\Omega} b(y)\gamma(x,y)u(t,y)\,dy$$

and f(u)(t,x) := -m(x, P(t))u(t,x). The operator A is the generator of a positive semigroup T(t). Let  $\lambda$  be a constant bigger than the bound of m. If we add and subtract  $\lambda u$  to (12) we get

$$\frac{\partial u}{\partial t} = (A - \lambda I)u + f(u(t)) + \lambda u(t),$$

The mild solutions of this new initial value problem, and therefore also those of problem (12), can be constructed by iterating a suitable variation of constants formula [21, 2]. More precisely, they are limits of the sequence  $(z_n)_{n\geq 0}$  of functions defined on  $[0, t_{\max})$  for some  $t_{\max} > 0$ , recursively defined by the formula

$$z_{n+1}(t) = \widetilde{T}(t)z_0 + \int_0^t \widetilde{T}(t-s) \big(f(z_n(s)) + \lambda z_n(s)\big) \, ds,$$

where  $\widetilde{T}(t)$  is the semigroup generated by the operator  $A - \lambda I$ , that is  $\widetilde{T}(t) = e^{-\lambda t}T(t)$ .

Since  $z_0$  is positive, the semigroup T(t) is positive and since  $\lambda$  is larger than the bound of m, we obtain that  $z_1$  is positive. By induction over n

we have that  $(z_n)_{n\geq 0}$  is positive. Finally, since the cone of the positive functions of  $L^1$  is closed, we obtain that z(t) is positive. Positivity of local solutions implies positivity of global solutions by a standard connectedness argument. Finally, using Theorem 2.4, the density of  $L^1(\Omega)$  in  $\mathcal{M}(\Omega)$  in the bounded Lipschitz distance gives us conservation of positivity in the space of measures.

3.2. A selection-mutation model with infinite-dimensional environment. Another example of a selection-mutation equation is

$$\frac{\partial u}{\partial t}(t,x) = \left((1-\varepsilon)b(x) - d_0(x) - \int_{\Omega} d(x,y)u(t,y)\,dy\right)u(t,x) 
+ \varepsilon \int_{\Omega} b(y)\gamma(x,y)u(t,y)\,dy =: N(u(t,\cdot))(x).$$
(13)

for the density of individuals u(t,x) with respect to an (abstract) evolutionary trait  $x \in \Omega$ . The difference with (5) is that here the trait-specific per capita death rate is given by the sum of the terms  $d_0(x)$  and  $\int_{\Omega} d(x,y)u(t,y) dy$ . The latter one models the interaction between individuals through competition for resources, and is the only nonlinear term in the equation (whose nonlinearity in this case is infinite dimensional).

This model was presented in [6], where the authors prove existence of steady states and also that their asymptotic profile when the mutation rate  $\varepsilon \to 0$  is a Cauchy distribution. Our well-posedness result in the space of measures for equation (13) is the following:

**Theorem 3.3.** Assume (H1), points (i) and (iii) in Theorem 3.1, and also that  $d_0$  and d are nonnegative functions satisfying

$$d_0: \Omega \to \mathbb{R} \text{ is in } W^{1,\infty}(\Omega), \tag{14}$$

and  $d: \Omega \times \Omega \to \mathbb{R}$  with  $d \in W^{1,\infty}(\Omega; W^{1,\infty}(\Omega))$ ; that is, there exists L > 0 such that

$$\|d(x,\cdot)\|_{W^{1,\infty}(\Omega)} \le L \quad \text{for all } x \in \Omega.$$
(15)

$$\|d(x,\cdot) - d(z,\cdot)\|_{W^{1,\infty}(\Omega)} \le L|x-z| \quad \text{for all } x, z \in \Omega.$$
(16)

Then the operator N in equation (13) satisfies the hypotheses of Theorem 2.4. Consequently, equation (13) is well-posed in the sense of Theorem 2.4.

*Proof.* As remarked in the proof of Theorem 3.1, we only need to check (H4) and (H5). As the other terms have the same form as the terms in (5) since (14) is satisfied, we only need to check (H4) and (H5) for the term which involves d.

First we notice that due to (15)–(16) the term  $\int_{\Omega} d(x, y)u(y) dy$  is in  $W^{1,\infty}(\Omega)$  for any  $u \in \mathcal{M}(\Omega)$ , as for all  $x \in \Omega$ ,

$$\left|\int_{\Omega} d(x,y)u(y)\,dy\right| \le \|d(x,\cdot)\|_{W^{1,\infty}(\Omega)}\,\|u\| \le L\|u\|.$$

and for any  $x, z \in \Omega$ ,

$$\left| \int_{\Omega} (d(x,y) - d(z,y)) u(y) \, dy \right| \le \| d(x,\cdot) - d(z,\cdot) \|_{W^{1,\infty}(\Omega)} \, \|u\| \le L |x-z| \, \|u\|$$

Actually, we have proved that for any  $w \in \mathcal{M}(\Omega)$ ,

$$\left\| \int_{\Omega} d(\cdot, y) w(y) \, dy \right\|_{W^{1,\infty}(\Omega)} \le L \|w\|.$$
(17)

In order to prove (H4) for the term involving d, take two measures u, v in  $\mathcal{M}(\Omega)$ . Then,

$$\begin{split} \left\| u \int_{\Omega} d(\cdot, y) u(y) \, dy - v \int_{\Omega} d(\cdot, y) v(y) \, dy \right\| \\ & \leq \left\| (u - v) \int_{\Omega} d(\cdot, y) u(y) \, dy \right\| + \left\| v \int_{\Omega} d(\cdot, y) (u(y) - v(y)) \, dy \right\| \\ & \leq \left\| u - v \right\| \left\| \int_{\Omega} d(\cdot, y) u(y) \, dy \right\|_{1,\infty} + \left\| v \right\| \left\| \int_{\Omega} d(\cdot, y) (u(y) - v(y)) \, dy \right\|_{1,\infty} \\ & \leq L \| u - v \| \| u \| + L \| v \| \| u - v \|, \end{split}$$

where we used (17) for the last step. This proves (H4). On the other hand, (H5) is easily proved since, in particular,  $\left|\int_{\Omega} d(x,y)u(y) \, dy\right| \leq L \|u\|_{TV}$  for all  $x \in \Omega$ .

3.3. A selection-mutation model with age structure. Let us consider the following equation

$$\frac{\partial u}{\partial t}(t,a,x) + \frac{\partial u}{\partial a}(t,a,x) = -m(a,x,P(t),Q(t))u(t,a,x)$$
(18a)

$$u(t,0,x) = (1-\varepsilon) \int_{x}^{\infty} b(a,x)u(t,a,x) \, da \tag{18b}$$

$$+ \varepsilon \int_0^\infty \int_y^\infty \gamma(x, y) b(a, y) u(t, a, y) \, da \, dy \quad (18c)$$

$$u(0, a, x) = u_0(a, x)$$
 (18d)

where u(t, a, x) is the density of individuals with age  $a \ge 0$  and maturation age  $x \ge 0$  (the evolutionary variable) at time t. P(t) and Q(t) denote, respectively, the total population of juveniles and adults, that is  $P(t) = \int_0^\infty \int_0^x u(t, a, x) \, da \, dx$ ,  $Q(t) = \int_0^\infty \int_x^\infty u(t, a, x) \, da \, dx$ , m is the mortality rate, b is the fertility rate and  $\gamma(x, y)$  is the probability density that the maturation age of the mutant offspring of an individual with maturation age y is x. As in the previous examples,  $\varepsilon$  stands for the probability of mutation.

This model is a slightly modified version of the one studied in [7], where the only difference is in the term of inflow of newborns. The difference of this model with the ones in the previous sections is that here, fixing the evolutionary variable, we still have an infinite-dimensional model, more precisely, an age-structured population model. In [7] well-posedness of the model was proved in the Banach space  $L^1(\mathbb{R}^2_+)$  (denoting  $\mathbb{R}^2_+ = [0, +\infty) \times$   $[0, +\infty)$ ), and also the existence of steady states. In order to show wellposedness in the space of measures we rewrite (18) as follows:

$$\partial_t u + \partial_a u = N_1(u) \tag{19a}$$

$$u(t, 0, x) = n_2(u)$$
 (19b)  
 $u(0, a, x) = u_0(a, x)$  (19c)

$$u(0, a, x) = u_0(a, x)$$
(19c)

where we call  $\Omega := \mathbb{R}^2_+$  and define, for  $u \in \mathcal{M}(\Omega)$ , 

$$N_1(u) := -m(a, x, P(u), Q(u))u,$$
  

$$n_2(u)(x) := (1 - \varepsilon) \int_x^\infty b(a, x)u(a, x) da$$
  

$$+ \varepsilon \int_0^\infty \int_y^\infty \gamma(x, y)b(a, y)u(t, a, y) da dy.$$

The model may be rewritten in the form (1) by extending it to an equation on  $\mathbb{R}^2$ , with an additional independent term. Let us be precise about the intended solutions:

**Definition 3.4.** Take  $T \in [0, +\infty]$ . We say a continuous function u:  $[0,T) \to \mathcal{M}(\Omega)$  is a solution of equation (19) on [0,T) with initial condition  $u_0$  when, for every  $\phi \in \mathcal{C}_0^{\infty}([0,T) \times \Omega)$ ,

$$-\int_0^T \int_\Omega u \partial_t \phi \, dx \, da \, dt - \int_\Omega \phi(0, x, a) u_0(x, a) \, dx \, da$$
$$-\int_0^T \int_\Omega u \partial_a \phi \, dx \, da \, dt - \int_0^T \int_0^\infty n_2(u(t)) \phi(t, x, 0) \, dx \, dt$$
$$= \int_0^T \int_\Omega N_1(u(t)) \phi \, dx \, da \, dt.$$

(When the variables of  $\phi$  or u are not specified, it is understood that they are (t, a, x)).

We now take a suitable extension of the functions m, b and  $\gamma$  to all of  $\mathbb{R}^2$ (for definiteness, by mirror symmetry first in x and then in a) and consider the following equation, posed in the whole set of  $(a, x) \in \mathbb{R}^2$ :

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = N_1(u) + n_2(u)\delta_{a=0}, \qquad (20a)$$

$$u(0) = u_0.$$
 (20b)

Equation (20) is of the form (1). Now, observe that a solution of (20), in the sense of Definition 2.3, is also a solution to (19) in the sense of Definition 3.4 when restricted to  $\mathbb{R}^2_+$ , provided it is zero on the set  $\mathbb{R}^2 \setminus \mathbb{R}^2_+$ . Hence, we just need to give conditions on m, b and  $\gamma$  so that (20) satisfies Hypotheses (H1)–(H5) and its solutions are supported on  $\mathbb{R}^2_+$ .

**Theorem 3.5.** We assume the following:

- (i)  $b \in W^{1,\infty}(\Omega)$ , and it is nonnegative.
- (ii)  $m: \Omega \times \mathbb{R} \times \mathbb{R} \to \mathbb{R}$  is a nonnegative function satisfying a condition similar to the one in Theorem 3.1: for each  $p,q \in \mathbb{R}, m(\cdot,p,q) \in$

 $W^{1,\infty}$ , and for each R > 0 there exists L > 0 such that

$$\|m(\cdot, p_1, q_1) - m(\cdot, p_2, q_2)\|_{1,\infty} \le L(|p_1 - p_2| + |q_1 - q_2|)$$

for all  $p_1, p_2, q_1, q_2 \in [-R, R]$ .

(iii) For each  $y \in \mathbb{R}$ ,  $\gamma(\cdot, y)$  is a positive probability measure on  $\mathbb{R}$  and there exists L > 0 such that

$$\|\gamma(\cdot, y) - \gamma(\cdot, z)\| \le L|y - z| \quad \text{for all } y, z \in \mathbb{R}.$$

Then the initial value problems (20) and (18) are well-posed in the sense of Theorem 2.4.

*Proof.* As remarked in the proof of Theorem 3.1, we only need to prove (H4) and (H5), and we can do it separately for each term.

The term  $N_1(u)$  can be treated in a similar way to the term m(x, P)u in (5), and we omit the details. For the term  $n_2(u)\delta_{a=0}$  we have

$$\|(n_2(u) - n_2(v))\delta_{a=0}\|_{\mathcal{M}(\mathbb{R}^2)} = \|n_2(u) - n_2(v)\|_{\mathcal{M}(\mathbb{R})}.$$

The term in  $n_2(u)$  which involves  $\gamma$  is of a similar form to the one in (5) and can be treated analogously. For the other term, taking any test function  $\phi \in W^{1,\infty}(\mathbb{R})$  with  $\|\phi\|_{1,\infty} \leq 1$ ,

$$\int_{\mathbb{R}} \int_{\mathbb{R}} \phi(x) b(a, x) (u(a, x) - v(a, x)) \, da \, dx \\ \leq \|u - v\| \, \|\phi \, b\|_{1,\infty} \leq \|u - v\| \, \|b\|_{1,\infty},$$

which shows that

$$\left\|\int_{\mathbb{R}} b(a, \cdot)(u(a, \cdot) - v(a, \cdot)) \, da\right\| \le \|u - v\| \, \|b\|_{1,\infty},$$

hence proving (H4) for this term. Condition (H5) for this term is easily seen to hold by using that b is bounded.

The above allows us to apply Theorem 2.4 to equation (20). We deduce that the problem (20) is well-posed, and we only have to show that its solutions have support on  $\mathbb{R}^2_+$ , so that they are also solutions to (18). In order to do this, we take any time T > 0 and any test function  $\phi_T \in \mathcal{C}^{\infty}(\mathbb{R}^2)$ with compact support on  $\mathbb{R}^2/\mathbb{R}^2_+$  and consider  $\phi : [0,T] \times \mathbb{R} \times \mathbb{R} \to \mathbb{R}$  to be the solution to

$$\frac{\partial \phi}{\partial t} - \frac{\partial \phi}{\partial a} = 0 \quad \text{on } (0,T) \times \mathbb{R} \times \mathbb{R},$$
(21)

with  $\phi(T, a, x) = \phi_T(a, x)$  for  $a, x \in \mathbb{R}$ . Then,

$$\frac{d}{dt} \int_{\mathbb{R}} \int_{\mathbb{R}} \phi u \, da \, dx = \int_{\mathbb{R}} \int_{\mathbb{R}} \phi(-\partial_a u + N_1(u) + n_2(u)\delta_{a=0}) \, da \, dx \\ + \int_{\mathbb{R}} \int_{\mathbb{R}} u \partial_a \phi \, da \, dx = \int_{\mathbb{R}} \int_{\mathbb{R}} \phi(N_1(u) + n_2(u)\delta_{a=0}) \, da \, dx = 0,$$

since for all  $t \in [0, T]$ ,  $\phi(t, \cdot, \cdot)$  has support contained in  $\mathbb{R}^2/\mathbb{R}^2_+$ , which can easily be seen since the solution to (21) is explicit. Hence, since the initial data is supported in  $\mathbb{R}^2_+$ , then

$$\int_{\mathbb{R}} \int_{\mathbb{R}} \phi_T(a, x) u(T, a, x) \, da \, dx = \int_{\mathbb{R}} \int_{\mathbb{R}} \phi(0, a, x) u_0(a, x) \, da \, dx = 0 \,,$$

and since  $\phi_T$  was arbitrary we deduce that at time T, u has support contained in  $\mathbb{R}^2_+$ .

3.4. An age-size structured model. Let us consider the following agesize structured model from [26]:

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} + \frac{\partial}{\partial x}(g(x)u) = -m(a, x, P(t))u$$
(22a)

for 
$$a \in (0, a_1), x \in (x_0, x_1), t > 0$$
 (22b)

$$u(t,0,x) = \int_0^{a_1} \int_{x_0}^{x_1} \beta(a,\hat{x},x)u(t,a,\hat{x}) \,d\hat{x} \,da \tag{22c}$$

for 
$$x \in (x_0, x_1), t > 0$$
 (22d)

 $u(0, a, x) = u_0(a, x)$  for  $a \in (0, a_1), x \in (x_0, x_1),$  (22e)

where u = u(t, a, x) denotes the density of individuals with age a, with  $0 \le a \le a_1 \le \infty$  and size x with  $0 \le x_0 \le x \le x_1 \le \infty$ . Size increases with time, in the same way for all individuals of the population, and the growth rate is given by the function g(x) which is assumed not to depend on environmental factors. Moreover it satisfies  $g(x) \ge 0$  and  $g(x_0) = 0$ . m denotes the mortality rate and  $\beta(a, \hat{x}, x)$  denotes the average number of offspring of size x produced per unit of time by an individual of age a and size  $\hat{x}$  and  $P(t) = \int_0^{a_1} \int_{x_0}^{x_1} u(t, a, x) dx da$ . Here, we denote by  $\Omega = (0, a_1) \times (x_0, x_1)$  the domain of definition of the equation.

Many versions of the model (22), both linear and nonlinear, have been studied, for instance in [20] and also in [24] where a more general nonlinear model containing an arbitrary number of structured variables is considered. The usual space to study these models is  $L^1(\Omega)$ . By using essentially the same ingredients as in the previous subsection, one can prove the following theorem that we state without proof.

**Theorem 3.6.** We assume the following:

(i) m : Ω × ℝ → ℝ is a nonnegative function satisfying a condition similar to the one in Theorem 3.1: for each p ∈ ℝ, m(·, p) ∈ W<sup>1,∞</sup>, and for each R > 0 there exists L > 0 such that

$$||m(\cdot, p_1) - m(\cdot, p_2)||_{1,\infty} \le L|p_1 - p_2|$$

for all  $p_1, p_2 \in [-R, R]$ .

- (ii)  $g \in W^{1,\infty}([x_0, x_1])$  with g(0) = 0 and  $g(x_1) > 0$ .
- (iii) The map  $\beta : \Omega \to \mathcal{M}([x_0, x_1])$  assigns  $(a, \hat{x}) \mapsto \beta(a, \hat{x}, \cdot)$  and verifies that  $W^{1,\infty}(\Omega, \mathcal{M}([x_0, x_1]))$ , i.e, it is bounded and there exists L > 0 such that

$$\|\beta(a_1, \hat{x}_1, \cdot) - \beta(a_2, \hat{x}_2, \cdot)\| \le L(|a_1 - a_2| + |\hat{x}_1 - \hat{x}_2|)$$

for all  $(a_1, \hat{x}_1), (a_2, \hat{x}_2) \in \Omega$ .

Then the initial boundary value problem to (22) is well-posed in the sense of Remark 3.7.

Remark 3.7. Let us mention that the extension outside the realistic domain  $\Omega$  to  $\mathbb{R}^2$  of the model ingredients  $m, \beta$ , and g while meeting the conditions in Theorem 2.4 may be done in many different ways. Once one has an extended

equation in  $\mathbb{R}^2$ , Theorem 2.4 applies, and all solutions to the extended equations lead to the same solution once restricted to  $\Omega$ . This is due to the fact that the characteristics associated to the transport field (1, g(x)) for the age and size variables (a, x) are not incoming at the boundaries:  $a = a_1, x = x_0$ , and  $x = x_1$ . A similar argument as in the proof of Theorem 3.5 shows that if the solutions for these extended systems are zero initially in the set of a < 0, then they remain so for all times.

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