

BASIC THEORY FOR A CLASS OF MODELS OF HIERARCHICALLY STRUCTURED POPULATION DYNAMICS WITH DISTRIBUTED STATES IN THE RECRUITMENT

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In this paper we present a proof of existence and uniqueness of solution for a class of PDE models of size structured populations with distributed state-at-birth and having nonlinearities defined by an infinite-dimensional environment. The latter means that each member of the population experiences an environment according to a sort of average of the population size depending on the individual size, rank or any other variable structuring the population. The proof of the local existence and uniqueness of solution as well as the continuous dependence on initial continuous is based on the general theory of quasi-linear evolution equations in nonreflexive Banach spaces, while the global existence proof is based on the integration of the local solution along characteristic curves.

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1. Introduction

Continuous structured population models consider a population described by a density $u(x, t)$ of individuals with respect to a variable x , sometimes called “internal”, “structuring”, or “physiological” variable, with $x \in [x_0, l)$, $l \leq \infty$, and $x_0 \geq 0$. Examples of these variables are age, size, height, body surface, energy reserve or maturity, and, in some cases, populations are described by densities with respect to more than one internal variable, i.e. with $x \in \Omega \subset \mathbb{R}^k$, $k \geq 2$.^{27,34} In their classical form, these models are formulated in terms of nonlocal first-order hyperbolic

PDE (a *balance law*) governing the dynamics of the density $u(x, t)$. In order to have a well-posed initial value problem (IVP) one needs an initial condition $u_0(x)$ and a boundary condition at $x = x_0$. Usually, this boundary condition describes the inflow of newborns in the population, i.e. the inflow of individuals having a value $x = x_0 \geq 0$ of the structuring variable (see Refs. 8, 15, 23 and 27). From now on we will call the structuring variable x *size* and will restrict ourselves to the one-dimensional case, i.e. to $x \in [x_0, l)$, $l \leq \infty$.

It is likely that this sort of boundary condition comes from the fact that the first structuring variable considered in the literature was age and, in this case, it is clear that all the newborns have exactly the same value of age-at-birth, namely $x_0 = 0$. Whether this is the reason or not, most of the structured population models assume a fixed value x_0 for the state-at-birth of an individual, even though it is not clear at all that this is always a good approximation. For instance, if x_0 denotes the size-at-birth of an individual, different newborns (or seeds in case of modelling plant populations) can have different values of x_0 , and such differences can play an important role in their survival during the childhood (or as seedlings). Such an assumption can be justified as a simplification introduced to model the dynamics of such structured populations and, for the same price, it provides these models with an added mathematical interest: a nonlinearity at the boundary condition. However, such a simplification is not always a suitable one. For instance, in cell populations where large enough cells with different sizes split into two new cells, there is not a fixed size for daughter cells coming in the cell population.^{27,34} Another example is given by the cell aggregation process where larger aggregates are formed from fusion of smaller ones by collisions.² An analogous situation which combines both processes, namely, division and aggregation, happens in a non-biological context when modelling fragmentation and coagulation in systems of reacting polymers.^{24,25,35} In all these examples, the recruitment/production process cannot be modelled by a nonlinear boundary condition or, at least, not only by means of it.²

On the other hand, if the previous simplification in the recruitment process also causes problems when proving the well-posedness of the model, even when it seems suitable from a modelling point of view, it is reasonable to overcome such difficulties by means of an alternative mathematical description of this process. A situation where such difficulties appear is when vital rates of an individual (growth, mortality and reproduction rates) depend on a variable obtained by applying an operator to $u(\cdot, t)$, usually called *environment* or *interaction variable*, here denoted by $E[u(t)](x)$, which reflects (resumes) the competition effects at time t on individuals having a size between x and $x + dx$. When the environment is only a functional of u , i.e. $E[u(t)]$, all the individuals in the population experience the same competition effect and the resulting competition is called *scramble competition* (see Ref. 10). In this case, there is no problem in proving, by means of the characteristics method, that the solutions of the corresponding IVP define a C^0 -semigroup in $L^1(x_0, l)$, $l \leq \infty$, which is the natural function space for $u(x, t)$ (see, for instance, Ref. 8 for the case $l = \infty$, Ref. 28 for the well-posedness of the IVP for $l < \infty$,

and Refs. 15, 34 for the well-posedness of models with age plus other structuring variables).

In other situations, the availability of resources is related to a hierarchical ranking among individuals in the population and, so, the competition effects experienced by a given individual depend on a structuring variable which reflects its rank or status in the population. Many times it is a physical feature of the organisms (height, size, age, etc.) which determines the amount of available resource. In other cases, badges of social status, as it can be certain plumage traits in some species of birds, structure the population in dominance classes each of them having a different availability of resources. In all these cases, it is said that there is a *competition* among individuals of the population (see, for instance, Ref. 10) and the environment experienced by these individuals is said to be *infinite-dimensional*: $E = E[u(t)](x)$. Under such environments governing the interactions among individuals, there is no general proof of the well-posedness of the resulting IVP assuming the classical nonlinear boundary condition at $x = x_0$. Proofs of well-posedness of particular models assuming both particular infinite-dimensional environments and a nonlinear boundary condition are given in Ref. 10 for the age-dependent case, and in Refs. 9, 23 for the size dependent case. In particular, in Ref. 9, the original nonlocal PDE model is transformed into a local PDE for the interaction variable E thanks to the fact that, as in Ref. 10, vital rates do not depend explicitly on x . In Ref. 23, there exists a dependence of the vital rates on size, and the existence and uniqueness of a C^0 -solution of an IVP with an infinite-dimensional environment and a nonlinear boundary condition is proved by transforming the original PDE model into characteristic coordinates (as in Ref. 15). In general, however, the well-posedness of PDE models with a set of infinite-dimensional environments with interactions among them is still an open question, even in the so-called *cumulative formulation*, an alternative approach to the deterministic modelling of structured populations (see Refs. 13, 12, 16 for details).

In this paper we consider a general PDE model where nonlinearities are defined by a vector of interaction variables $E = (E_1, \dots, E_n)$ such that its components satisfy the so-called *generalized mass action* introduced in Ref. 12. More precisely, the following hierarchical structure among the components of E is assumed:

$$E_i = L_i(x, E_1, \dots, E_{i-1}), \quad i \geq 2$$

and $E_1 = L_1(x)$. Here, given x, E_1, \dots , and E_{i-1} , L_i are linear functionals of the population density u . This structure guarantees that each component of E will be Lipschitzian (in suitable norms) with respect to u whenever L_i is Lipschitzian with respect E_1, \dots, E_{i-1} . Of course, the particular case in which all the E_i are finite-dimensional, as in most of the models in the literature, clearly satisfies this assumption.

By means of considering newborns distributed with respect to their size-at-birth with $x_0 = 0$, which implies no-inflow of individuals at $x = 0$, i.e. a boundary condition given by $V(0, E[u(t)](0)) u(0, t) = 0$ for all $t \geq 0$, we prove the existence and uniqueness of solution of the resulting IVP. Under this assumption but for a

general form for the *recruitment term*, $R[u(t)](x)$, we can use results on quasi-linear evolution equations in non-reflexive Banach spaces (see Ref. 22) to prove that the unique solution to our IVP belongs to

$$\mathcal{C}([0, T]; W_0^{1,1}(0, \infty)) \cap \mathcal{C}^1([0, T]; L^1(0, \infty)).$$

As we have commented before, the main difficulty for proving it is that, in general, it is not possible to reduce the dimension of the problem by transforming it into a system of coupled ODE, as it happens when the environment is finite dimensional, or to transform the model into a simpler one. On the other hand, the natural function space to work with in population dynamics is $L^1(a, b)$, $a \geq 0, b \leq \infty$, but this is a non-reflexive space. Hence, when proving the convergence of a sequence of iterations to a limit function (the candidate to be a solution) in a bounded closed subset $M \subset Y = W_0^{1,1}(0, \infty)$, $Y \subset X = L^1(0, \infty)$, it is not sufficient to work with the L^1 -norm to guarantee that the limit belongs also to M . One has to work simultaneously with the L^1 -norm and the $W^{1,1}$ -norm (see Ref. 20). In Ref. 22, conditions for having guaranteed that this limit function is actually an element of M are obtained for an arbitrary non-reflexive Banach space X .

In the following section we present the IVP governing a dynamics as the one described before and the assumptions on the ingredients of the model guaranteeing its well-posedness. A brief summary of the required definitions and results of the general theory of quasi-linear evolution equations in Banach spaces is given in Sec. 3. The well-posedness of the IVP is proved in Sec. 4 while the continuous dependence on initial conditions in L^1 and positivity of solutions are studied in Sec. 4. Section 5 deals with the global existence of solution. Finally, in Sec. 7, we discuss briefly some biological situations that are in agreement with the assumptions on the ingredients of the model presented in Sec. 2.

2. The Model

The IVP corresponding to a class of models as the one described at the Introduction is given by

$$\begin{cases} \frac{\partial}{\partial t} u(x, t) + \frac{\partial}{\partial x} (V(x, E[u(t)](x)) u(x, t)) \\ \quad = R[u(t)](x) - m(x, E[u(t)](x)) u(x, t), & x \in [0, \infty), t > 0, \\ V(0, E[u(t)](0)) u(0, t) = 0, & t > 0, \\ u(x, 0) = u_0(x), & x \in [0, \infty), \end{cases} \quad (2.1)$$

where $u(x, t)$ is population density, at time t , with respect to the individual size x , $R[u(t)](x)$ is the recruitment of new individuals at time t having a size x , $E[u](y)$ is the environment experienced by an individual with size y when the population density is $u(x)$, $m(x, E(x))$ is the mortality rate of an individual of size x when the environment is E , $V(x, E(x))$ is the growth rate of an individual of size x experiencing an environment E , and, finally, $u_0(x)$ is the initial population density.

The following hypotheses will be assumed on R , m , V and E in order to guarantee the existence and uniqueness of solution to the IVP (2.1). For a given $K > 0$, let $\Omega := [0, \infty) \times [0, K]^N$. Then, we assume that

(A1) Let $M_n := \{v \in (L^\infty(0, \infty))^N : v' \in (W^{n,1})^N\}$. Then, the operator

$$E : L^1 \rightarrow M_0 \quad \text{and} \quad E : W^{1,1} \rightarrow M_1,$$

satisfies $E[0] = 0$, and its components are Lipschitzian in the norms $\|\cdot\|_0 = \|\cdot\|_\infty + \|D(\cdot)\|_{L^1}$ and $\|\cdot\|_1 = \|\cdot\|_\infty + \|D(\cdot)\|_{W^{1,1}}$.

(A2) $R : L^1(0, \infty) \rightarrow W^{1,1}(0, \infty)$ is a Lipschitz operator on bounded sets such that $R[0] = 0$.

(A3) $m(x, E)$ is a non-negative C^1 -function, with partial derivatives m_x and m_{E_i} being Lipschitzian functions in both arguments for all $1 \leq i \leq N$. Moreover, m , $|m_x|$ and $|m_{E_i}|$ are uniformly bounded by m^0 , m_x^0 , and $m_{E_i}^0$, respectively, for all $(x, E) \in \Omega$ and for all $1 \leq i \leq N$.

(A4) $V(x, E)$ is a strictly positive C^2 -function for all $x, E \geq 0$, upper bounded by V^0 and lower bounded by $V_0 > 0$ for all $(x, E) \in \Omega$. Moreover, for all $(x, E) \in \Omega$ and for all $1 \leq i, j \leq N$, the absolute value of the first-order partial derivatives $|V_x|$ and $|V_{E_i}|$ are upper bounded by V_1^0 , and the absolute value of the second-order partial derivatives $|V_{x E_i}|$ and $|V_{E_i E_j}|$ are upper bounded by V_2^0 . Finally, the second-order partial derivatives $V_{xx}(x, E)$, $V_{x E_i}(x, E)$, and $V_{E_i E_j}(x, E)$ are Lipschitzian functions with respect to E .

Note that the strict positivity of V assumed in (A4) and the boundary condition given by (2.1)₂ implies that $u(0, t) = 0$ for all $t \geq 0$.

3. Definitions and Preliminary Results

We begin this section introducing some definitions, general hypotheses and two basic results concerning to a non-autonomous linear evolution equation in a Banach space which are essential to understand the hypotheses we need for the well-posedness of our model (see Refs. 20, 22 and 30 for detailed explanations).

Let X and Y be two real Banach spaces, endowed with the norm $\|\cdot\|_X$ and $\|\cdot\|_Y$. Moreover, let $\mathcal{B}(Y, X)$ be the set of all bounded linear operators from Y to X and $\mathcal{B}(X) := \mathcal{B}(X, X)$.

Let T be a positive constant and $\{A(t)\}_{t \in [0, T]}$ be a family of negative generators of C^0 -semigroups in X which is denoted by $\{e^{-sA(t)}\}_{s \geq 0}$. This family of generators is said to be *stable* if there exist two constants M and β such that

$$\left\| \prod_{j=1}^k e^{-s_j A(t_j)} \right\|_X \leq M e^{\beta(s_1 + \dots + s_k)}$$

for every finite family $0 \leq t_1 \leq t_2 \leq \dots \leq t_k \leq T$, $k \geq 1$ and $s_j \geq 0$, $1 \leq j \leq k$. The operator product on the left is time-ordered: $e^{-s_j A(t_j)}$ is to the left of $e^{-s_i A(t_i)}$ if $t_j > t_i$.

The pair (M, β) is called *stability index* for $\{A(t)\}_{t \in [0, T]}$ and the set of all stable families of negative generators of \mathcal{C}^0 -semigroups in X with stability index (M, β) is denoted by $S(X, M, \beta)$. Notice that if, for each $t \in [0, T]$, $-A(t)$ is the generator of a contraction semigroup, then the family $\{A(t)\}_{t \in [0, T]}$ is stable and belongs to $S(X, 1, 0)$.

Now let us consider the following nonlinear IVP

$$\frac{du(t)}{dt} + A(t, u(t))u(t) = f(t, u(t)), \quad 0 \leq t \leq T, \quad u(0) = u_0, \tag{3.1}$$

and let us introduce the following hypotheses on $X, Y, \{A(t, w)\}_{t \in [0, T]}$, and $f(t, w)$:

- (H1) Y is densely and continuously embedded in X . Moreover, there is an isomorphism S of Y onto X .
- (H2) There exist an open subset W of Y and a constant $T_0 > 0$ such that $A(t, w)$ is a linear operator in X defined for each $t \in [0, T_0]$ and $w \in W$. Moreover, for each $\rho \geq 0$, there exist two constants $M \geq 1$ and $\alpha \geq 0$ such that

$$\{A(t, v(t))\}_{t \in [0, T_0]} \in S(X, M, \alpha) \quad \forall v(\cdot) \in \mathcal{D}_\rho,$$

where $\mathcal{D}_\rho := \{v \in \mathcal{C}([0, T_0]; W) : \|v(t) - v(s)\|_X \leq \rho|t - s|, 0 \leq s < t \leq T_0\}$.

- (H3) For any $w \in W$, there exists a strongly measurable operator valued function $B(\cdot, w)$ on $[0, T_0]$ to $\mathcal{B}(X)$ such that

$$SA(t, w)S^{-1} = A(t, w) + B(t, w), \quad t \in [0, T_0], \quad w \in W,$$

where S is the isomorphism defined in (H1).

Moreover, there exist two positive numbers λ_B and μ_B such that

$$\|B(t, w)\|_X \leq \lambda_B \quad \text{and} \quad \|B(t, w) - B(t, z)\|_X \leq \mu_B \|w - z\|_Y$$

for $t \in [0, T_0]$ and $w, z \in W$.

- (H4) For each $t \in [0, T_0]$ and $w \in W$, $\mathcal{D}(A(t, w)) \supset Y$ (and, therefore, $A(t, w) \in \mathcal{B}(Y, X)$ by the closed graph theorem because, under (H2), it is the negative generator of a \mathcal{C}^0 -semigroup). For each $w \in W$, $A(\cdot, w)$ is strongly continuous in $\mathcal{B}(Y, X)$ on $[0, T_0]$. There exists a constant $\mu_A > 0$ such that

$$\|A(t, w) - A(t, z)\|_{Y, X} \leq \mu_A \|w - z\|_X, \quad t \in [0, T_0], \quad w, z \in W.$$

- (H5) For each $t \in [0, T_0]$ and $w \in W$, let $f(t, w)$ be a defined function belonging to Y . Moreover, for each $w \in W$, $f(\cdot, w)$ is continuous in X on $[0, T_0]$ and is strongly measurable in Y . Finally, there exist positive numbers λ_f, μ_f and $\bar{\mu}_f$ such that

$$\begin{aligned} \|f(t, w)\|_Y &\leq \lambda_f, \\ \|f(t, w) - f(t, z)\|_X &\leq \mu_f \|w - z\|_X, \\ \|f(t, w) - f(t, z)\|_Y &\leq \bar{\mu}_f \|w - z\|_Y \end{aligned}$$

for $t \in [0, T_0]$ and $w, z \in W$.

The previous hypotheses guarantee the well-posedness of the IVP (3.1) and the existence of an *evolution operator* (or *solution operator* in Pazy’s terminology) $\{U(t, s)\}$ associated to the family $\{A(t, u(t))\}_{t \in [0, t]}$. More precisely, if $\Delta := \{(t, s) \in [0, T] \times [0, T] : 0 \leq s \leq t \leq T\}$, we have the following results:

Theorem I. (Kobayasi & Sanekata) *Under hypotheses (H1)–(H5), for each initial condition $u_0 \in W$, there exists a time $T \in [0, T_0]$ such that (3.1) has a unique solution*

$$u \in \mathcal{C}([0, T]; W) \cap \mathcal{C}^1([0, T]; X).$$

Theorem II. (Kobayasi & Sanekata) *Under hypotheses (H1)–(H5), $A(t, u(t))$ with $u(t)$ being a solution to (3.1) generates a unique family of operators $\{U(t, s)\}$, $(t, s) \in \Delta$ with the following properties:*

(a) $U(t, s)$ is strongly continuous in $\mathcal{B}(X)$ on Δ and

$$\|U(t, s)\|_X \leq M e^{\alpha(t-s)}, \quad (t, s) \in \Delta.$$

(b) $U(t, s)U(s, r) = U(t, r)$ and $U(s, s) = I$ for $(t, s), (s, r) \in \Delta$.

(c) $U(t, s)Y \subset Y$, $U(t, s)$ is strongly continuous in $\mathcal{B}(Y)$ on Δ and

$$\|U(t, s)\|_Y \leq \tilde{M} e^{\tilde{\alpha}(t-s)}, \quad (t, s) \in \Delta,$$

where $\tilde{M} = M \|S\|_{Y, X} \|S^{-1}\|_{X, Y}$ and $\tilde{\alpha} = \lambda_B M + \alpha$.

(d) $\partial U(t, s)/\partial t = -A(t, u(t))U(t, s)$ and $\partial U(t, s)/\partial s = U(t, s)A(s, u(s))$, where the derivatives exist in the strong sense in $\mathcal{B}(Y, X)$ and are strongly continuous in $\mathcal{B}(Y, X)$ on Δ .

4. Local Existence and Uniqueness of Solution

Let us verify the previous hypotheses and, hence, apply Theorems I and II to the IVP (2.1).

Hypothesis (H1). The spaces X and Y are $L^1(0, \infty)$ and $W_0^{1,1}(0, \infty)$, respectively. The isomorphism $S : W_0^{1,1} \rightarrow L^1$ is $Su = u' + u$.

Clearly, S is bijective because, for every $f \in L^1(0, \infty)$, there exists a unique function $u(x) = e^{-x} \int_0^x e^s f(s) ds \in W_0^{1,1}(0, \infty)$, such that $u' + u = f$ and $u(0) = 0$.

Moreover, if $u \in W_0^{1,1}$, there exist two positive constants c_1, c_2 such that $c_1 \|u\|_{W^{1,1}} \leq \|Su\|_{L^1} \leq c_2 \|u\|_{W^{1,1}}$. In fact, from the previous expression of u , it is immediate to determine such constants. First, we have

$$\|u\|_{W^{1,1}} = \int_0^\infty |u| + \int_0^\infty |u'| \geq \int_0^\infty |u + u'| = \|Su\|_{L^1} \Rightarrow c_2 = 1.$$

Second, since

$$\begin{aligned} \|u\|_{L^1} &= \int_0^\infty |u| \leq \int_0^\infty e^{-x} \int_0^x e^s |f(s)| ds dx \\ &= \int_0^\infty \left(\int_s^\infty e^{-x} dx \right) e^s |f(s)| ds = \|f\|_{L^1} = \|Su\|_{L^1}, \end{aligned}$$

we have

$$\int_0^\infty |u'| = \int_0^\infty |f - u| \leq \int_0^\infty |f| + \int_0^\infty |u| \leq 2 \int_0^\infty |f|,$$

and, so,

$$\|u\|_{W^{1,1}} = \int_0^\infty |u| + \int_0^\infty |u'| \leq 3 \int_0^\infty |f| = 3 \|Su\|_{L^1} \Rightarrow c_1 = 1/3.$$

Hypothesis (H2). For a given $v \in \mathcal{D}_\rho$, let us consider the linear problem associated to (3.1), namely,

$$\frac{du(t)}{dt} + A(t, v(t)) u(t) = 0, \quad t > 0 \quad \text{with } u(t_0) = u_0.$$

In terms of our original model this problem is equivalent to

$$\begin{cases} u_t + (V(x, E[v(t)](x)) u)_x = 0, & x \in [0, \infty), \quad t > 0, \\ V(0, E[v(t)](0)) u(0, t) = 0, & t > 0, \\ u(x, t_0) = u_0(x), & x \in [0, \infty). \end{cases} \tag{4.1}$$

As the open subset W of Y in (H2) let us consider a bounded set contained in the closed ball in $W_0^{1,1}$ with center 0 and radius $r > \|u_0\|_Y$, denoted by \mathcal{B}_r . Let $D := d/dx$ and $u \in W_0^{1,1}$. For a given $w \in \mathcal{B}_r$, the operator A associated to the linear problem (4.1) does not depend explicitly on t and it is given by

$$\begin{aligned} A(w)u &= D(V(x, E^w) u) \\ &= V(x, E^w) Du + (V_x(x, E^w) + \nabla_E V(x, E^w) \cdot E_x^w) u \\ &=: A_1(w)u + A_2(w)u, \end{aligned} \tag{4.2}$$

where, for simplicity in notation, $E^w := E[w]$, $\nabla_E V = (\partial_{E_1} V, \dots, \partial_{E_N} V)$, and $E_x = (\partial_x E_1, \dots, \partial_x E_N)$. Therefore, for each $t \in [0, \infty)$ ($T_0 = \infty$) and $w \in \mathcal{B}_r$, $A(w)$ is a linear operator in L^1 .

Since the operator A does not depend on t we can take $T_0 = \infty$ and, in order to prove the stability of the family $\{A(v(t))\}_{t \in [0, T]}$ we only have to see that, for each $w \in \mathcal{B}_r$, $-A(w)$ generates a contraction semigroup. Hence, $-A(v(t))$ with $v \in \mathcal{D}_\rho$ generates a contraction semigroup for all t .

A characterization of the generator of a positive contraction semigroup in a Banach lattice is given by the Phillips theorem (see Refs. 29 and 31). This theorem

says that a densely defined linear operator $-A$ is the generator of a positive contraction semigroup if and only if the range of $\lambda I + A$ is X for some $\lambda > 0$ and, for any $u \in \mathcal{D}(A)$, there is a positive linear form $\varphi \in X^*$ such that $\|\varphi\| \leq 1$, $\langle u, \varphi \rangle = \|u^+\|$, and $\langle -Au, \varphi \rangle \leq 0$.

The first hypothesis is checked directly by solving explicitly the non-homogeneous first-order linear differential equation

$$\lambda u + (V(x, E^w)u)_x = f$$

with initial condition $u(0) = 0$ and noticing that the solution belongs to $Y = W_0^{1,1}(0, \infty)$ whenever $f \in X = L^1(0, \infty)$ and $\lambda > 0$.

The second hypothesis is fulfilled by taking φ as the sign function of the positive part of u , i.e. $\varphi = \text{sgn}(u^+)$. Indeed, $\varphi \in L_+^\infty(0, \infty)$, $\|\varphi\|_\infty \leq 1$, $\int_0^\infty u\varphi = \int_0^\infty u^+ = \|u^+\|$, and

$$\begin{aligned} \langle -Au, \varphi \rangle &= -\int_0^\infty D(Vu) \text{sgn}(u^+) = -\int_0^\infty D(Vu) \text{sgn}(Vu^+) \\ &= -\int_0^\infty D((Vu)^+) = 0, \end{aligned}$$

where, for simplicity in notation, the arguments of V are omitted, and it is used that, under (A4), V is strictly positive.

Hypothesis (H3). Since $A = A(w)$, the operator $B = SAS^{-1} - A$ does not depend explicitly on t and we can take $T_0 = \infty$. In this case, the condition for $B(w) \in \mathcal{B}(X)$ with $\|B(w)\|_X \leq \lambda_B$, $\lambda_B > 0$, is given by

$$\|(SA(w) - A(w)S)S^{-1}u\|_X \leq \lambda_B \|u\|_X$$

for all $u \in X$.

Let us compute the ‘‘commutator’’ $SA - AS$:

$$\begin{aligned} (SA - AS)u &= D(VD + DV)u - (VD + DV)Du \\ &= (DV)Du + VD^2u + D(DVu) - VD^2u - (DV)Du \\ &= D(DVu) = (D^2V)u + (DV)Du, \end{aligned}$$

where the arguments of V are again omitted for simplicity of notation, $S = D + I$ with $D = d/dx$ and I the identity operator, $u \in W_0^{1,1}$, and $Au = VDu + (DV)u$ with

$$DV(x, E(x)) := V_x(x, E(x)) + \nabla_E V(x, E(x)) \cdot E_x(x).$$

Therefore, the operator $B = (SA - AS)S^{-1}$ in (H3) can be written as

$$Bu = D^2V(D + I)^{-1}u + (DV)D(D + I)^{-1}u, \quad \forall u \in L^1.$$

Let us see that, under (A4), the operator B is uniformly bounded for all $w \in \mathcal{B}_r \subset W_0^{1,1}(0, \infty)$. Let $u \in L^1$ and $v = (D + I)^{-1}u = S^{-1}u \in W_0^{1,1}$. Under (H1), we have that $\|v\|_\infty \leq \|v\|_{W^{1,1}} \leq 3\|u\|_{L^1}$ and, hence, it follows

$$\begin{aligned} \|Bu\|_{L^1} &\leq \|D^2Vv\|_{L^1} + \|(DV)Dv\|_{L^1} \\ &\leq \|V_{xx}v\|_{L^1} + 2\|V_{xE} \cdot E_x^w v\|_{L^1} + \|(E_x^w)^T V_{EE} E_x^w v\|_{L^1} \\ &\quad + \|\nabla_E V \cdot E_{xx}^w v\|_{L^1} + \|V_x Dv\|_{L^1} + \|(\nabla_E V \cdot E_x^w) Dv\|_{L^1} \\ &\leq V_2^0 \|v\|_{L^1} + (2\|V_{xE} \cdot E_x^w\|_{L^1} + \|(E_x^w)^T V_{EE} E_x^w\|_{L^1} \\ &\quad + \|\nabla_E V \cdot E_{xx}^w\|_{L^1}) \|v\|_\infty + (V_1^0 + \|\nabla_E V \cdot E_x^w\|_\infty) \|Dv\|_{L^1} \\ &\leq [V_2^0 + 3(2V_2^0 \| |E_x^w|_1 \|_{L^1} + V_2^0 \|E_x^w \cdot E_x^w\|_{L^1} \\ &\quad + V_1^0(1 + \| |E_{xx}^w|_1 \|_{L^1} + \| |E_x^w|_1 \|_\infty))] \|u\|_{L^1}, \end{aligned} \tag{4.3}$$

where V_{EE} denotes the matrix of the second derivatives with respect to E and $V_{xE} = \nabla_E V_x$, and $|E|_1 := \sum_{i=1}^N |E_i|$. From now on, let us follow such a convention in the notation.

The last two terms on the R.H.S. of the previous inequality can be bounded for all $w \in \mathcal{B}_r$ using that, under (A1), E is a bounded operator from $W^{1,1}$ to M_1 . Precisely, there exists a constant $c > 0$ such that, for all $w \in \mathcal{B}_r$,

$$\| |E_x^w|_1 \|_\infty \leq c \quad \text{and} \quad \| |E_{xx}^w|_1 \|_{L^1} \leq \| |E_x^w|_1 \|_{W^{1,1}} \leq c.$$

Similarly, for the second term we have $\| |E_x^w|_1 \|_{L^1} \leq \| |E_x^w|_1 \|_{W^{1,1}} \leq c \forall w \in \mathcal{B}_r$.

With respect to the third term of the R.H.S. in (4.3), first note that, using that $f \in \mathcal{B}_r \subset W_0^{1,1}$, it follows that

$$\int_0^\infty f^2 = \int_0^\infty |f| |f| \leq \|f\|_\infty \|f\|_{L^1} \leq \|f\|_{W^{1,1}}^2.$$

Hence, for all $w \in \mathcal{B}_r$,

$$\|E_x^w \cdot E_x^w\|_{L^1} \leq \| |E_x^w|_1 \|_\infty \| |E_x^w|_1 \|_{L^1} \leq c^2,$$

where the constant c depends on \mathcal{B}_r . Hence,

$$\|B(w)\|_{L^1} \leq V_2^0 + 3 [c(c + 2) V_2^0 + V_1^0(2c + 1)] =: \lambda_B.$$

That is, $B(w) \in \mathcal{B}(L^1)$ for all $w \in \mathcal{B}_r$, and it is uniformly bounded.

Finally, we have to verify the condition $\|B(w_1) - B(w_2)\|_{L^1} \leq \mu_B \|w_1 - w_2\|_{W^{1,1}}$ with $w_1, w_2 \in \mathcal{B}_r$. Writing the expression of $B(w)$ it follows

$$\begin{aligned} (B(w_1) - B(w_2))u &= D(DV(x, E^{w_1}) - DV(x, E^{w_2}))S^{-1}u \\ &= [V_{xx}(x, E^{w_1}) - V_{xx}(x, E^{w_2}) + 2[(V_{xE}(x, E^{w_1}) - V_{xE}(x, E^{w_2})) \cdot E_x^{w_1} \\ &\quad - V_{xE}(x, E^{w_2}) \cdot (E_x^{w_2} - E_x^{w_1})] + (E_x^{w_1})^T (V_{EE}(x, E^{w_1}) - V_{EE}(x, E^{w_2})) E_x^{w_1} \\ &\quad - (E_x^{w_2} - E_x^{w_1})^T V_{EE}(x, E^{w_2}) E_x^{w_1} + (E_x^{w_2})^T V_{EE}(x, E^{w_2}) (E_x^{w_1} - E_x^{w_2}) \\ &\quad + (\nabla_E V(x, E^{w_1}) - \nabla_E V(x, E^{w_2})) \cdot E_{xx}^{w_1} \\ &\quad + \nabla_E V(x, E^{w_2}) \cdot (E_{xx}^{w_1} - E_{xx}^{w_2})] S^{-1}u. \end{aligned}$$

Taking the L^1 -norm in the previous equality, bounding each term on the R.H.S., and using that, under (A1), E is Lipschitzian with respect to w from $W^{1,1}$ to M_1 and bounded, we have

$$\begin{aligned} & \| (B(w_1) - B(w_2)) u \|_{L^1} \\ & \leq L_2 \| |E^{w_1} - E^{w_2}|_1 S^{-1} u \|_{L^1} + 2L_2 \| |E^{w_1} - E^{w_2}|_1 |E_x^{w_1}|_1 S^{-1} u \|_{L^1} \\ & \quad + 2V_2^0 \| |E_x^{w_1} - E_x^{w_2}|_1 S^{-1} u \|_{L^1} + L_2 \| |E^{w_1} - E^{w_2}|_1 |E_x^{w_1}|_1 \cdot |E_x^{w_2}|_1 S^{-1} u \|_{L^1} \\ & \quad + V_2^0 \| (E_x^{w_1} - E_x^{w_2}) \cdot |E_x^{w_1}|_1 S^{-1} u \|_{L^1} + V_2^0 \| |E_x^{w_2}|_1 \cdot (E_x^{w_1} - E_x^{w_2}) S^{-1} u \|_{L^1} \\ & \quad + V_1^0 \| |E^{w_1} - E^{w_2}|_1 |E_{xx}^{w_1}|_1 S^{-1} u \|_{L^1} + V_1^0 \| |E_{xx}^{w_1} - E_{xx}^{w_2}|_1 S^{-1} u \|_{L^1} \\ & \leq [(1 + 2c) \|u\|_{L^1} + c^2 \|S^{-1} u\|_{\infty}] L_2 \| |E^{w_1} - E^{w_2}|_1 \|_{\infty} \\ & \quad + (2 + c) V_2^0 \| |E_x^{w_1} - E_x^{w_2}|_1 \|_{\infty} \|u\|_{L^1} + cV_2^0 \| |E_x^{w_1} - E_x^{w_2}|_1 \|_{\infty} \|u\|_{L^1} \\ & \quad + cV_1^0 \| |E^{w_1} - E^{w_2}|_1 \|_{\infty} \|S^{-1} u\|_{\infty} + V_1^0 \| |E_x^{w_1} - E_x^{w_2}|_1 \|_{W^{1,1}} \|S^{-1} u\|_{\infty} \\ & \leq L_E [(1 + 2c + 3c^2)L_2 + 2(1 + c)V_2^0 + 3(c + 1)V_1^0] \|w_1 - w_2\|_{W^{1,1}} \|u\|_{L^1}, \end{aligned}$$

where it is used that V satisfies (A4), that $\|S^{-1} u\|_{L^1} \leq \|u\|_{L^1}$, and that $\|S^{-1} u\|_{\infty} \leq \|S^{-1} u\|_{W^{1,1}} \leq 3\|u\|_{L^1}$. Moreover, for any $w \in \mathcal{B}_r$, L_2 is the maximum of the Lipschitz constants of V_{xx} , V_{xE_i} and $V_{E_i E_j}$, and L_E is equal to N times the maximum of the set of Lipschitz constants of the components of $E : W^{1,1}(0, \infty) \rightarrow M_1$ for all $w \in \mathcal{B}_r$.

Hence, the constant μ_B in Hypothesis (H3) is

$$\mu_B = L_E [(1 + 2c + 3c^2)L_2 + 2(1 + c)V_2^0 + 3(c + 1)V_1^0].$$

Hypothesis (H4). Clearly, $\mathcal{D}(A(w)) = W_0^{1,1}(0, \infty) = Y$. So, $A(w) \in \mathcal{B}(W^{1,1}, L^1)$ and, under (A4), it satisfies

$$\begin{aligned} \|A(w)u\|_{L^1} & \leq \|V(x, E^w)Du\|_{L^1} + \|V'(x, E^w)u\|_{L^1} \\ & \leq V^0 \|Du\|_{L^1} + V_1^0 (1 + \| |E_x^w|_1 \|_{\infty}) \|u\|_{L^1} \\ & \leq (V^0 + (1 + c)V_1^0) \|u\|_{W^{1,1}}. \end{aligned}$$

On the other hand, for a given w , $A(w)$ is an autonomous first-order differential operator. Therefore, $A(w) : [0, T_0] \rightarrow \mathcal{B}(Y, X)$ is strongly continuous with $T_0 = \infty$.

We have to see that there exists a constant $\mu_A > 0$ such that $\|A(w_2) - A(w_1)\|_{W^{1,1}, L^1} \leq \mu_A \|w_2 - w_1\|_{L^1}$, for any $w_1, w_2 \in \mathcal{B}_r$. Under hypotheses (A1) and (A4), and using that $A = A_1 + A_2$ (see Eq. (4.2)), we have that, if L_0 is equal to N times the maximum of the N Lipschitz constants corresponding to the components of $E : L^1(0, \infty) \rightarrow M_0$ for all $w \in \mathcal{B}_r$, then

$$\| (A(w_2) - A(w_1)) u \|_{L^1} \leq \| (A_1(w_2) - A_1(w_1)) u \|_{L^1} + \| (A_2(w_2) - A_2(w_1)) u \|_{L^1}$$

with

$$\begin{aligned} \|(A_1(w_2) - A_1(w_1))u\|_{L^1} &\leq \| [V(x, E^{w_2}) - V(x, E^{w_1})] Du \|_{L^1} \\ &\leq V_1^0 \| |E^{w_2} - E^{w_1}|_1 \|_\infty \| Du \|_{L^1} \\ &\leq L_0 V_1^0 \|w_2 - w_1\|_{L^1} \|u\|_{W^{1,1}} \end{aligned}$$

and

$$\begin{aligned} \|(A_2(w_2) - A_2(w_1))u\|_{L^1} &\leq \| (DV(x, E^{w_2}) - DV(x, E^{w_1})) u \|_{L^1} \\ &\leq \| (V_x(x, E^{w_2}) - V_x(x, E^{w_1})) u \|_{L^1} \\ &\quad + \| (\nabla_E V(x, E^{w_2}) - \nabla_E V(x, E^{w_1})) \cdot E_x^{w_2} u \|_{L^1} \\ &\quad + \| \nabla_E V(x, E^{w_1}) \cdot (E_x^{w_2} - E_x^{w_1}) u \|_{L^1} \\ &\leq V_2^0 \| |E^{w_2} - E^{w_1}|_1 \|_\infty \|u\|_{L^1} \\ &\quad + V_2^0 \| |E_x^{w_2}|_1 \|_\infty \| |E^{w_2} - E^{w_1}|_1 \|_\infty \|u\|_{L^1} \\ &\quad + V_1^0 \| |E_x^{w_2} - E_x^{w_1}|_1 \|_{L^1} \|u\|_\infty \\ &\leq L_0((1 + c) V_2^0 + V_1^0) \|w_2 - w_1\|_{L^1} \|u\|_{W^{1,1}}. \end{aligned}$$

Therefore, $\|A(w_2) - A(w_1)\|_{W^{1,1}, L^1} \leq \mu_A \|w_2 - w_1\|_{L^1}$ with $\mu_A := L_0(2V_1^0 + (1 + c)V_2^0)$.

Hypothesis (H5). Imposing hypotheses (A2) and (A3) to the ingredients R and m of the model, respectively, it follows the bounds of $f(t, w)$ in (H5) with

$$f(t, w) = R[w] - m(x, E^w) w,$$

$\|R[w]\|_{L^1} \leq R_1$, and $\|R_x[w]\|_{L^1} \leq R'_1$ for all $w \in \mathcal{B}_r$. Moreover, since f does not depend on t , we can take $T_0 = \infty$.

More precisely, if L_R and L_{R_x} are the Lipschitz constants of R and R_x with respect to w in \mathcal{B}_r respectively, L_{m_x} is the Lipschitz constant of $m_x(x, E^w)$ for all $w \in \mathcal{B}_r$, L_{m_E} is the maximum of the Lipschitz constants of $m_{E_i}(x, E^w)$ with respect to E_i for all $w \in \mathcal{B}_r$ and for all $1 \leq i \leq N$, and $\|m(\cdot, E^w)\|_\infty \leq m^0$, $\|m_x(\cdot, E^w)\|_\infty \leq m_x^0$, $\| |\nabla_E m(\cdot, E^w)|_1 \|_\infty \leq m_E^0$ for all $w \in \mathcal{B}_r$, then

$$\begin{aligned} \|f(w)\|_{W^{1,1}} &\leq \|m(\cdot, E^w) w\|_{W^{1,1}} + \|R[w]\|_{W^{1,1}} \\ &\leq (m^0 + m_x^0 + m_E^0 \| |E_x^w|_1 \|_\infty) \|w\|_{W^{1,1}} + R_1 + R'_1 \\ &\leq (m^0 + m_x^0 + c m_E^0) r + R_1 + R'_1 =: \lambda_f, \end{aligned}$$

$$\begin{aligned} \|f(w_1) - f(w_2)\|_{L^1} &\leq \|m(\cdot, E^{w_1}) w_1 - m(\cdot, E^{w_2}) w_2\|_{L^1} + \|R[w_1] - R[w_2]\|_{L^1} \\ &\leq \| [m(\cdot, E^{w_1}) - m(\cdot, E^{w_2})] w_1 \|_{L^1} \\ &\quad + \|m(\cdot, E^{w_2})(w_1 - w_2)\|_{L^1} + L_R \|w_1 - w_2\|_{L^1} \end{aligned}$$

$$\begin{aligned}
 &\leq m_E^0 \| |E^{w_1} - E^{w_2}|_1 \|_{L^1} \|w_1\|_\infty + (m^0 + L_R) \|w_1 - w_2\|_{L^1} \\
 &\leq (m_E^0 L_0 r + m^0 + L_R) \|w_1 - w_2\|_{L^1} =: \mu_f \|w_1 - w_2\|_{L^1}, \\
 \|f(w_1) - f(w_2)\|_{W^{1,1}} &\leq \left\| [m_x(\cdot, E^{w_1}) - m_x(\cdot, E^{w_2})] w_1 + m_x(\cdot, E^{w_2})(w_1 - w_2) \right\|_{L^1} \\
 &\quad + \left\| [\nabla_E m(\cdot, E^{w_1}) \cdot E_x^{w_1} - \nabla_E m(\cdot, E^{w_2}) \cdot E_x^{w_2}] w_1 \right\|_{L^1} \\
 &\quad + \left\| (w_1 - w_2) \nabla_E m(\cdot, E^{w_2}) \cdot E_x^{w_2} \right\|_{L^1} \\
 &\quad + \left\| [m(\cdot, E^{w_1}) - m(\cdot, E^{w_2})] w'_1 + m(\cdot, E^{w_2})(w'_1 - w'_2) \right\|_{L^1} \\
 &\quad + \|R_x[w_1] - R_x[w_2]\|_{L^1} + \mu_f \|w_1 - w_2\|_{L^1} \\
 &\leq L_{m_x} \|w_1\|_{L^1} \| |E^{w_1} - E^{w_2}|_1 \|_\infty + m_x^0 \|w_1 - w_2\|_{L^1} \\
 &\quad + m_E^0 \| |E_x^{w_1} - E_x^{w_2}|_1 \|_{L^1} + L_{m_E} \|E_x^{w_2}\|_\infty \| |E^{w_1} - E^{w_2}|_1 \|_{L^1} \\
 &\quad + c m_E^0 \|w_1 - w_2\|_{L^1} + m_E^0 \|w'_1\|_{L^1} \| |E^{w_1} - E^{w_2}|_1 \|_\infty \\
 &\quad + m^0 \|w_1 - w_2\|_{W^{1,1}} + L_{R_x} \|w_1 - w_2\|_{L^1} + \mu_f \|w_1 - w_2\|_{L^1} \\
 &\leq [L_0(r L_{m_x} + m_E^0(r+1) + L_{m_E} c) + c m_E^0 + m_x^0 + m^0 \\
 &\quad + L_{R_x} + \mu_f] \|w_1 - w_2\|_{W^{1,1}} =: \bar{\mu}_f \|w_1 - w_2\|_{W^{1,1}}
 \end{aligned}$$

for all $w, w_1, w_2 \in \mathcal{B}_r$.

Therefore, the hypotheses of Theorems I and II are fulfilled with $T_0 = \infty$ and W any open set contained in an arbitrary closed ball $\mathcal{B}_r \subset W_0^{1,1}(0, \infty)$ with $r > \|u_0\|_{W^{1,1}}$, and, hence, we have the following

Theorem 1. *Under hypotheses (A1)–(A4) and for any $u_0 \in W_0^{1,1}(0, \infty)$, there exists a time $T > 0$ such that the IVP (2.1) has a unique solution*

$$u \in \mathcal{C}([0, T]; W_0^{1,1}(0, \infty)) \cap \mathcal{C}^1([0, T]; L^1(0, \infty)).$$

Moreover, the family of operators $\{U(t, s)\}$, $(t, s) \in \Delta$, generated by $\{A(t, u(t))\}_{t \in [0, T]}$ is stable with stability index $(M, \alpha) = (1, 0)$ in $L^1(0, \infty)$ and $(\tilde{M}, \tilde{\alpha}) = (3, V_2^0 + 3c[(c+2)V_2^0 + V_1^0])$ in $W_0^{1,1}(0, \infty)$, and it satisfies the properties of Theorem II.

5. Continuous Dependence on Initial Conditions and Positivity of Solutions

Under hypotheses (H1)–(H5) and since the evolution operator of (3.1) satisfies Theorem II, it follows that:

Theorem 2. *Let T be a common local existence time and let u and v be solutions of (3.1) with initial conditions u_0 and v_0 respectively. Then, for all $0 < t < T$, there exists a constant $\xi(r, T)$ such that*

$$\|u(t) - v(t)\|_X \leq M e^{\alpha t} \|u_0 - v_0\|_X (1 + t \xi(r, T))$$

with $r > \max\{\|u_0\|_Y, \|v_0\|_Y\}$.

Proof. Let \mathcal{B}_r be a closed ball in Y with center 0 and radius $r > \max\{\|u_0\|_Y, \|v_0\|_Y\}$ containing W , and let \mathcal{M} be the following set

$$\mathcal{M} := \{v \in \mathcal{C}([0, T]; Y) : v(t) \in \mathcal{B}_r \ \forall t \in [0, T] \text{ and } \|v(t) - v(s)\|_X \leq \rho_0|t - s|, \ 0 \leq s \leq t \leq T\}$$

with ρ_0 being a suitable positive constant (see Ref. 22 for details).

Moreover, let Ψ be an operator from \mathcal{M} into $\mathcal{C}([0, T]; Y)$ defined by

$$\Psi[v](t) = U^v(t, 0)u_0 + \int_0^t U^v(t, s)f^v(s) \, ds, \quad 0 \leq t \leq T, \tag{5.1}$$

with $\{U^v(t, s)\}, (t, s) \in \Delta$, being the evolution operator generated by $\{A(t, v(t))\}_{t \in [0, T]}$, $v \in \mathcal{M}$, and $f^v(s) := f(s, v(s))$.

Under hypotheses (H1)–(H5), Theorem II guarantees the existence of the evolution operator $\{U^u(t, s)\}, (t, s) \in \Delta$, generated by $\{A(t, u(t))\}_{t \in [0, T]}$ with $u(t)$ being the unique solution of the IVP (3.1) in the sense of Theorem I. In particular, given the solutions $u(t)$ and $v(t)$ of (3.1) with initial conditions $u(0) = u_0$ and $v(0) = v_0$, respectively, the corresponding evolution operators $U^u(t, s)$ and $U^v(t, s)$ satisfy, for $(t, s) \in \Delta$ and $y \in Y$,

$$\|U^u(t, s)y - U^v(t, s)y\|_X \leq \mu_A M \tilde{M} e^{\tilde{\alpha}(t-s)} \|y\|_Y \int_s^t \|u(\tau) - v(\tau)\|_X \, d\tau,$$

where $\tilde{M} = M \|S\|_{Y, X} \|S^{-1}\|_{X, Y}$ and $\tilde{\alpha} = \lambda_B M + \alpha$ (see Theorem II). The proof of this inequality follows from the derivative of $U^u(t, \sigma)U^v(\sigma, s)y$ with respect to σ , using property (d) in Theorem II, and then integrating the resulting expression between 0 and t (for details, see Ref. 22, Lemma 2.4, taking into account that $u(t)$ and $v(t)$ belong to \mathcal{M} if $0 \leq t \leq T$). It is worth noticing that the condition $y \in Y$ is needed in order to obtain the previous inequality, otherwise the term $A(t, v(t))U^v(t, s)y$ appearing in the previous derivative is not defined because, under (H4), $A(t, w) \in \mathcal{B}(Y, X)$ for $w \in W$. This fact restricts the continuous dependence on initial conditions to be in the X -norm.

Since $u(t)$ and $v(t)$ are the solutions to (3.1) in the sense of Theorem I, with initial condition $u(0) = u_0$ and $v(0) = v_0$ respectively, they are fixed points of Ψ and, then, $\|u(t) - v(t)\|_X = \|\Psi[u](t) - \Psi[v](t)\|_X$. From the definition of Ψ it follows

$$\begin{aligned} \Psi[u](t) - \Psi[v](t) &= U^u(t, 0)(u_0 - v_0) + (U^u(t, 0) - U^v(t, 0))v_0 \\ &\quad + \int_0^t U^u(t, s)[f^u(s) - f^v(s)] \, ds \\ &\quad + \int_0^t (U^u(t, s) - U^v(t, s))f^v(s) \, ds. \end{aligned}$$

Now, using the hypotheses (H1)–(H5), the previous upper bound of $\|U^u(t, s)y - U^v(t, s)y\|_X$, and since $u(t), v(t) \in \mathcal{B}_r$ for all $t \in [0, T]$, it follows

$$\begin{aligned} \|u(t) - v(t)\|_X &\leq \|U^u(t, 0)(u_0 - v_0)\|_X + \|(U^u(t, 0) - U^v(t, 0))v_0\|_X \\ &\quad + \int_0^t \|U^u(t, s)[f^u(s) - f^v(s)]\|_X ds \\ &\quad + \int_0^t \|(U^u(t, s) - U^v(t, s))f^v(s)\|_X ds \\ &\leq Me^{\alpha t} \left[r\mu_A \tilde{M} e^{\lambda_B M t} (1 + t\lambda_f) \int_0^t \|u(\tau) - v(\tau)\|_X d\tau \right. \\ &\quad \left. + \|u_0 - v_0\|_X + \int_0^t \|f^u(s) - f^v(s)\|_X ds \right] \\ &\leq Me^{\alpha t} \left\{ \|u_0 - v_0\|_X + [r\mu_A \tilde{M} e^{\lambda_B M t} (1 + t\lambda_f) + \mu_f] \right. \\ &\quad \left. \times \int_0^t \|u(s) - v(s)\|_X ds \right\}. \end{aligned}$$

Finally, applying Gronwall’s inequality, it follows

$$\|u(t) - v(t)\|_X \leq Me^{\alpha t} \|u_0 - v_0\|_X [1 + tM\beta(r, t)e^{t(Me^{\alpha t}\beta(r, t) + \alpha)}],$$

where $\beta(r, t) := r\mu_A \tilde{M} e^{\lambda_B M t} (1 + t\lambda_f) + \mu_f$, and, hence, the constant in the statement is $\xi(r, T) := M\beta(r, T)e^{T(Me^{\alpha T}\beta(r, T) + \alpha)}$. □

In particular, in our case, since $-A(t, u(t))$ is the generator of a contraction semigroup, $M = 1$ and we have

Corollary 1. *Let T be a common local existence time and let u and v be solutions of (2.1) with initial conditions u_0 and v_0 , respectively, in $W^{1,1}(0, \infty)$. Then, under hypotheses (A1)–(A4), there exists a constant $\xi(r, T)$ such that*

$$\|u(t) - v(t)\|_{L^1} \leq e^{\alpha t} (1 + t\xi(r, T)) \|u_0 - v_0\|_{L^1} \quad \forall t \in [0, T].$$

Theorem 3. *Let T be a common local existence time and let R be a positive operator and $u_0 \geq 0$. Then, under hypotheses (A1)–(A4), the solution of the IVP (2.1) is non-negative for any $t \in [0, T]$.*

Proof. Let $\bar{U}^v(t, s)$ be the evolution operator generated by $\bar{A}(t, v(t)) := A(t, v(t)) + m^0I$ and $\bar{f}^v(t) := f(t, v(t)) + m^0v$. It is clear that $\bar{A}(t, v(t))$ and $\bar{f}^v(t)$ satisfy (H2)–(H5) and that the solution to the IVP (2.1) is the limit of the sequence of iterations $\{u^n\}$ with $u^n = \bar{\Psi}[u^{n-1}]$ and $\bar{\Psi}$ being the operator defined by the R.H.S. of (5.1) with U^v and f^v replaced by \bar{U}^v and $\bar{f}^v(t)$, respectively, with $u^0 = u_0$.²²

Note that \bar{U}^v is positive since it is the solution of the linear IVP (4.1) with $u_0 \geq 0$ and the R.H.S. of (4.1)₁ replaced by $-m^0u$. Moreover, $\bar{f}^v \geq 0$ by construction (recall that m^0 is an upper bound of $m(x, E)$ and that $f(x, v) = R[v](x) - m(x, E^v)v$). Hence, under the assumption of the positivity of R , $u^n(t) \geq 0$ from (5.1) and, since $u(t) = \lim_{n \rightarrow \infty} u^n(t)$ in the $W_0^{1,1}$ -norm for all $t \in [0, T]$ (see Ref. 22, Lemma 3.7), it follows that $u(t) \geq 0$. □

In particular, in many population models, the recruitment is given by

$$R[u](x) = \int_0^\infty \beta(x, y, E[u](y)) u(y) dy$$

with $\beta(x, y, E[u](y))$ being the contribution to the recruitment of newborns of size x from individuals of size y , which is also a function of the environmental conditions of the latter, $E[u](y)$, when the population density is u .

6. Global Existence of Solution

6.1. Integration of the IVP along characteristic curves

The smoothness of the local solution obtained in the previous section allows us to integrate (2.1) along characteristic curves. In fact, we can identify each element $u(t)(x)$ in the space

$$L_T := \mathcal{C}([0, T]; W_0^{1,1}(0, \infty)) \cap \mathcal{C}^1([0, T]; L^1(0, \infty))$$

with an element $\bar{u}(x, t)$ of the space $W^{1,1}(\Omega_T; R)$, where $\Omega_T := (0, \infty) \times [0, T]$. For simplicity, let us denote this element by $u(x, t)$. In particular, $u(x, t)$ has classical gradient defined almost everywhere in Ω_T (see, for instance, Ref. 26, Theorem 1, p. 8) and, moreover, the chain rule holds (Ref. 26, Prop. IX.6).

Therefore, given a (local) solution $u(x, t)$ of (2.1), if $\varphi(t; t_0, x_0)$ is the *characteristic curve* passing through $(x_0, t_0) \in \Omega_T$, i.e. if it is the solution of

$$\frac{\partial \varphi}{\partial t} = V(\varphi(t; t_0, x_0), E[u(t)](\varphi(t; t_0, x_0))), \quad \varphi(t_0; t_0, x_0) = x_0,$$

and $\tilde{u}(t) := u(\varphi(t; t_0, x_0), t)$, we can consider (2.1)₁ as a directional derivative and, so, for a fixed (x_0, t_0) , we have

$$\frac{d}{dt} \tilde{u}(t) = \frac{\partial u}{\partial t} + V \frac{\partial u}{\partial x} = G[u], \tag{6.1}$$

where

$$G[u(t)](x) := R[u(t)](x) - DV(x, E[u(t)](x)) u(x, t) - m(x, E[u(t)](x)) u(x, t).$$

Now, let τ be implicitly given by $\varphi(\tau; t, x) = 0$. Then integrating (6.1) from τ to t for $\tau > 0$, and from 0 to t otherwise, and imposing the initial and boundary conditions of (2.1), we have that, if u is a (local) solution of (2.1), then u satisfies

the following integral equation

$$u(x, t) = \begin{cases} \int_{\tau}^t e^{-\int_{\zeta}^t m(\varphi(s; t, x), E[u(s)](\varphi(s; t, x))) ds} R[u(\zeta)](\varphi(\zeta; t, x)) \varphi_x(\zeta; t, x) d\zeta, & x < z(t), \\ u_0(\varphi(0; t, x)) e^{-\int_0^t m(\varphi(s; t, x), E[u(s)](\varphi(s; t, x))) ds} \varphi_x(0; t, x) \\ + \int_0^t e^{-\int_{\zeta}^t m(\varphi(s; t, x), E[u(s)](\varphi(s; t, x))) ds} R[u(\zeta)](\varphi(\zeta; t, x)) \varphi_x(\zeta; t, x) d\zeta, & x > z(t), \end{cases} \quad (6.2)$$

where $z(t) := \varphi(t; 0, 0)$ is the characteristic curve coming from the origin, and

$$\varphi_{x_0}(t; t_0, x_0) := \exp\left(\int_{t_0}^t DV(\varphi(s; t_0, x_0), E[u(s)](\varphi(s; t_0, x_0))) ds\right) \quad (6.3)$$

is the Jacobian of the change of variable $x \rightarrow x_0 := \varphi(0; t, x)$, which gives the infinitesimal change of volume in the x -space when going from t_0 to t . Note that, taking into account that $\exp(-\int_{t_0}^t m(\varphi(s; t, x), E[u(s)](\varphi(s; t, x))) ds)$ is the *survival function*, the expression of the solution along characteristics can be easily interpreted. For instance, for $x > z(t)$, $u(x, t)$ is equal to the density of individuals of the same cohort already present at time zero that still survive at time t times the infinitesimal change of volume of the space of sizes, plus the sum of the newborns with different size-at-birth that have been recruited in that cohort and that still survive at time t , all of them affected by the change of volume in the x -space from their time at birth ζ up to time t .

6.2. *A priori estimates of the solution*

In order to obtain an *a priori* estimate of the $W^{1,1}$ -norm of the solution, it will be convenient to assume the following hypothesis

(A5) For any positive integrable function u , $\frac{\partial V(x, E)}{\partial E_i} \frac{\partial E_i[u](x)}{\partial x} \geq 0$ for all $1 \leq i \leq N$.

Note that this hypothesis is trivially fulfilled for those components of E that are finite-dimensional, i.e. for those $E_i = E_i(t)$. For the rest of the components, (A5) says that, regardless of other physiological effects, an increase of size always has positive consequences for the individual growth with respect to the environment. In fact, from (A5), it follows that $\nabla_E V \cdot E_x \geq 0$.

Lemma 1. *Let us assume hypotheses (A1)–(A5) and let $u(x, t)$ be a positive solution of the IVP (2.1) up to time T . Then the $W^{1,1}$ -norm of $u(x, t)$ is upper bounded by a positive continuous function of t for all $t \in [0, T]$.*

Proof. Since $u \in L_T$, one can integrate (2.1)₁ with respect to x . Moreover, under (A2), we can choose a constant $R^0 := \max\{R^1, R^\infty\}$ with $\|R[u]\|_{L^1} \leq R^1 \|u\|_{L^1}$ and $\|R[u]\|_\infty \leq R^\infty \|u\|_{L^1}$. Then, from the positivity of $u(t)$ and $m(x, E)$, it follows that

$$\frac{d}{dt} \|u(t)\|_{L^1} = \int_0^\infty (R[u(t)](s) - m(s, E[u(t)](s)) u(s, t)) ds \leq R^0 \|u(t)\|_{L^1}.$$

Hence, we have the following upper bound of the L^1 -norm of the solution $u(x, t)$:

$$\|u(t)\|_{L^1} \leq \|u_0\|_{L^1} e^{R^0 t}. \tag{6.4}$$

Second, with respect to the sup-norm of the solutions, from (6.1) it follows that

$$\frac{d\tilde{u}(t)}{dt} = R[u(t)](x) - \lambda(x, t) \tilde{u}(t) \leq R^0 \|u(t)\|_{L^1} - \lambda_0 \tilde{u}(t),$$

where $\lambda(x, t) := DV(x, E(x, t)) + m(x, E(x, t))$ and $\lambda_0 = \inf_{x, t > 0} \{V_x(x, E(x, t))\}$ provided that the latter is negative, and $\lambda_0 = 0$ otherwise (recall that $\nabla_{EV} \cdot E_x$ and $m(x, E)$ are non-negative).

Therefore, using (6.4) we have that if $\lambda_0 \neq -R^0$ then

$$\|u(t)\|_\infty \leq \|u_0\|_\infty e^{-\lambda_0 t} + \frac{R^0 \|u_0\|_{L^1}}{R^0 + \lambda_0} e^{R^0 t} =: g_1(t). \tag{6.5}$$

Otherwise, i.e. $\lambda_0 = -R^0 < 0$, we have

$$\|u(t)\|_\infty \leq (\|u_0\|_\infty + R^0 \|u_0\|_{L^1} t) e^{R^0 t} =: g_2(t). \tag{6.6}$$

Now, let us compute $u_x(x, t)$ in order to obtain an *a priori* estimation of the $W^{1,1}$ -norm of the solutions. First, let us consider u as a function of t and $\xi := \varphi(0; t, x)$ for $x > z(t)$, and as a function of t and τ , with τ given by $\varphi(\tau; t, x) = 0$ for $x < z(t)$, i.e.

$$u(x, t) = \bar{u}(t, \tau(x, t)), \quad 0 < x < z(t), \quad u(x, t) = \bar{\bar{u}}(t, \xi(x, t)), \quad x > z(t).$$

Hence, we have

$$u_x(x, t) = \begin{cases} \bar{u}_\tau(t, \tau) \partial_x \tau(x, t) & \text{if } x < z(t), \\ \bar{\bar{u}}_\xi(t, \xi) \partial_x \xi(x, t) & \text{if } x > z(t), \end{cases}$$

and, so, we can express the L^1 -norm of u_x as

$$\begin{aligned} \|u_x(t)\|_{L^1} &= \int_0^{z(t)} |u_x(x, t)| dx + \int_{z(t)}^\infty |u_x(x, t)| dx \\ &= \int_0^t |\bar{u}_\tau(t, \tau)| d\tau + \int_0^\infty |\bar{\bar{u}}_\xi(t, \xi)| d\xi. \end{aligned} \tag{6.7}$$

The expressions of \bar{u}_τ and $\bar{\bar{u}}_\xi$ computed from (6.2) (see the Appendix for details) and the previous upper bounds of the sup-norm and L^1 -norm of the

solution lead, after changing the order of integration, to the following bound of the L^1 -norm of u_x :

$$\begin{aligned} \|u_x(t)\|_{L^1} &\leq \|u'_0\|_{L^1} e^{-\lambda_0 t} + tR^0 \|u_0\|_{L^1} e^{(R^0-\lambda_0)t} \\ &\quad + tR_x^0 \|u_0\|_{L^1}^2 e^{-\lambda_0 t} [e^{2R^0 t} + e^{-\lambda_0 t}] \\ &\quad + t(m_x^0 + V_2^0) \|u_0\|_{L^1} (e^{-\lambda_0 t} + e^{R^0 t}) \\ &\quad + t(m_E^0 + V_2^0) (\|u_0\|_\infty e^{-\lambda_0 t} + g(t)) c' \|u_0\|_{L^1} e^{R^0 t} \\ &\quad + [\|u_0\|_\infty e^{-\lambda_0 t} + g(t)] \left(V_2^0 \int_0^t \|E_x(s) \cdot E_x(s)\|_{L^1} ds \right. \\ &\quad \left. + V_1^0 \int_0^t \| |E_{xx}(s)|_1 \|_{L^1} ds \right) \end{aligned} \tag{6.8}$$

with $g(t)$ being equal to $g_1(t)$ if $\lambda_0 \neq -R^0$ or to $g_2(t)$ if $\lambda_0 = -R^0$. In particular, after changing the order of integration and grouping terms, we have used that

$$\begin{aligned} &\int_0^s \bar{u}(t, \tau) (-\varphi_\tau(s; \tau, 0)) d\tau + \int_0^\infty \bar{u}(t, \xi) \varphi_\tau(s; 0, \xi) d\xi \\ &= \int_0^{z(s)} u(t, x) dx + \int_{z(s)}^\infty u(t, x) dx = \|u(t)\|_{L^1} \leq \|u_0\|_{L^1} e^{R^0 t}, \end{aligned}$$

and, by (6.3), that

$$\int_0^\infty u_0(\xi) e^{-\int_0^t \lambda(s, \xi) ds} \varphi_\xi(s; 0, \xi) d\xi \leq \|u_0\|_{L^1} e^{-\lambda_0(t-s)}.$$

Moreover, under (A1) and (A2), $\| |E_x(t)|_1 \|_{L^1} \leq c' \|u(t)\|_{L^1}$, and $\|R_x[u]\|_{L^1} \leq R_x^0 \|u\|_{L^1}$.

Using that $\| |E_x(t)|_1 \|_\infty \leq \| |E_x(t)|_1 \|_{W^{1,1}} \leq c'' \|u(t)\|_{W^{1,1}}$, the last two integrals in (6.8) can be bounded as follows

$$\begin{aligned} \int_0^t \|E_x(s) \cdot E_x(s)\|_{L^1} ds &\leq \int_0^t \| |E_x(s)|_1 \|_\infty \| |E_x(s)|_1 \|_{L^1} ds \\ &\leq c' \|u_0\|_{L^1} e^{R^0 t} \int_0^t \| |E_x(s)|_1 \|_\infty ds \\ &\leq c' \|u_0\|_{L^1} e^{R^0 t} c'' \int_0^t (\|u(s)\|_{L^1} + \|u_x(s)\|_{L^1}) ds \end{aligned}$$

and

$$\int_0^t \| |E_{xx}(s)|_1 \|_{L^1} ds \leq c'' \int_0^t (\|u(s)\|_{L^1} + \|u_x(s)\|_{L^1}) ds.$$

Denoting by $f_1(t)$ all the terms of the R.H.S. of (6.8) with the exception of the last one and if

$$f_2(t) := c'' [\|u_0\|_\infty e^{-\lambda_0 t} + g(t)] (V_2^0 c' \|u_0\|_{L^1} e^{R^0 t} + V_1^0),$$

it follows that

$$\begin{aligned} \|u_x(t)\|_{L^1} &\leq f_1(t) + f_2(t) \left(\int_0^t \|u(s)\|_{L^1} ds + \int_0^t \|u_x(s)\|_{L^1} ds \right) \\ &\leq f(t) + f_2(t) \int_0^t \|u_x(s)\|_{L^1} ds, \end{aligned}$$

where $f(t) := f_1(t) + f_2(t) \|u_0\|_{L^1} (e^{R^0 t} - 1)/R^0$.

Finally, once Gronwall's lemma is applied, (6.8) becomes

$$\|u_x(t)\|_{L^1} \leq f(t) + f_2(t) \int_0^t f(s) \exp\left(\int_s^t f_2(\zeta) d\zeta\right) ds. \tag{6.9}$$

That is, we have bounded $\|u_x\|_{L^1}$ by means of an increasing and continuous function of time which only depends on the $W^{1,1}$ -norm of the initial condition and on the functions appearing in the model ingredients (throughout $R^0, R_x^0, \lambda_0, V_1^0, V_2^0, m_x^0, m_E^0$). Therefore, we have that

$$\|u(t)\|_{W^{1,1}} = \|u(t)\|_{L^1} + \|u_x(t)\|_{L^1} \leq \|u_0\|_{W^{1,1}} e^{R^0 t} + N_2(t, \|u_0\|_{W^{1,1}}),$$

where $N_2(t, \|u_0\|_{W^{1,1}})$ denotes the R.H.S. of (6.9) with $\|u_0\|_{L^1}$ and $\|u_0\|_\infty$ replaced by $\|u_0\|_{W^{1,1}}$. □

6.3. Existence of a global solution

Let \mathcal{M}_Y be the set

$$\mathcal{M}_Y := \{v \in \mathcal{C}([0, T]; Y) : v(t) \in \mathcal{B}_r \ \forall t \in [0, T]\},$$

which is a complete metric space if endowed with the distance $d_Y(v, w) := \sup_{t \in [0, T]} \|v(t) - w(t)\|_Y$. Moreover, given a solution u of the IVP (3.1) in the sense of Theorem I, let us consider the mapping $\Phi_u : \mathcal{M}_Y \rightarrow \mathcal{C}([0, T]; Y)$ defined by

$$\Phi_u[v](t) = S^{-1}U^u(t, 0)Su_0 + \int_0^t S^{-1}U^u(t, s)\{Sf^v(s) - B^v(s)Sv(s)\}ds, \quad 0 \leq t \leq T,$$

where $\{U^u(t, s)\}, (t, s) \in \Delta$, is the evolution operator generated by $\{A(t, u(t))\}_{t \in [0, T]}$, $B^w(t) := B(t, w(t))$ is the operator valued function given in (H3), and, for convenience of notation, $f^v(t) := f(t, v(t))$. This mapping has u as a unique fixed point in \mathcal{M}_Y .²²

The local existence time is determined from requiring, first, that the operator Ψ defined in the proof of Theorem 2 is a mapping from \mathcal{M} into \mathcal{M} (see Lemma 3.1 in Ref. 22) and, second, that the operator Φ_u is a mapping from \mathcal{M}_Y into \mathcal{M}_Y (see Lemma 3.5 in Ref. 22). For instance, imposing that $\Psi : \mathcal{M} \rightarrow \mathcal{M}$ amounts to the following inequality

$$r_2 \exp\{\lambda_B M e^{\beta T} \|S\|_{Y, X} \|S^{-1}\|_{X, Y} T\} < r,$$

where $r_2 := r_1 + M e^{\beta T} \|S\|_{Y,X} \|S^{-1}\|_{X,Y} (\lambda_f + \lambda_B \|\phi\|) T$ with $r_1(\|u_0 - \phi\|_Y) = r_1(\|u_0\|_Y) < r$ (in our case, $\phi \equiv 0$) being an increasing function of $\|u_0\|_Y$ (see the proof of Lemma 3.1 in Ref. 22). A similar inequality follows from imposing $\Phi : \mathcal{M}_Y \rightarrow \mathcal{M}_Y$. What is relevant here is that such inequalities imply that the maximal time T_0 for which $\Psi : \mathcal{M} \rightarrow \mathcal{M}$ and $\Phi : \mathcal{M}_Y \rightarrow \mathcal{M}_Y$ is a strictly decreasing function of $\|u_0\|_Y$: $T_0 = T_0(\|u_0\|_Y)$. Using this fact, we can state the following

Theorem 4. *Under hypotheses (A1)–(A5) with R a positive operator and for any $T^* > 0$, the IVP (2.1) has a unique solution up to time T^* , which is positive whenever the initial condition $u_0 > 0$.*

The proof of this theorem is omitted since it proceeds along the same lines as that of Theorem 3 in Ref. 8 replacing L^1 -norm by $W^{1,1}$ -norm.

7. Biological and Concluding Remarks

In this paper we have proved the well-posedness as well as the global existence of solution of a class of PDE models arising in the so-called hierarchically structured population dynamics. A first feature of these models is that the nonlinearities appear in the model by means of an infinite-dimensional environment in such a way that, if the latter is known, the model becomes linear. Environments in such models can be written as the following integral operator

$$E[u](x) = \int_0^\infty \gamma(x, y) u(y) dy. \tag{7.1}$$

For environments with more than one component, the more general structure assumed in the literature is given by the so-called “generalized mass action”,¹² i.e. with components of the form $E_i[u] = E[u]$ and, for $i > 1$,

$$E_i[u](x) = \int_0^\infty \gamma_i(x, y, E_1(y), \dots, E_{i-1}(y)) u(y) dy,$$

where $\gamma_i(x, y, E_1(y), \dots, E_{i-1}(y))$ represents the contribution of individuals with ranks/sizes between y and $y + dy$ to the environment experienced by an individual of size x . Therefore, as long as γ_i , $i \geq 1$, is globally bounded and Lipschitzian with respect to the “previous” environmental components E_1, \dots, E_{i-1} , hypothesis (A1) is fulfilled. In other words, the existence and uniqueness of solution of the corresponding IVP is compatible with the generalized mass action.

It is worth noticing that it is shown elsewhere a lack of uniqueness of solution of nonlinear transport equations with nonlocal nonlinearities when the positivity condition on the individual growth rate V is not satisfied and a non-Lipschitzian γ_i is assumed.¹⁴ As in the present paper, the key point is the assumption of a nonlinear individual growth rate with a nonlocal dependence on the solution. This fact provokes a lack of uniqueness under certain non-smooth initial conditions due to the development of singularities when V vanishes in those regions where γ_i is either discontinuous or non-Lipschitzian. Hence the source of this nonuniqueness is

different from the one in hyperbolic equations with local nonlinearities, namely, the occurrence of shock waves due to the intersection of characteristics curves.

The dependence among environmental components seems to be the case, for instance, when there are interferences in the acquisition of essential resources as light, water or mineral nutrients, in plant populations; i.e. when individuals have to balance availability of different resources and individual demand which results in multiple resource limitation (see, for instance, Refs. 17, 18 and 33). In this case, the hypothesis of a generalized mass action offers a suitable framework when the availability of resources is the result, first, of their environmental supply and, second, of the population consumption, and, moreover, there exists a hierarchical dependence in their acquisition as it happens, for instance, between light and essential mineral nutrients.

Of course, when all the components E_i are independent of each other, we are in a particular situation of the one considered in this paper. A simple example appears in Ref. 9 where it is considered that vital rates of any individual with a given rank/size depend on a linear combination of the number of individuals in the population with higher ranks and those individuals with a lower rank (size-related competition). Under such an assumption, the environment experienced by an individual of size/rank x when the population density is $u(x, t)$ is given by

$$E[u(t)](x) = \delta \int_0^x u(y, t) dy + (1 - \delta) \int_x^\infty u(y, t) dy, \quad 0 \leq \delta \leq 1, \quad (7.2)$$

i.e. $\gamma(x, y) = \delta \mathcal{X}_{[0, x]} + (1 - \delta) \mathcal{X}_{[x, \infty)}$. It is easy to check that this environment satisfies hypothesis (A1) for $N = 1$. On the other hand, each of the previous integrals can be considered as a particular environmental variable and, so, $E[u] = (E_1[u], E_2[u])$ as it was done, for instance, in Refs. 10 and 11 in order to model competition in hierarchical age-dependent populations. In this case, given an age x , $E_1(x)$ corresponds to the sub-population size of younger individuals and $E_2(x)$ to that of older individuals. Also in Ref. 10, the environment given by (7.2), with $\delta \in [0, 1/2]$, was the one considered for modelling different ways by which individuals can interact, ranging from asymmetrical or contest competition ($\delta = 0$) to symmetrical or scramble competition ($\delta = 1/2$). Other examples of such a sort of environments with different γ are, for instance, in Refs. 1, 5, 6, 7, 21 and 23.

In the example of an environment given by (7.2), the restriction $\delta \in [0, 1/2]$ assumed in Ref. 10 implies that $\partial E[u(t)](x)/\partial x \leq 0$. This fact says that, for a given age x , the competition effects caused by older individuals on an x -aged individual are stronger than those of the younger individuals. So, when an individual becomes older, he/she feels less competition pressure from the rest of the population relatively to those that are younger. A similar situation occurs when the individual state x is size instead of age, as in Ref. 9. In such a case and when a nonlinear individual growth is considered, the hypothesis (A5) used in the proof of global existence of solution, namely, $(\partial V(x, E)/\partial E)(\partial E[u(t)](x)/\partial x) \geq 0$, amounts to the condition $\partial V(x, E)/\partial E \leq 0$ which says that an increase in the value of the environmental variable is translated into negative effects on the growth because, in this context,

E is a measure of competition. The converse happens when E is positively related to the resource abundance as, for instance, in populations with cannibalism. In this case $\partial V(x, E)/\partial E$ should be positive and, hence, $\partial E[u(t)](x)/\partial x \geq 0$ in order to satisfy the hypothesis (A5). Note that a hypothesis analogous to (A5) has also been assumed elsewhere to guarantee the existence of a global continuous solution in a hierarchically structured forest model with an environment similar to the one given by (7.1) with $\gamma(x, y) = \alpha(y) 1_{y \geq x}$ (see Theorem 2 in Ref. 23).

A second feature of the model appears in the recruitment term $R[u(t)](x)$. Here it is assumed that the size-at-birth is distributed, i.e. different newborns (or seedlings, etc.) have different sizes. A typical assumption about this term is to take it as

$$R[u(t)](x) = \int_{x_0}^{\infty} \beta(x, y, E[u(t)](y)) u(y, t) dy, \quad x_0 \geq 0,$$

where $\beta(x, y, E)$ is the (re)production rate of newborns of size x of an individual of size y experiencing an environment E at time t (see Ref. 34 for a model with age and size as internal variables and a similar recruitment term). In particular, such a choice of the recruitment term implies that there is no-inflow of individuals through the boundary $x = x_0$ since $u(x_0, t) = 0$ for all $t \geq 0$. Again, as long as β is regular enough and uniformly bounded, $R[u(t)](x)$ will satisfy hypothesis (A2). Similar recruitment terms appear in structured population models dealing with cell division²⁷ and in modelling reacting polymers by means of fragmentation models.^{24,25,35} In the latter case, a production rate β as the one considered here would correspond to the so-called multiple fragmentation kernel. For instance, if $a(y)$ denotes the overall break-up rate of a particle of mass y and $b(y, x)$ is the distribution of particles of mass x formed from a particle of mass y splitting, then $\beta(x, y) = a(y) b(y, x) 1_{y \geq x}$.^{24,35}

Recently, an alternative way to model the dynamics of structured populations, the so-called *cumulative formulation*, has been developed.^{12,13} In some sense, this approach recover the classical approach in demography considered, for instance, by Sharpe and Lotka.³² Roughly speaking, the equations governing the dynamics of the population are integral equations (instead of PDEs) and the state variables are measures on the so-called individual state-space. More recently, the study of a linearized stability principle has been addressed by introducing as state variables a pair of functions over time axis, namely, the number of newborns per time unit and a weighted average of the population as the total population, the total biomass, or, in general, a finite dimensional environment $E = (E_1, \dots, E_n)$ where each component E_i is a scalar function of t . Under such an approach, less smoothness is required for the vital rates with respect to that of the PDE approach, and $u(x, t)$ and $u_0(x)$ can be measures instead of densities (see Chap. 3 in Ref. 16). However, it still remains open the well-posedness of the problem when some of the components E_i are infinite-dimensional in the sense given at the Introduction.

Finally, it is worth mentioning that another mathematical approach to the study of complex biological systems with internal structure as, for instance, multicellular systems, is the one based on the mathematical kinetic theory. The idea behind this

modelling approach is to apply methods of nonequilibrium statistical mechanics that allow a mathematical description of the collective behaviour of complex systems ranging from the microscopic (or individual) level to the macroscopic (or populational) level (see Refs. 3, 4 and 19 for recent reviews on mathematical methods for generalized kinetic models). Under this framework, the approach to the study of population dynamics presented in this paper would correspond to the so-called *mesoscopic modelling*.³

Appendix

The expression of the solution of (2.1) along characteristics for $x < z(t)$ is given by

$$u(x, t) = \int_{\tau}^t e^{-\int_{\zeta}^t \lambda(s, \tau) ds} R[u(\zeta)](\varphi(\zeta; \tau, 0)) d\zeta,$$

where $\lambda(s, \tau) := m(\varphi(s; \tau, 0), E(\varphi(s; \tau, 0), s)) + DV(\varphi(s; \tau, 0), E(\varphi(s; \tau, 0), s))$ and DV is the total derivative of $V(x, E(x, t))$ with respect to x , and $E(\varphi(s; \tau, 0), s) := E[u(s)](\varphi(s; \tau, 0))$ for simplicity of notation. Hence, it follows that

$$\begin{aligned} \bar{u}_{\tau}(t, \tau) = & - \left(R[u(\tau)](0) e^{-\int_{\tau}^t \lambda(s, \tau) ds} \right. \\ & + \int_{\tau}^t \left\{ \int_{\zeta}^t [m_x(\varphi(s; \tau, 0), E) + \nabla_E m(\varphi(s; \tau, 0), E) \right. \\ & \cdot E_x(\varphi(s; \tau, 0), s)] \varphi_{\tau}(s; \tau, 0) ds \\ & + \int_{\zeta}^t [V_{xx}(\varphi(s; \tau, 0), E) + V_{xE}(\varphi(s; \tau, 0), E) \\ & \cdot E_x(\varphi(s; \tau, 0), s)] \varphi_{\tau}(s; \tau, 0) ds \\ & + \int_{\zeta}^t (E_x(\varphi(s; \tau, 0), s))^T V_{EE}(\varphi(s; \tau, 0), E) E_x(\varphi(s; \tau, 0), s) \varphi_{\tau}(s; \tau, 0) ds \\ & \left. + \int_{\zeta}^t \nabla_E V(\varphi(s; \tau, 0), E) \cdot E_{xx}(\varphi(s; \tau, 0), s) \varphi_{\tau}(s; \tau, 0) ds \right\} \\ & \cdot e^{-\int_{\zeta}^t \lambda(s, \tau) ds} R[u(\zeta)](\varphi(\zeta; \tau, 0)) d\zeta \\ & - \int_{\tau}^t e^{-\int_{\zeta}^t \lambda(s, \tau) ds} R_x[u(\zeta)](\varphi(\zeta; \tau, 0)) \varphi_{\tau}(\zeta; \tau, 0) d\zeta \Big), \end{aligned}$$

where $\bar{u}(t, \tau) = \bar{u}(t, \tau(x, t)) = u(x, t)$ for $0 < x < z(t)$ and, for brevity, the arguments of E have been omitted whenever E appears as an argument of another function.

Changing the order of integration in all terms with a double integral leads to

$$\begin{aligned} |\bar{u}_{\tau}(t, \tau)| \leq & |R[u(\tau)](0)| e^{-\int_{\tau}^t \lambda(s, \tau) ds} + \bar{u}(t, \tau) \left((m_x^0 + V_2^0) \int_{\tau}^t (-\varphi_{\tau}(s; \tau, 0)) ds \right. \\ & \left. + (m_E^0 + V_2^0) \int_{\tau}^t |E_x(\varphi(s; \tau, 0), s)|_1 (-\varphi_{\tau}(s; \tau, 0)) ds \right) \end{aligned}$$

$$\begin{aligned}
 &+ V_2^0 \int_{\tau}^t E_x(\varphi(s; \tau, 0), s) \cdot E_x(\varphi(s; \tau, 0), s) (-\varphi_{\tau}(s; \tau, 0)) ds \\
 &+ V_1^0 \int_{\tau}^t |E_{xx}(\varphi(s; \tau, 0), s)|_1 (-\varphi_{\tau}(s; \tau, 0)) ds \Big) \\
 &+ \int_{\tau}^t e^{-\int_{\zeta}^t \lambda(s, \tau) ds} |R_x[u(\zeta)](\varphi(\zeta; \tau, 0))| (-\varphi_{\tau}(\zeta; \tau, 0)) d\zeta, \tag{A.1}
 \end{aligned}$$

where we have used that, $\forall s \in [\tau, t]$, $\varphi_{\tau}(s; \tau, 0) < 0$ and

$$\begin{aligned}
 &\int_{\tau}^s e^{-\int_{\zeta}^t \lambda(s, \tau) ds} R[u(\zeta)](\varphi(\zeta; \tau, 0)) d\zeta \\
 &\leq \int_{\tau}^t e^{-\int_{\zeta}^t \lambda(s, \tau) ds} R[u(\zeta)](\varphi(\zeta; \tau, 0)) d\zeta = \bar{u}(t, \tau).
 \end{aligned}$$

For $x > z(t)$ and using the same convention for the notation as before but now with $\lambda(s, \xi) := m(\varphi(s; 0, \xi), E(\varphi(s; 0, \xi), s)) + DV(\varphi(s; 0, \xi), E(\varphi(s; 0, \xi), s))$, it follows that the solution of (2.1) is

$$u(x, t) = u_0(\xi) e^{-\int_0^t \lambda(s, \xi) ds} + \int_0^t e^{-\int_{\zeta}^t \lambda(s, \xi) ds} R[u(\zeta)](\varphi(\zeta; 0, \xi)) d\zeta$$

and its derivative with respect to ξ is

$$\begin{aligned}
 \bar{u}_{\xi}(t, \xi) = &e^{-\int_0^t \lambda(s, \xi) ds} \left(u_0'(\xi) - u_0(\xi) \int_0^t \{ m_x(\varphi(s; 0, \xi), E) \right. \\
 &+ \nabla_E m(\varphi(s; 0, \xi), E) \cdot E_x(\varphi(s; 0, \xi), s) \\
 &+ V_{xx}(\varphi(s; 0, \xi), E) + V_{xE}(\varphi(s; 0, \xi), E) \cdot E_x(\varphi(s; 0, \xi), s) \\
 &+ (E_x(\varphi(s; 0, \xi), s))^T V_{EE}(\varphi(s; 0, \xi), E) E_x(\varphi(s; 0, \xi), s) \\
 &\left. + \nabla_E V(\varphi(s; 0, \xi), E) \cdot E_{xx}(\varphi(s; 0, \xi), s) \} \varphi_{\xi}(s; 0, \xi) ds \right) \\
 &- \int_0^t \left(\int_{\zeta}^t \{ m_x(\varphi(s; 0, \xi), E) + m_E(\varphi(s; 0, \xi), E) \right. \\
 &\cdot E_x(\varphi(s; 0, \xi), s) \\
 &+ V_{xx}(\varphi(s; 0, \xi), E) + V_{xE}(\varphi(s; 0, \xi), E) \cdot E_x(\varphi(s; 0, \xi), s) \\
 &+ (E_x(\varphi(s; 0, \xi), s))^T V_{EE}(\varphi(s; 0, \xi), E) E_x(\varphi(s; 0, \xi), s) \\
 &\left. + \nabla_E V(\varphi(s; 0, \xi), E) \cdot E_{xx}(\varphi(s; 0, \xi), s) \} \varphi_{\xi}(s; 0, \xi) ds \right) \\
 &\cdot e^{-\int_{\zeta}^t \lambda(s, \xi) ds} R[u(\zeta)](\varphi(\zeta; 0, \xi)) d\zeta \\
 &+ \int_0^t e^{-\int_{\zeta}^t \lambda(s, \xi) ds} R_x[u(\zeta)](\varphi(\zeta; 0, \xi)) \varphi_{\xi}(\zeta; 0, \xi) d\zeta.
 \end{aligned}$$

Proceeding along the same lines as for $|u_\tau(t)|$, one obtains the following upper bound

$$\begin{aligned}
 |\bar{u}_\xi(t, \xi)| &\leq |u'_0(\xi)| e^{-\int_0^t \lambda(s, \xi) ds} + \left(u_0(\xi) e^{-\int_0^t \lambda(s, \xi) ds} + \bar{u}(t, \xi) \right) \\
 &\quad \times \left((m_x^0 + V_2^0) \int_0^t \varphi_\xi(s; 0, \xi) ds \right. \\
 &\quad + (m_E^0 + V_2^0) \int_0^t |E_x(\varphi(s; 0, \xi), s)|_1 \varphi_\xi(s; 0, \xi) ds \\
 &\quad + V_2^0 \int_0^t E_x(\varphi(s; 0, \xi), s) \cdot E_x(\varphi(s; 0, \xi), s) \varphi_\xi(s; 0, \xi) ds \\
 &\quad \left. + V_1^0 \int_0^t |E_{xx}(\varphi(s; 0, \xi), s)|_1 \varphi_\xi(s; 0, \xi) ds \right) \\
 &\quad + \int_0^t e^{-\int_\zeta^t \lambda(s, \xi) ds} |R_x[u(\zeta)](\varphi(\zeta; 0, \xi))| \varphi_\xi(\zeta; 0, \xi) d\zeta, \quad (\text{A.2})
 \end{aligned}$$

where, as before, we have used that

$$\begin{aligned}
 &\int_0^s e^{-\int_\zeta^s \lambda(s, \xi) ds} R[u(\zeta)](\varphi(\zeta; 0, \xi)) d\zeta \\
 &\leq \int_0^t e^{-\int_\zeta^t \lambda(s, \xi) ds} R[u(\zeta)](\varphi(\zeta; 0, \xi)) d\zeta = \bar{u}(t, \xi).
 \end{aligned}$$

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