

# Asymptotic behaviour of a model of hierarchically structured population dynamics<sup>★</sup>

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**Abstract.** A hierarchically structured population model with a dependence of the vital rates on a function of the population density (*environment*) is considered. The existence, uniqueness and the asymptotic behaviour of the solutions is obtained transforming the original non-local PDE of the model into a local one. Under natural conditions, the global asymptotical stability of a nontrivial equilibrium is proved. Finally, if the environment is a function of the biomass distribution, the existence of a positive total biomass equilibrium without a nontrivial population equilibrium is shown.

**Key words:** Rank competition – Structured population dynamics – Asymptotic behaviour

## 1 Introduction

Most of the models in population dynamics, even in structured population modelling, introduce the resource competition through total population variables as, for instance, the total biomass or the total population (see, for instance, [2, 13, 18]). In a more general way, such introduction can be done by considering a dependence of the vital rates (growth, fecundity and mortality rates) on the resource level at time  $t$ , and assuming a dynamics for the resource that depends on some total population variable (see [8, 12]). Both approaches have, however, the same implicit assumption, namely, that all the individuals in the population have the same availability of resources.

Nevertheless, this assumption is not always a suitable one because it ignores that individual differences not only have direct implications on the

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vital rates, but also on the availability of resources, i.e., on the efficiency that an individual has in the competition among members of the same population (*intraspecific competition*). For instance, very often the size of an individual determines what species can be its prey and, moreover, by what species it can be eaten (as well as the values of its vital rates). The same thing happens if one considers the competition for sunlight in a forest: the taller is a tree, the higher is the availability of light it has. In other words, (body) size is a variable that introduces a *hierarchy* in populations of many species, the intraspecific predation or *cannibalism* being the most dramatic expression of such hierarchy (see [14] for a review of field evidences of intraspecific predation, and [20]).

The role of the hierarchy (and social organization) in Ecology has been always associated to the idea of a stabilizing mechanism in population dynamics, and it has motivated several theoretical works on this topic (see [9, 10, 17]). The basic idea can be summarized by the following statement: “the feeding success of individual animals is closely related to their position in a social hierarchy”. This sentence appears in [9], one of the first attempts to study the implications of hierarchy in population dynamics from a mathematical point of view. In this work, however, the authors do not use the structured population modelling framework (see [12]). In fact, under certain hypotheses, they reduce the problem to study the dynamics of two total population variables: the population feeding function and the total number of individuals.

Of course, one can think of other (continuous) attributes (different to size) that can structure populations in a hierarchical way by means of affecting the ability to obtain resources (food, light, . . .) of individuals and, consequently, the vital rates values. However, any of such attributes has to “grow” during the individual life, and its development has to show plasticity, i.e., it should be influenced by environmental conditions, in order to be a suitable candidate to structure the population. For instance, the extent of color patches in the plumage of some species of birds seems to be badges of social status in the population (see [16]). Nevertheless, a non-genetic determination of this character (or, at least, a not very high degree of such determination) is a necessary condition for this attribute to show plasticity during the development in the same way that it is assumed in structured population modelling.

Linking both aspects, hierarchy and asymmetrical competition, is the notion of *rank(size)-related competition* that appears when resource use is a function of *rank(size)*. In such case, the competitive effects on a given member of a population will depend not only on its *rank(size)* but, also, on the *rank(size)* distribution of the population (see [1]). So, in order to model the competitive effects experienced by an individual, one has also to take into account members of the population with *rank(sizes)* different from the *rank(size)* of such individual. From a mathematical point of view, *rank(size)-related competition* introduces nonlinearities or feedbacks into the structured population models through functions of the population density that appear in the submodels of the vital rates. In particular, in many structured models (see, for instance, [1, 3, 18, 19]) such nonlinearities are introduced by means of a functional of the population density which is usually named *environment* or control function.

In this paper we study a model inspired by those of Cushing that model cannibalism and hierarchical organization in age- and size-structured populations (see [4, 5, 6, 7]). More precisely, we consider a rank-structured population model with a nonlinear individual growth rate and with newborns having all the same state (rank), and we study the corresponding dynamics of the model under natural conditions on the vital rates. The main novelties of this work are those for a rank dependent population model with a non-linear growth rate: 1) we obtain results about the behaviour of the population density (not only about total population variables) for a particular environment that is function of the rank distribution; 2) we compare these results with those that are obtained by considering the biomass distribution as the factor that defines the environment; in particular, we show that having an equilibrium for the total biomass does not always imply an equilibrium for the population density.

Mathematically, our model is given by a nonlinear nonlocal first order partial differential equation of hyperbolic type. The corresponding initial boundary value problem (IBVP) is presented in Sect. 2 along with the hypotheses that guarantee the existence and uniqueness of solution of the problem.

Section 3 starts with the transformation (in Subsect. 3.1) of the original nonlocal problem into a local one by means of a change of variable similar to that used in the age-dependent case (see [6], proof of Theorem 3). Moreover, a decoupled ordinary differential equation (ODE) is also obtained for the total population  $P(t)$ . However, the main difference to the age-dependent case is that the transformed model can not be considered as an ODE for the new variable because, now, characteristics are not straight lines in the  $(x, t)$ -plane; in fact, they are not known *a priori* because they depend on the solution of the problem, as it is usual in nonlinear size-dependent population models. In Subsect. 3.2, the existence and uniqueness of solution for the transformed model is proved and, from that, the existence and uniqueness of solution to the original problem follows.

Once we know the existence of stationary solutions given by the equilibria of the ODE for the total population (Sect. 4), the  $L^1$ -convergence of the solution towards a stationary solution is proved in Sect. 5. To do that it is necessary, firstly, to prove the convergence (in the sup-norm) of the solution of the local problem to the stationary solution corresponding to  $P^*$ , the (unique) equilibrium of  $P(t)$ .

When size is the significant variable, it is natural to consider that, in some situations, the environment can be determined by the biomass distribution of the population rather than by the size distribution. This is the case we consider in Sect. 6. This assumption can give rise to a situation in which, even though the total biomass  $B(t)$  tends to a constant value  $B^* > 0$ , the corresponding population density does not tend to any non-zero *stationary* population density. More precisely, in this situation the total biomass tends to be constant, the total population tends to zero and the surviving individuals in the population become bigger and bigger as time increases – in order to have a constant biomass.

## 2 The model

Let  $u(x, t)$  be the density of individuals at time  $t$  having a rank between  $x$  and  $x + dx$ , and let us assume that all the vital rates only depend on a function of the population density, the *environment*, given by

$$E(x, t) = \alpha \int_{x_0}^x u(s, t) ds + \int_x^\infty u(s, t) ds, \quad 0 \leq \alpha < 1. \tag{1}$$

The coefficient  $\alpha$  is related with the degree of hierarchy in the population structure. More precisely,  $\alpha$  is the weight of the lower ranks in the competition for resources. So,  $\alpha = 0$  represents an absolute hierarchical social structure, i.e., *contest* or *asymmetric competition*, whereas values of  $\alpha$  tending to 1 mean that the effect of higher ranks (in the competition for resources) tends to be similar to the effect of lower ranks, i.e., *scramble competition*. The limit case  $\alpha = 1$  corresponds to an environment given by the total population at time  $t$ , i.e., without any kind of social structure, and it is studied, for instance, in the references given in the beginning of this paper.

With respect to the vital rates, we will assume that they depend on the energy uptake, which is a function of the environment. So, for simplicity, we will consider that the individual *growth rate*,  $V$ , the *reproduction rate*,  $\beta$ , and the *mortality rate*,  $m$ , are only functions of  $E$ .

According to such hypotheses we have the following IBVP

$$\begin{cases} u_t + (V(E(x, t))u)_x = -m(E(x, t))u, & x > x_0, t > 0, \\ V(E(x_0, t))u(x_0, t) = \int_{x_0}^\infty \beta(E(s, t))u(s, t) ds, & t > 0, \\ u(x, 0) = u_0(x), & x \in [x_0, \infty), \end{cases} \tag{2}$$

where  $x_0 \geq 0$  is the rank (size) of a newborn and  $\beta(E(s, t))$  is the *reproduction rate*: the number of offspring per unit time of an individual of rank (size)  $s$  when its environment is  $E(s, t)$ .

Notice that the vital rates depend on size through the environment  $E(x, t)$ , that is, they do not depend on size in an explicit way. In particular, the reproduction rate depends on parent's size  $s$  only through the environment  $E(s, t)$  they have at time  $t$ .

Let us assume the following hypotheses for the functions appearing in the model:

- (H1)  $V(E)$  is a strictly positive function of class  $\mathcal{C}^2(0, \infty)$ , bounded from above by  $V^0$  and from below by  $V_0 > 0$ . Moreover,  $|V'|$  and  $|V''|$  are bounded from above by  $V'^0$  and  $V''^0$ , respectively.
- (H2)  $\beta(E)$  is a nonnegative function bounded from above by  $\beta^0$ .
- (H3)  $m(E)$  is a nonnegative function, continuously differentiable and bounded from above by  $m^0$  and from below by  $m_0 > 0$ , and  $m^0$  being an upper bound of  $|m'(E)|$ .

*Remark:* The existence and uniqueness of solution to (2) with a general environment  $E(x, t)$ -an arbitrary function of the solution  $u(x, t)$ - is, as far as we

know, an open question that has an answer in [15] under some regularity conditions on the vital rates and on  $E(x, t)$  and assuming distributed states for the newborns.

### 3 The transformed IBVP

#### 3.1 Derivation of the transformed problem

Let  $u(x, t)$  be an integrable  $C^1$  function satisfying (2) and  $\lim_{x \rightarrow \infty} u(x, t) = 0$  (i.e., a “classical solution”). Taking the derivative of  $E$  with respect to  $x$  in (1) we have  $E_x = (\alpha - 1)u$  and, hence,  $u = E_x/(\alpha - 1)$ ,  $u_t = E_{xt}/(\alpha - 1)$ . Therefore, substituting  $u$  by  $E_x/(\alpha - 1)$  in (2)<sub>1</sub> and multiplying it by  $(\alpha - 1)$  we obtain

$$\begin{cases} E_{xt} + (V(E)E_x)_x = -(M(E))_x, & x > x_0, t > 0, \\ E(x, 0) = \alpha \int_{x_0}^x u_0(s) ds + \int_x^\infty u_0(s) ds, & x > x_0, \\ V(E(x_0, t))E_x(x_0, t) = - \int_{\alpha P(t)}^{P(t)} \beta(\eta) d\eta, & t > 0, \\ E(x_0, t) = P(t), & t > 0, \end{cases} \tag{3}$$

where  $M(\eta) := \int_0^\eta m(\xi) d\xi$  and  $P(t) := \int_{x_0}^\infty u(x, t) dx$  is the total population at time  $t$ . In particular, the reproduction term gives

$$\int_{x_0}^\infty \beta(E(s, t))u(s, t) ds = \frac{1}{\alpha - 1} \int_{x_0}^\infty \beta(E) E_s ds = \frac{1}{1 - \alpha} \int_{\alpha P(t)}^{P(t)} \beta(E) dE .$$

Now (3)<sub>1</sub> implies  $\frac{\partial}{\partial x} [E_t + V(E)E_x + M(E)] = 0$ . Therefore, it follows that

$$E_t + V(E)E_x + M(E) = F(t) , \tag{4}$$

where  $F(t)$  is an unknown function.

Evaluating (4) at  $x = x_0$  and at  $x = \infty$ , we obtain

$$\begin{cases} P'(t) + V(E(x_0, t))E_x(x_0, t) + M(P(t)) = F(t) , \\ \alpha P'(t) + V(E(\infty, t))E_x(\infty, t) + M(\alpha P(t)) = F(t) . \end{cases}$$

Because of the boundary condition for  $E_x$  given by (3)<sub>3</sub> and the fact that  $E_x(\infty, t) = 0$  we have, firstly, that  $F(t)$  is given by

$$F(t) = P'(t) + M(P(t)) - \int_{\alpha P(t)}^{P(t)} \beta(\eta) d\eta \tag{5}$$

and, secondly, subtracting the second equation from the first one it results in the following ODE for the total population  $P(t)$

$$P'(t) = \frac{1}{1 - \alpha} \int_{\alpha P(t)}^{P(t)} [\beta(\eta) - m(\eta)] d\eta =: f(P(t)) . \tag{6}$$

This equation is similar to eq. (14) obtained by Cushing in [6].

Finally, the transformed IBVP is

$$\begin{cases} E_t + V(E)E_x = P'(t) + M(P(t)) - M(E) - \int_{\alpha P(t)}^{P(t)} \beta(\eta) d\eta, & x > x_0, t > 0, \\ E(x, 0) = E_0(x), & x > x_0, \\ E(x_0, t) = P(t), & t > 0, \end{cases} \tag{7}$$

where the function  $P(t)$  is given by the solution of the ODE (6) with initial condition  $P(0) = P_0$ . In particular, each initial condition  $u_0$  of (2) determines  $E_0(x) = \alpha \int_{x_0}^x u_0(s) ds + \int_x^\infty u_0(s) ds$  and  $P_0 = \int_{x_0}^\infty u_0(x) dx$ .

*Remark:* Even if the vital rates depend also on  $P(t)$  and/or some of them depend on one of the integrals appearing in (1) -instead of depending on  $E(x, t)$ -, a derivation of a local IBVP and a decoupled ODE for  $P(t)$  is possible along the same lines.

### 3.2. Analysis of the transformed problem

From now on we are going to deal with the IBVP given by (7). Its derivation has been heuristic and it has used the definition of  $E(x, t)$  in order to obtain some results, for instance, equation (6). For this reason it is necessary to prove that every solution of this IBVP satisfies the properties we have assumed in such derivation. In particular, the derivative of  $E$  with respect to  $x$  has to be nonpositive because it is equal to  $(\alpha - 1)u(x, t)$ , where  $\alpha < 1$  and  $u \geq 0$  ( $u$  is a population density).

For this purpose we will use the characteristic system of (7), namely,

$$\begin{cases} \tilde{x}' = V(\tilde{E}), \\ \tilde{E}' = M(P(t)) - M(\tilde{E}) - \int_{\alpha P(t)}^{P(t)} \beta(\eta) d\eta + P'(t). \end{cases} \tag{8}$$

Hence,  $\tilde{E}(t) = E(\tilde{x}(t), t)$  is the solution to (7) along the characteristic curves given by  $\tilde{x}(t)$ , the solution to (8)<sub>1</sub>. The corresponding initial conditions of this system are

$$\tilde{x}(0) = \xi, \quad \tilde{E}(0) = E_0(\xi), \quad \text{or} \quad \tilde{x}(\tau) = x_0, \quad \tilde{E}(\tau) = P(\tau), \tag{9}$$

depending on the point where the characteristic curve comes from, namely,  $(\xi, 0)$  and  $(x_0, \tau)$ , respectively.

**Theorem 1** *Assume hypothesis (H1)–(H3) of the previous section and, further, that  $V' \leq 0$ . Then, for every initial condition  $E_0(x)$  in  $\mathcal{C}^1$  satisfying the following compatibility conditions*

$$\text{i) } E_0(x_0) = P_0 \quad \text{and} \quad \text{ii) } V(P_0)E'_0(x_0) = - \int_{\alpha P_0}^{P_0} \beta(\eta) d\eta,$$

and such that  $E'_0(x) \leq 0$ ,  $E_0(x) \rightarrow \alpha P_0$  and  $E'_0(x) \rightarrow 0$  as  $x \rightarrow \infty$ , there exists a unique continuously differentiable solution  $E(x, t)$  to (7) for all time and, further, this solution has the following properties

- a)  $E_x(x, t) \leq 0$  for all  $x \geq 0$  and  $t > 0$ ,
- b)  $\lim_{x \rightarrow \infty} E(x, t) = \alpha P(t)$ ,  $t > 0$ ,
- c)  $\lim_{x \rightarrow \infty} E_x(x, t) = 0$ ,  $t > 0$ .

*Proof.* According to the characteristic system and using that  $m$ ,  $\beta$ ,  $P(t)$  and  $P'(t)$  are bounded functions, in order to prove the global existence of solution we only have to prove that shocks of the characteristic curves in the  $(x, t)$ -plane are not possible.

To see that, let us consider the solution  $(\tilde{x}, \tilde{E})$  to (8)–(9) as a one-parameter family with parameter  $\zeta$ . Then, the system of variation of (8) is given by

$$\begin{cases} \tilde{x}'_\zeta = V'(\tilde{E})\tilde{E}_\zeta, & \tilde{x}_\zeta(0; \zeta) = 1, \\ \tilde{E}'_\zeta = -m(\tilde{E})\tilde{E}_\zeta, & \tilde{E}_\zeta(0; \zeta) = E'_0(\zeta). \end{cases} \tag{10}$$

A simple analysis of (10) shows that, under such initial condition,  $\tilde{x}_\zeta \geq 1$  and  $\tilde{E}_\zeta \leq 0$ . So, for the characteristics coming from  $t = 0$  shocks are not possible because  $\tilde{x}_\zeta \geq 1$ .

Now, considering  $\tau$  as the parameter of the family defined by the solutions of (8)–(9), we have the system of variation of (8)–(9) given by

$$\begin{cases} \tilde{x}'_\tau = V'(\tilde{E})\tilde{E}_\tau, & \tilde{x}_\tau(\tau; \tau) = -V(P(\tau)), \\ \tilde{E}'_\tau = -m(\tilde{E})\tilde{E}_\tau, & \tilde{E}_\tau(\tau; \tau) = \int_{\alpha P(\tau)}^{P(\tau)} \beta(\eta) d\eta. \end{cases} \tag{11}$$

In particular, the initial condition for  $\tilde{E}_\tau$  comes from the fact that the total derivative of  $\tilde{E}(\tau; \tau)$  with respect to  $\tau$  is  $\tilde{E}_\tau(\tau; \tau) + \tilde{E}_t(\tau; \tau) = P'(\tau)$  and, on the other hand, that  $\tilde{E}_t(\tau; \tau) = P'(\tau) - \int_{\alpha P(\tau)}^{P(\tau)} \beta(\eta) d\eta$  as one can see evaluating (8)<sub>2</sub> at  $x = x_0$ .

As in the previous case, the analysis of (11) reveals that, under such initial condition,  $\tilde{x}_\tau < 0$  and  $\tilde{E}_\tau \geq 0$ ; that is, shocks are again not possible because now  $\tilde{x}_\tau < 0$ . Therefore, we have seen that the solution to (8)–(9) exists for all positive time.

From the analysis of the previous systems, statement (a) of the theorem is immediately obtained. Indeed, denoting by  $(x_0, t_0)$  the initial condition in the  $(x, t)$ -plane and using the chain rule, one obtains

$$E_x(x, t) = \begin{cases} \tilde{E}_\zeta(t; \zeta(x))\zeta_x = \tilde{E}_\zeta(t; \zeta(x))/\tilde{x}_\zeta \leq 0, & \text{if } (\tilde{x}(0), 0) = (\zeta, 0), \\ \tilde{E}_\tau(t; \tau(x))\tau_x = \tilde{E}_\tau(t; \tau(x))/\tilde{x}_\tau \leq 0, & \text{if } (\tilde{x}(\tau), \tau) = (x_0, \tau), \end{cases} \tag{12}$$

that is, it follows that  $E_x(x, t) \leq 0$  for all  $t \geq 0$ . Notice that the compatibility conditions imply that (12) holds for the points  $(x, t)$  on the characteristic coming from  $(x_0, 0)$ .

In order to prove statement (b) and using (6), let us write (8)<sub>2</sub> in the following manner

$$\tilde{E}' = \alpha P'(t) - \int_{\alpha P(t)}^{\tilde{E}} m(\eta) d\eta . \tag{13}$$

Now, defining  $y(t) := \tilde{E} - \alpha P(t)$  and using (H3), it follows that  $|y'(t)| \leq m^0 |y(t)|$ .

Let us choose  $L = L(\varepsilon)$  satisfying that, for all  $(x, t) \in [L, \infty) \times [0, T]$ ,  $|y(0)| = |\tilde{E}(0, \xi(x)) - \alpha P(0)| = |E_0(\xi(x)) - \alpha P_0| \leq \varepsilon$ . We have

$$|y(t)| \leq |y(0)| + \int_0^t |y'(s)| ds \leq \varepsilon + m^0 \int_0^t |y(s)| ds \leq \varepsilon e^{m^0 t} ,$$

where, in the last inequality, we have used Gronwall’s lemma. Therefore, for every given  $\varepsilon_0 > 0$  we can choose  $L > 0$  such that

$$|\tilde{E}(t; \xi(x)) - \alpha P(t)| = |E(x, t) - \alpha P(t)| < \varepsilon_0 \quad \forall x > L, \quad \forall t \in [0, T] .$$

This proves statement (b) of the theorem.

Finally, statement (c) follows directly from (10) and (12). □

We understand by a *solution* of (2) in a *weak sense* the function  $u := E_x/(\alpha - 1)$ . From the previous theorem,  $u$  is a non-negative, continuous and integrable function tending to 0 as  $x \rightarrow \infty$ . Moreover, statement (b) implies that (1) holds for this function  $u$ . Finally, if  $E_{xx}$  is continuous, then  $u$  is a classical solution of (2).

### 4 Equilibria

If  $u^*(x)$  is an equilibrium solution of (2) with total population  $P^*$ , then  $P^*$  is a solution of  $f(P) = 0$ , with  $f(P)$  given by the RHS of (6). Therefore, there are as many total equilibrium populations  $P^*$  as zeros of  $f(P)$ .

**Proposition 1** *Let us assume the following hypotheses on  $\beta$  and  $m$ :  $\beta'(\eta) < 0$ ,  $m'(\eta) > 0$  with  $\beta(0) > m(0)$  and  $\beta(\eta) \rightarrow 0$  when  $\eta \rightarrow \infty$ . Then, there exists a unique value  $P^* > 0$  of  $P$  such that  $f(P) = 0$ . Moreover,  $P^*$  is a globally asymptotically stable equilibrium of (6) for any positive initial condition.*

*Proof.* Under such hypotheses,  $\beta(\eta) - m(\eta)$  is monotonously decreasing, positive for  $\eta < \eta_0$  and negative for  $\eta > \eta_0$ ,  $\eta_0$  being the unique value of  $\eta$  such that  $\beta(\eta_0) = m(\eta_0)$ . Therefore, the existence and uniqueness of  $P^* > 0$  and the property of being globally asymptotically stable follows from the fact that  $f(P)$  is positive for all  $0 < P < \eta_0$ , and negative for all  $P > \eta_0/\alpha$  and, finally, because  $f'(P) = (\beta(P) - m(P) - \alpha[\beta(\alpha P) - m(\alpha P)])/(1 - \alpha) < 0$  for all  $\eta_0 < P < \eta_0/\alpha$ . □

Notice that Allee-like effects can give rise to the existence of more than one equilibrium. This situation can be conceivable, for instance, in some species in

which dominant individuals (i.e., individuals of the highest ranks and, so, with the lowest environments) have higher mortality rates than those that are subordinate. In such cases, this is due to the fact that the dominant individuals defend the group from predators or from competitors of other species. Moreover, in other cases (for instance, in some species of birds), having a high rank is not always correlated with being more successful in finding a mate.

For simplicity, however, from now on we are going to consider the hypotheses of monotony for  $\beta$  and  $m$ . On the other hand, the results we present only assume convergence of the total population to a constant value. Therefore, they are also valid in case of having several equilibria for the total population because, even in this case,  $P(t)$  tends monotonously to a stable equilibrium.

Once we have guaranteed the existence of an equilibrium  $P^*$  for the total population, we have to know how many equilibrium distributions  $u^*$  correspond to a given  $P^*$ . By an *equilibrium solution* of (2), we define a nonnegative  $\mathcal{C}^1$ -function that satisfies (2)<sub>1</sub> and (2)<sub>2</sub> with  $u_t = 0$ . Equivalently, we look for the  $C^2$ -equilibria  $E^*$  of (7) because  $u^*(x) = E^*(x)/(\alpha - 1)$ . In particular,  $u^* \geq 0$  if  $E^* \leq 0$ .

We mean by *equilibrium solution* of (7) a  $\mathcal{C}^2$ -function that satisfies the autonomous initial value problem

$$\begin{cases} V(E)E'(x) = M(P^*) - M(E) - \int_{\alpha P^*}^{P^*} \beta(\eta) d\eta, & x > x_0, \\ E(x_0) = P^* . \end{cases} \tag{14}$$

**Proposition 2** *Under the hypotheses of Proposition 1, there exists a unique equilibrium solution,  $E^*$ , of (7) (and therefore a unique equilibrium  $u^*$  of (2)). Furthermore,  $E^*(x) < 0 \forall x \geq x_0$  and  $E^*(x) \rightarrow \alpha P^*$  when  $x \rightarrow \infty$ , where  $P^* > 0$  is the unique positive equilibrium of (6).*

*Proof.* It follows from the fact that the right hand side of (14)<sub>1</sub> is a smooth strictly decreasing function vanishing at  $\alpha P^*$ . □

### 5 The dynamics

Under the hypotheses of Proposition 1, there exists a unique equilibrium  $P^* > 0$  which is globally asymptotically stable of (6) and, therefore, the total population tends monotonously towards this equilibrium. Thus, given an initial population density  $u_0(x)$  and if  $P_0 := \int_{x_0}^{\infty} u_0(x) dx$ , then  $P(t) \leq \max\{P_0, P^*\} =: P^{**}$ .

Along this section we assume the hypotheses (H1)–(H3) as well as those corresponding to Proposition 1. We will see that, when the total population  $P(t)$  tends to a constant value  $P^*$ , then the solution  $u(t)$  tends (in  $L^1$ -norm) to the equilibrium solution  $u^*$  when  $t \rightarrow \infty$ . To do that, we will prove that  $P(t) \rightarrow P^*$  implies  $E(x, t) \rightarrow E^*(x)$  in the sup-norm when  $t \rightarrow \infty$ . Hence, it will follow that  $u \rightarrow u^*$ .

5.1 Convergence of  $E(x, t)$  (in the sup-norm) to  $E^*(x)$

The proof is based on splitting the rank/size space in two parts: the “low ranks/small sizes” part and “high ranks/large sizes” part. The reason of this division is to make use of the fact that, for times large enough and “small” values of  $x$ , the differential equations and the initial conditions for  $E$  and  $E^*$  tend to be the same, while for  $x$ -values large enough and also for times large enough,  $E$  and  $E^*$  tend to  $\alpha P^*$ .

If  $E^*$  is considered as a function of  $x$  and  $t$ , then we can write the characteristic system of (14) similar to the corresponding one for  $E$ , namely,

$$\begin{cases} \tilde{x}^*{}' = V(\tilde{E}^*) , \\ \tilde{E}^*{}' = M(P^*) - M(\tilde{E}^*) - \int_{\alpha P^*}^{P^*} \beta(\eta) d\eta , \end{cases} \tag{15}$$

with a suitable initial condition. In this case, however, the characteristics in the  $(x, t)$ -plane,  $\tilde{x}^*(t)$ , are constant curves, that is, all of them are vertical translations of a given curve satisfying (15)<sub>1</sub> with an arbitrary initial time  $t_0$ ,  $\tilde{x}^*(t; t_0)$ .

5.1.1 Convergence for “small” values of  $x$

For large time values, characteristics corresponding to small values of  $x$  for systems (8) and (15) come from the time axis. So, the initial conditions of both systems are given by the second term of (9) and

$$\tilde{x}^*(\tau) = x_0, \quad \tilde{E}^*(\tau) = P^* , \tag{16}$$

respectively. Notice that the initial condition of (15) is constant, that is, independent of the initial time  $\tau$ .

We are going to use two results in order to study the convergence towards the equilibrium distribution  $E^*(x)$  for finite values of  $x$  or, equivalently, for recent initial times. The first one is that  $P(t)$  tends to  $P^*$  and  $P'(t)$  tends to zero when  $t \rightarrow \infty$ . This is due to the fact that  $P(t)$  is a solution and  $P^*$  is an asymptotically stable equilibrium of (6), a scalar ODE.

The second result is continuity of solutions as functions of the data  $f(x, t)$  and, also, as functions of initial conditions in ODEs. This classical result is stated in the following lemma that we give without proof.

**Lemma 1** *Let  $W \subset \mathcal{M} \times \mathbf{R}$  be an open set with  $\mathcal{M}$  a normed vector space, and  $f, g: W \rightarrow \mathcal{M}$  continuous functions. Suppose that*

$$|f(x, t) - g(x, t)| < \varepsilon \quad \forall (x, t) \in W .$$

*Further, let  $K$  be a Lipschitz constant in  $x$  for  $f(x, t)$ . If  $x(t), y(t)$  are solutions to  $x'(t) = f(x, t)$  and  $y'(t) = g(y, t)$ , respectively, on an interval  $J := [t_0, T]$  such that  $(x(t), t) \in W$  and  $(y(t), t) \in W$  for all  $t \in J$ , and  $|x(t_0) - y(t_0)| < \delta$  with  $\delta$  a positive constant, then for all  $t \in J$ :*

$$|x(t) - y(t)| \leq \frac{\varepsilon}{K} (e^{K(t-t_0)} - 1) + \delta e^{K(t-t_0)} .$$

In our case, the solution of the system is given by the pair  $(x, E)$  and  $\mathcal{M} \equiv \mathbf{R}^2$  endowed with the norm  $|x| = \sum_{i=1}^2 |x_i|$ . Moreover, systems (8) and (15) satisfy the conditions of the previous lemma. In particular, if  $\bar{x} := (x, E)$ , then

a) For all  $\varepsilon > 0$  there is  $T_\varepsilon > 0$  such that  $|f(\bar{x}, t) - g(\bar{x}, t)| < \varepsilon \forall \bar{x} \in \mathbf{R}^{2+}$  and  $t > T_\varepsilon$ :

Let  $f(\bar{x}, t)$  and  $g(\bar{x}, t)$  be the right hand side of (8) and (15) respectively. Then

$$|f(\bar{x}, t) - g(\bar{x}, t)| \leq (m^0 + (1 + \alpha)\beta^0)|P(t) - P^*| + |P'(t)| \rightarrow 0 \quad \text{as } t \rightarrow \infty$$

uniformly in  $\bar{x}$ , because the right hand part of the inequality does not depend on  $x$  neither  $E$  and, furthermore,  $|P(t) - P^*|$  and  $|P'(t)|$  tend to zero when  $t \rightarrow \infty$ . Therefore, given  $\varepsilon > 0$ , we can always choose a value  $T_\varepsilon$  large enough such that the first hypothesis of the lemma is satisfied with  $W = \mathbf{R}^{2+} \times (T_\varepsilon, \infty)$ .

b)  $g(\bar{x})$  is Lipschitz in  $\bar{x}$ :  $|g(\bar{x}) - g(\bar{y})| \leq (V^0 + m^0)|E_1 - E_2| \leq K|\bar{x} - \bar{y}|$ .

Let  $(\tilde{x}, \tilde{E})$  be the solution of (8) and  $(\tilde{x}^*, \tilde{E}^*)$  the one corresponding to (15). The inequality for the difference of solutions of ODEs stated in the previous lemma is enough to prove the following.

**Lemma 2** *Let us assume the hypotheses of Theorem 1 and Proposition 1. Then, for any  $x_\varepsilon > x_0$ ,  $|E(x, t) - E^*(x)|$  tends to zero uniformly in  $x$  on  $[x_0, x_\varepsilon]$  when  $t \rightarrow \infty$ .*

*Proof.* For simplicity let us assume  $x_0 = 0$ . Then, for a given  $t$ , let us consider the two characteristics passing through each  $x$  with  $x \in [0, x_\varepsilon]$ : one of them being the solution of (8)<sub>1</sub>,  $\tilde{x}(t; \tau)$ , and the other,  $\tilde{x}^*(t; \tau')$ , being the solution of (15)<sub>1</sub>. The initial conditions for (8) and (15) are given by  $(\tilde{x}(\tau), \tilde{E}(\tau)) = (0, P(\tau))$  and  $(\tilde{x}^*(\tau'), \tilde{E}^*(\tau')) = (0, P^*)$  respectively, where  $\tau$  and  $\tau'$  are the corresponding times of the intersection of each characteristic with the  $t$ -axis. Further, let us assume without loss of generality that  $\tau' > \tau$ .

As we have mentioned above, the characteristic  $\tilde{x}^*(t; \tau')$  is a vertical translation of the curve  $\tilde{x}^*(t; 0)$ , i.e., with  $\tau' = 0$ , because  $E^*$  is an equilibrium solution of (7). Having this point in mind, one can consider the characteristic that is a solution of (15)<sub>1</sub> with initial condition  $(0, \tau)$ ,  $\tilde{x}^*(\cdot; \tau)$ , and its value at time  $t$ :  $\tilde{x}^*(t; \tau) = y$ . Graphically the situation is shown in Fig. 1.

Then, the difference between the solution of (7) at time  $t$ ,  $E(x, t)$ , and the equilibrium solution,  $E^*(x)$ , at a given point  $x$  can be bounded in the following manner:

$$|E(x, t) - E^*(x)| \leq |\tilde{E}(t; \tau) - \tilde{E}^*(t; \tau)| + |\tilde{E}^*(t; \tau) - \tilde{E}^*(t; \tau')|,$$

where  $\tilde{E}(t; \tau)$  denotes the solution of (8)<sub>2</sub> with initial condition given at time  $\tau$ .

Now, as  $E^*$  is an equilibrium solution,  $\tilde{E}^*(t, \tau') = \tilde{E}^*(t_1, \tau)$  with  $t_1$  implicitly given by  $\tilde{x}^*(t_1; \tau) = x$ . Therefore, the resulting inequality is

$$|E(x, t) - E^*(x)| \leq |\tilde{E}(t; \tau) - \tilde{E}^*(t; \tau)| + |\tilde{E}^*(t; \tau) - \tilde{E}^*(t_1; \tau)|. \quad (17)$$

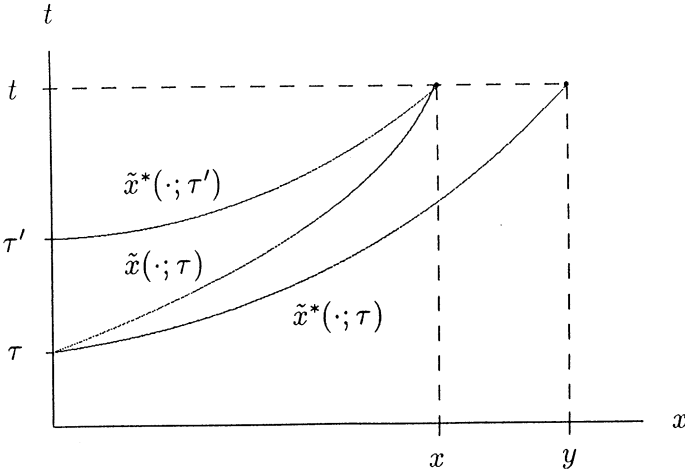


Fig. 1.

The RHS of (17) can be bounded using Lemma 1 because the initial time of the initial conditions is the same:  $t_0 = \tau$ . The initial difference of the solutions to (8) and (15) is given by

$$|\tilde{x}(\tau; \tau) - \tilde{x}^*(\tau; \tau)| + |\tilde{E}(\tau; \tau) - \tilde{E}^*(\tau; \tau)| = |P(\tau) - P^*| \leq c\varepsilon(\tau) =: \delta$$

with  $c^{-1} := (m^0 + (1 + \alpha)\beta^0)$  and  $\varepsilon(\tau) := c^{-1}|P(\tau) - P^*| + |P'(\tau)|$ . So, the statement of the lemma in our case is

$$|\tilde{x}(t; \tau) - \tilde{x}^*(t; \tau)| \leq \varepsilon(\tau) \left( \frac{1}{K} [e^{K(t-\tau)} - 1] + ce^{K(t-\tau)} \right) =: \varepsilon(\tau)l(t - \tau).$$

This means, while the difference  $(t - \tau)$  is bounded,  $\tau \rightarrow \infty$  when  $t \rightarrow \infty$  and, hence,  $\varepsilon(\tau) \rightarrow 0$  because  $|P(\tau) - P^*|$  and  $|P'(\tau)|$  tend to zero. In other words, we can make the differences  $|\tilde{x}(t; \tau) - \tilde{x}^*(t; \tau)|$  and  $|\tilde{E}(t; \tau) - \tilde{E}^*(t; \tau)|$  as small as we want for a fixed value of  $x_\varepsilon$  because, given  $x_\varepsilon$ ,  $(t - \tau) \leq x_\varepsilon/V_0$ .

The second term on the right of (17) goes to zero uniformly in  $x$  when  $t$  tends to  $\infty$  because  $|\tilde{E}^*(t; \tau) - \tilde{E}^*(t_1; \tau)| = |E^*(\tilde{x}^*(t; \tau)) - E^*(\tilde{x}^*(t_1; \tau))|$  and  $E^*$  is uniformly continuous on  $[0, x_\varepsilon]$ . □

Notice that as the value  $x_\varepsilon$  is arbitrary, it will be chosen when proving the convergence for large values of  $x$ .

### 5.1.2 Convergence for “large” values of $x$

To study this convergence we have to focus our attention again on equation (13) and, furthermore, on the corresponding equation for  $\tilde{E}^*$ , namely,

$$\tilde{E}^{*'} = - \int_{\alpha P^*}^{E^*} m(\eta) d\eta. \tag{18}$$

From both equations we have the following.

**Lemma 3** *Under the hypotheses of Theorem 1 and Proposition 1, and for all  $\varepsilon > 0$ , there exist  $x_\varepsilon > 0$  and  $T_\varepsilon > 0$  such that*

$$|E(x, t) - E^*(x)| < \varepsilon \quad \forall x > x_\varepsilon \quad \text{and} \quad \forall t > T_\varepsilon .$$

*Proof.* From Theorem 1, we know that  $E(x, t) - \alpha P(t) \geq 0$  for all  $x \in [x_0, \infty)$ . Now, using (13), we have  $\tilde{E}(t) - \alpha P(t) \leq P^{**}e^{-m_0(t-\tau)}$ , with  $\tau$  satisfying that either  $\tilde{x}(\tau; \tau) = 0$ , or  $\tau = 0$  if the characteristic  $\tilde{x}(t)$  comes from  $t = 0$ .

Similarly, from (18), we obtain  $\tilde{E}^*(t) - \alpha P^* \leq P^{**}e^{-m_0(t-\tau^*)}$ , with  $\tau^*$  satisfying that either  $\tilde{x}^*(\tau^*; \tau^*) = 0$ , or  $\tau^* = 0$  if the characteristic  $\tilde{x}^*(t)$  comes from  $t = 0$ .

Now, given  $\varepsilon > 0$ , let us choose a value  $T_\varepsilon > 0$  such that  $P^{**}e^{-m_0T_\varepsilon} < \varepsilon/3$  and  $|\alpha|P(T_\varepsilon) - P^*| \leq \varepsilon/3$ . Then, for all  $0 \leq \tau \leq t - T_\varepsilon$ , we have

$$\tilde{E}(t) - \alpha P(t) \leq \frac{\varepsilon}{3} \quad \text{and} \quad \tilde{E}^*(t) - \alpha P^* \leq \frac{\varepsilon}{3} .$$

Moreover, we use  $T_\varepsilon$  to choose the number  $x_\varepsilon$  that splits the  $x$ -axis in small and large values by defining  $x_\varepsilon := V^0 T_\varepsilon$ .

Finally, for all  $x > x_\varepsilon$  and  $t > T_\varepsilon$ , we have  $t - \tau \geq T_\varepsilon$  and hence,

$$\begin{aligned} |E(x, t) - E^*(x)| &= |\tilde{E}(t) - \tilde{E}^*(t)| \leq \\ &|\tilde{E}(t) - \alpha P(t)| + |\alpha P^* - \tilde{E}^*(t)| + \alpha|P(t) - P^*| \leq \varepsilon . \end{aligned} \quad \square$$

**Theorem 2** *Let us suppose the hypotheses of Theorem 1 and Proposition 1, and let  $E(x, t)$  and  $E^*(x)$  be the solution of (7) and (14), respectively. Then, for all  $\varepsilon > 0$ , there exists a time  $T > 0$  such that*

$$\sup_x |E(x, t) - E^*(x)| < \varepsilon \quad \forall t > T .$$

*Proof.* It follows directly from the last two lemmas choosing, given  $\varepsilon > 0$ , the interval  $[0, x_\varepsilon]$  appearing in Lemma 2 with  $x_\varepsilon$  obtained in Lemma 3, and with  $T \geq \max\{T_1, T_2\}$  where  $T_1$  and  $T_2$  are the corresponding times from which solutions differ from each other less than  $\varepsilon$  on  $(x_\varepsilon, \infty)$  and  $[0, x_\varepsilon]$ , respectively. □

### 5.2 Convergence of $u(t)$ (in the $L^1$ -norm) to $u^*$

By definition,  $u(x, t) = E_x(x, t)/(\alpha - 1)$ . So, in order to prove the convergence of  $u(x, t)$  to an equilibrium solution,  $u^*(x) = E^*(x)/(\alpha - 1)$ , we will use again the system of variation of (8) given by (10) or (11) depending on the initial condition.

We will evaluate the  $L^1$ -norm of the difference of  $u$  and  $u^*$  by means of the following decomposition

$$\begin{aligned} \int_{x_0}^{\infty} |u(x, t) - u^*(x)| dx &= \int_{x_0}^{x_\varepsilon} |u(x, t) - u^*(x)| dx \\ &+ \int_{x_\varepsilon}^{\infty} |u(x, t) - u^*(x)| dx . \end{aligned} \quad (19)$$

with  $x_\varepsilon$  a positive value that, as before, splits the rank (size) space in two parts.

5.2.1 Convergence for “small” values of  $x$

For times large enough, characteristics that at time  $t$  pass through small values of  $x$  come from  $x = x_0$ . Then, the parameter of the initial condition is  $\tau$ . On the other hand, in order to see that the first integral of (19) tends to zero, it is only necessary to see that  $E_x \rightarrow E_x^*$  on a finite interval  $[x_0, x_1]$ .

**Lemma 4** *Let us suppose the hypotheses of Theorem 1 and Proposition 1. Then, for all  $\varepsilon > 0$  and  $x_1 > x_0$ , there exists  $T_\varepsilon > 0$  such that*

$$\left| \frac{\partial E(x, t)}{\partial x} - \frac{dE^*(x)}{dx} \right| < \varepsilon$$

in  $[x_0, x_1]$  for all  $t > T_\varepsilon$ .

*Proof.* Integrating (11) we have

$$\begin{cases} \tilde{x}_\tau(t; \tau) = \int_\tau^t V'(\tilde{E}(s; \tau)) \tilde{E}_\tau(s; \tau) ds - V(P(\tau)) , \\ \tilde{E}_\tau(t; \tau) = (\int_{xP(\tau)}^{P(\tau)} \beta(\eta) d\eta) e^{-\int_\tau^t m(\tilde{E}(s; \tau)) ds} . \end{cases} \tag{20}$$

Now, substituting  $P(\tau)$  by  $P^*$ ,  $\tilde{E}$  by  $\tilde{E}^*$  and  $\tilde{x}$  by  $\tilde{x}^*$  in (20), we obtain similar integral equations for  $\tilde{x}_\tau^*$  and  $\tilde{E}_\tau^*$  respectively.

Using them and the fact that  $P(t) \rightarrow P^*$ ,  $\tilde{E} \rightarrow \tilde{E}^*$  and  $\tilde{x} \rightarrow \tilde{x}^*$ , it follows that the differences  $|\tilde{E}_\tau(t; \tau) - \tilde{E}_\tau^*(t; \tau^*)|$  and  $|\tilde{x}_\tau(t; \tau) - \tilde{x}_\tau^*(t; \tau^*)|$  tend to zero as  $t$  tends to  $\infty$  uniformly in  $x$  on every finite interval. In particular, if we assume without loss of generality that  $\tau(x) < \tau^*(x)$ , then, from (20)<sub>2</sub>, it results

$$\begin{aligned} |\tilde{E}_\tau(t; \tau) - \tilde{E}_\tau^*(t; \tau^*)| &\leq \beta^0(1 + \alpha) |P(\tau) - P^*| \\ &\quad + \beta^0(1 - \alpha) P^{**} [m^0 |\tau(x; t) - \tau^*(x; t)| \\ &\quad + m^0 \int_\tau^t |\tilde{E}(s; \tau) - \tilde{E}^*(s; \tau^*)| ds] . \end{aligned} \tag{21}$$

Now, for any finite interval  $[x_0, x_1]$ , the difference  $t - \tau(x)$  is bounded by  $(x_1 - x_0)/V_0$  for all  $x$  in this interval. Then  $\tau(x) \rightarrow \infty$  as  $t \rightarrow \infty \forall x \in [x_0, x_1]$ . So, there exists  $T_0 > 0$  such that  $\beta^0(1 + \alpha) |P(\tau(x; t)) - P^*| < \varepsilon/2 \forall t > T_0$  and  $\forall x \in [x_0, x_1]$ .

Using a similar scheme of characteristics as in proof of Lemma 2 (now with  $\tau^*$  instead of  $\tau'$  and taking  $\tau^* > \tau$ ), it follows that  $|\tau(x) - \tau^*(x)| \leq |\tilde{x}^*(t; \tau) - \tilde{x}(t; \tau)|/V_0$ . From the proof of Lemma 2, it follows that this upper bound tends to 0 as  $t \rightarrow \infty$  uniformly in  $x$  on any compact interval. From the same proof and, moreover, because the length of the integration interval,  $t - \tau(x)$ , is uniformly bounded in  $[x_0, x_1]$ , the last integral of (21) tends to 0 as  $t \rightarrow \infty$  uniformly.

Then, for any given  $\varepsilon$ , we can choose  $T > 0$  such that, for all  $t > T$ , the RHS of (21) is less than  $\varepsilon$  in  $[x_0, x_1]$ .

On the other hand, from (20)<sub>1</sub> we have

$$\begin{aligned}
 |\tilde{x}_\tau(t; \tau) - \tilde{x}_\tau^*(t; \tau^*)| &\leq V'^0 \int_{\tau^*}^t |\tilde{E}_\tau(s; \tau) - \tilde{E}_\tau^*(s; \tau^*)| ds \\
 &\quad + V''^0 \int_{\tau^*}^t |\tilde{E}_\tau(s; \tau)| |\tilde{E}(s; \tau) - \tilde{E}^*(s; \tau^*)| ds \\
 &\quad + V'^0 \int_{\tau}^{\tau^*} |\tilde{E}_\tau(s; \tau)| ds + V'^0 |P(\tau) - P^*|.
 \end{aligned}$$

In a similar way as we have done with the upper bound of  $|\tilde{E}_\tau(t; \tau) - \tilde{E}_\tau^*(t; \tau^*)|$  and using that this difference also tends to zero uniformly in  $x$  on finite intervals, it can be seen that each term of the RHS of the previous inequality tends to zero as  $t \rightarrow \infty$  uniformly on  $[x_0, x_1]$ .

Finally, recalling that  $E_x(x, t) = \tilde{E}_\tau(t; \tau(x))/\tilde{x}_\tau$  and taking into account that  $|\tilde{x}_\tau|$  and  $|\tilde{x}_\tau^*|$  are bounded from below by strictly positive constants, the statement of the lemma trivially follows.  $\square$

From this lemma and as  $E_x(x, t) = (\alpha - 1)u(x, t)$  and  $E^{*'}(x) = (\alpha - 1)u^*(x)$ , we have the following.

**Corollary 1** *On any finite interval  $[x_0, x_1]$ ,  $\int_{x_0}^{x_1} |u(x, t) - u^*(x)| dx \rightarrow 0$  when  $t \rightarrow \infty$ .*

### 5.2.2 Convergence for “large” values of $x$

**Lemma 5** *Under the hypotheses of Theorem 1 and Proposition 1, and for all  $\varepsilon > 0$ , there exist  $x_\varepsilon > 0$  and  $T^* > 0$  such that  $\int_{x_\varepsilon}^\infty |u(x, t) - u^*(x)| dx < \varepsilon \forall t > T^*$ .*

*Proof.* Given  $\varepsilon > 0$ , we choose  $T^*$  such that  $2P^{**}e^{-m_0T^*} < \varepsilon$ . Then, for  $t > T^*$  and  $x > x_0 + V^0T^* =: x_\varepsilon$ , we have that the characteristic passing through the point  $(x, t)$  comes from a point  $(\xi, t - T^*)$  with  $\xi > x_0$ . Therefore, from (10)<sub>2</sub> and taking  $E_0(\xi) = E(\xi, t - T^*)$  as initial condition, we have

$$\frac{\partial E}{\partial x} = \frac{\partial \tilde{E}}{\partial \xi} \frac{\partial \xi}{\partial x} = E'_0(\xi(x)) e^{-\int_{t-T^*}^t m(E(s)) ds} \frac{\partial \xi}{\partial x} \quad \forall x > x_\varepsilon,$$

and, similarly,

$$\frac{\partial E^*}{\partial x} = E_0^{*'}(\xi^*(x)) e^{-\int_{t-T^*}^t m(E^*(s)) ds} \frac{\partial \xi^*}{\partial x} \quad \forall x > x_\varepsilon.$$

Hence recalling that  $u(x, t) = E_x(x, t)/(\alpha - 1)$ , the integral of the statement can be bounded as follows

$$\begin{aligned}
 \int_{x_\varepsilon}^\infty |u(x, t) - u^*(x)| dx &\leq e^{-m_0T^*} \left( \int_{x_0}^\infty u(\xi, t - T^*) d\xi + \int_{x_0}^\infty u^*(\xi) d\xi \right) \\
 &\leq (P(t - T^*) + P^*) e^{-m_0T^*} \\
 &\leq 2P^{**} e^{-m_0T^*} < \varepsilon \quad \forall t > T^*. \quad \square
 \end{aligned}$$

**Theorem 3** Assume the hypotheses of Theorem 1 and Proposition 1. Let  $u(x, t)$  be the solution of (2) in the weak sense defined at the end of Section 3, and let  $u^*(x)$  be the unique equilibrium of (2). Then, for all  $\varepsilon > 0$ , there exists  $T > 0$  such that  $\int_{x_0}^{\infty} |u(x, t) - u^*(x)| dx < \varepsilon \forall t > T$ .

*Proof.* Let us consider the value of  $x_{\varepsilon/2}$  obtained in Lemma 5. By Corollary 1, we can choose  $T_\varepsilon$  such that  $\int_{x_0}^{x_{\varepsilon/2}} |u(x, t) - u^*(x)| dx < \frac{\varepsilon}{2} \forall t > T_\varepsilon$ . Further, let us choose  $T^*$  such that Lemma 5 is satisfied for  $\varepsilon/2$ . Then, the statement of the theorem follows taking  $T \geq \max\{T_\varepsilon, T^*\}$ . □

### 6 $E(x, t)$ defined by the biomass distribution

In this section we are going to consider that the environment  $E(x, t)$  is determined by the biomass distribution in the population. So, as we have mentioned in the introduction, we are assuming implicitly that the rank of an individual is given by its body size. Several situations are related with such kind of environments. For instance, in a forest, the availability of light of an individual is more concerned with the distribution of volumes of the crowns (of the trees) than with the distribution of individuals (which is the case that has been considered in the previous section). The same thing happens if one considers populations of unicellular organisms where the uptake of nutrients is usually related with the body surface (see [5, 12]).

In particular, we will consider individual *biomass* as the measure of the individual size and the environment as a function of the biomass distribution in the population. Therefore,  $E$  is given by

$$E(x, t) = \alpha \int_{x_0}^x u(s, t) s ds + \int_x^{\infty} u(s, t) s ds, \quad 0 \leq \alpha < 1,$$

We assume that the energy uptake rate per unit of biomass only depends on the environment. So, the *growth rate* will be equal to the biomass  $x$  times a function  $V$  of  $E$ . (See [5, 12] for examples of similar growth rates). Finally, the *mortality rate*  $m$  and the *reproduction rate*  $\beta$  (now the number of offspring per unit of time and per unit of biomass) will be also functions of  $E$ .

Under these hypotheses and taking, without loss of generality,  $x_0 = 1$ , it follows

$$\begin{cases} u_t + (xV(E(x, t))u)_x = -m(E(x, t))u, & x > 1, t > 0, \\ V(E(1, t))u(1, t) = \int_1^{\infty} \beta(E(s, t))su(s, t) ds, & t > 0, \\ u(x, 0) = u_0(x), & x \in [1, \infty), \end{cases} \tag{22}$$

where  $u$  is assumed to be an integrable function with respect to  $x$  with a weight  $\rho = x$ .

As we have done with problem (2), we can transform this non-local problem into a local one by means of a similar change of variable. In this case,

however,  $E_x = (\alpha - 1)xu$  and, so, we have to multiply (22)<sub>1</sub> by  $(\alpha - 1)x$  and, afterwards, to substitute  $u$  by  $E_x/[(\alpha - 1)x]$ . After doing that, one obtains

$$\begin{cases} E_{xt} + x(V(E)E_x)_x = -(M(E))_x, & x > 1, t > 0, \\ V(E(1, t))E_x(1, t) = -\int_{\alpha B(t)}^{B(t)} \beta(\eta) d\eta, \\ E(x, 0) = E_0(x), & x > 1, \\ E(1, t) = B(t), & t > 0, \end{cases} \tag{23}$$

where  $M(\eta) := \int_0^\eta m(\xi) d\xi$  and  $B(t) := \int_1^\infty u(s, t) s ds$  is the total biomass of the population at time  $t$ .

An ODE for the total biomass  $B(t)$  analogous to (6) is obtained from (23) in the same way as before. Now, (23)<sub>1</sub> implies

$$\frac{\partial}{\partial x} [E_t + xV(E)E_x - G(E) + M(E)] = 0$$

with  $G(\eta) := \int_0^\eta V(s) ds$ . So, it follows that

$$E_t + xV(E)E_x - G(E) + M(E) = F(t), \tag{24}$$

with  $F(t)$  an unknown function.

Evaluating (24) at  $x = 1$  and  $x = \infty$  and using (23)<sub>2</sub>, (23)<sub>4</sub>, and assuming that  $\lim_{x \rightarrow \infty} \{x E_x(x, t)\} = 0$ , we obtain the following system of equations

$$\begin{cases} B'(t) - \int_{\alpha B(t)}^{B(t)} \beta(\eta) d\eta - G(B(t)) + M(B(t)) = F(t), \\ \alpha B'(t) - G(\alpha B(t)) + M(\alpha B(t)) = F(t), \end{cases}$$

where the first equation determines the function  $F(t)$  and, subtracting the second equation from the first one, we have the following ODE

$$B'(t) = \frac{1}{1 - \alpha} \int_{\alpha B(t)}^{B(t)} [\beta(\eta) + V(\eta) - m(\eta)] d\eta. \tag{25}$$

with initial condition  $B_0 = \int_1^\infty u_0(x) x dx$ .

Finally, introducing the expression of  $F(t)$  in (24) one obtains from (23) the following transformed IBVP

$$\begin{cases} E_t + xV(E)E_x = B'(t) + M(B(t)) - M(E) + G(E) - G(B(t)) - \int_{\alpha B(t)}^{B(t)} \beta(\eta) d\eta, \\ E(x, 0) = E_0(x), & x \geq 1, \\ E(1, t) = B(t), & \lim_{x \rightarrow \infty} E(x, t) = \alpha B(t), & t > 0. \end{cases} \tag{26}$$

As in the IBVP (7), each initial condition  $u_0$  of the original problem determines  $E_0(x) = \alpha \int_1^x u_0(s) s ds + \int_x^\infty u_0(s) s ds$ .

The remarkable point, in this case, are the equilibria of (25) and their relationship with the equilibria of (22). It is clear that if  $u^*$  is an equilibrium of

(22) with total biomass  $B^*$ , then  $B^*$  is an equilibrium of (25). Moreover,

$$E^*(x) = \alpha \int_{x_0}^x u^*(s) s ds + \int_x^\infty u^*(s) s ds, \quad 0 \leq \alpha < 1,$$

is an equilibrium of (26), i.e., a solution of the IVP with  $x$  as independent variable

$$\begin{cases} xV(E)E' = M(B^*) - M(E) + G(E) - G(B^*) - \int_{\alpha B^*}^{B^*} \beta(\eta) d\eta \\ \qquad \qquad \qquad = \int_{\alpha B^*}^E [V(\eta) - m(\eta)] d\eta =: g(E), \quad x > 1, \\ E(1) = B^*, \end{cases} \quad (27)$$

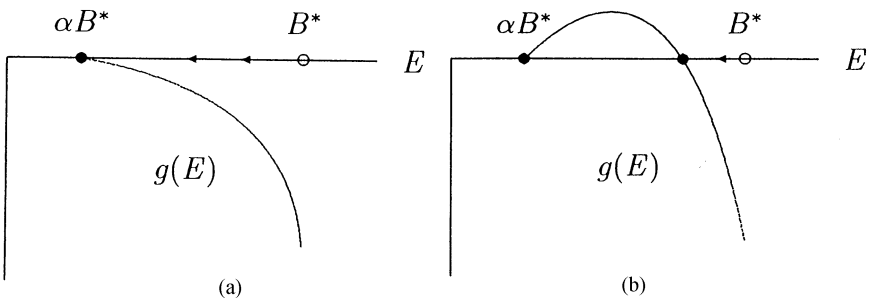
such that  $\lim_{x \rightarrow \infty} E(x) = \alpha B^*$ .

On the other hand, under “natural” hypotheses of monotony ( $\beta' < 0$ ,  $V' < 0$  and  $m' > 0$ ), and assuming  $\beta(0) + V(0) > m(0)$  and  $\lim_{\eta \rightarrow \infty} [\beta(\eta) + V(\eta) - m(\eta)] < 0$ , the same argument used in the proof of Proposition 1 shows the existence and uniqueness of a positive equilibrium  $B^*$  of (25) which is globally (for  $B(0) > 0$ ) asymptotically stable. This gives a (unique) nontrivial equilibrium of (22) in the form  $u^*(x) = E^*(x)/[(\alpha - 1)x]$ , where  $E^*(x)$  is the solution of (27) for this  $B^*$  (satisfying  $E^*(x) \rightarrow \alpha B^*$  as  $x \rightarrow \infty$ ), if and only if  $g$  is monotonous in the interval  $(\alpha B^*, B^*)$ , i.e., if and only if  $g'(\alpha B^*) \leq 0$  (see Fig. 2a). (Otherwise, as  $g(B^*) \leq 0$  and  $g'' < 0$ , there is a zero of  $g$  in the interval  $(\alpha B^*, B^*)$ , which is necessarily the limit of the solution of (27), see Fig. 2b).

The condition  $g'(\alpha B^*) \leq 0$  is obviously fulfilled if  $V(0) \leq m(0)$ . Otherwise, it is equivalent to  $\eta_1 \leq \alpha B^*$  with  $\eta_1 > 0$  such that  $V(\eta_1) = m(\eta_1)$  and, therefore, to

$$\int_{\eta_1}^{\eta_1/\alpha} [\beta(\eta) + V(\eta) - m(\eta)] d\eta \geq 0, \quad (28)$$

due to the definition of  $B^*$  and the monotony of  $V(\eta) - m(\eta)$ . So, if (28) does not hold, then there is a positive total biomass equilibrium but there is not a nontrivial equilibrium density, i.e., a positive equilibrium of (22).



Figs. 2a and b.

In particular, let us assume further that there are no births in the population, i.e.,  $\beta(E) \equiv 0$  for all  $E \geq 0$ . In this case, (28) does not hold (now the solution of (27) is  $E(x) \equiv B^*$ ). As a result of this situation, there is an equilibrium  $B^*$  of the total biomass with the total population  $P(t) \rightarrow 0$  when  $t \rightarrow \infty$  (integrating (22)<sub>1</sub> with respect to  $x$  with  $\beta \equiv 0$  it follows that  $P(t) < P_0 e^{-m_0 t}$ ). Consequently,  $u(\cdot, t)$  evolves with  $t$ , moving to larger values of  $x$  and, at the same time, with its integral tending to zero. In other words, the surviving members of the population are bigger and bigger but their number decreases incessantly.

### 7 Discussion

This paper deals with the introduction of hierarchy in a model of size (rank)-structured populations. Such introduction has been done by means of a dependence of the vital rates on an environment  $E$  defined, for every individual of size(rank)  $x$ , as a linear combination of the number of individuals smaller (with rank lower) than  $x$  and the number of individuals bigger (with rank higher) than  $x$  (in a similar way as in [6]). In such combination, the weight of the number of higher ranked individuals is constant whereas the weight  $\alpha$  affecting the number of lower ranked individuals can be considered as a parameter that measures the degree of hierarchy in the population.

As long as  $\alpha$  is a fixed parameter of the model and only questions about existence/uniqueness of solution and asymptotic behaviour are dealt with (as in the present paper), the choice of the environment  $E$  is equivalent to the one appearing in [6], Sub-sect. 5.1 and 5.2, for the age-dependent case, namely,

$$E^\gamma(x, t) := \gamma \int_{x_0}^x u(s, t) ds + (1 - \gamma) \int_x^\infty u(s, t) ds . \tag{29}$$

In fact,  $E^\gamma(x, t) = (1 - \gamma)E(x, t)$  with  $\alpha = \gamma/(1 - \gamma) \in [0, 1)$  if  $\gamma \in [0, 1/2)$ . However, when evolutionary questions (as in [1]) or optimization criteria (as in [6]) about hierarchy are formulated, the particular dependence of environment on  $\alpha$  (or whatever parameter we introduce as measure of the asymmetric competition) could become essential.

For instance, one possible optimization criterium could be to maximize the total equilibrium population  $P^*$  (or the total equilibrium biomass) under different degrees of hierarchy in the population in order to see what kind of competition is more “stable” (see [11]). The result of the analysis of such criterium in the age-dependent case with an environment  $E$  given by (29) is stated by Theorem 5 in [6], which says that  $P^*$  is maximized when  $\gamma = 0$  (asymmetric competition) and it is minimized when  $\gamma = 1$  (scramble competition). Note that, for this choice of  $E$ , it is not clear at first glance what value of  $\gamma$  will maximize  $P^*$ . The reason is that, for a given individual of age  $x$ , increasing  $\gamma$  results in an increase or a decrease of  $E$  – the environment that it

feels—depending on whether the number of individuals older than  $x$  is less or greater than the number of individuals younger than  $x$ , respectively.

Under the present election of  $E$ , from (6) it is straightforward to see that  $P^*$  is a decreasing function of  $\alpha$ . Hence, the maximum equilibrium population is attained when  $\alpha = 0$ , that is, under the contest competition as in the age-dependent case. This result can be anticipated realising that an increase of  $\alpha$  results in an increase of the environment experienced by any individual of the population. In other words, a decrease of the hierarchy is disfavourable for everybody.

The kind of competition represented by an environment as the one considered here seems to be suitable when modelling competition for light in a forest where, for a given individual (tree) of height  $x$ ,  $E(x, t)$  can be interpreted as a measure of the interference—at time  $t$ —of the other trees in its availability of light (*shadow*). In this case, the weight of higher individuals in the expression of  $E$  ((1) or (29)) can be assumed to be independent of  $\alpha$ . In general, we think that this choice of  $E$  is appropriate in situations where size (or other attribute) introduces strong differences among individuals.

Another aspect related to modelling hierarchy in populations has to do with the definition of the integrals appearing in the expression of  $E$ . In this paper, we have considered two definitions of  $E$ . In the first one,  $E$  is determined by the size(rank)-distribution of the population whereas, in the second one,  $E$  is determined by the biomass distribution. The main difference between them is the possibility of having, in the second case, a positive equilibrium for the total biomass without having a positive equilibrium for the population density. The key point is that when competition for resources is based on the distribution of individuals in the population, as in (2), an equilibrium is achieved only when the total number of births is equal to the total number of deaths (per unit of time), see (6), and this implies an equilibrium for the population density. Nevertheless, a new possibility of having an equilibrium arises when competition is based on the distribution of biomass in the population. In this case, think of forest growth for instance, the loss of biomass per unit of time due to deaths is partially compensated by the increase of biomass corresponding to the growth of individuals that remain alive. In fact, even if there is no gain of biomass due to the newborns, this loss could be totally compensated under certain assumptions on the growth rate; of course, this is not a realistic picture of a forest but we think that it illustrates what is going on with the biomass balance. On the other hand, this kind of competition is related with that appearing in many situations of management of resources, for instance in forest exploitations, where it is possible to be interested in maintaining constant the total biomass of the population (the forest) rather than in obtaining an equilibrium of the distribution of trees.

Of course, this is not the only option of modelling *rank(size)-related competition*. The own definition of  $E$  in terms of the previous integrals is indeed questionable. Sometimes the effects of competition coming from individuals with a similar rank(size) are more strongly felt than those coming from individuals with a very different rank(size) (this is known as “like vs like

competition”). Conversely, in the example of the forest growth, the shading effect caused by higher individuals can be more intensive than the one caused by lower individuals. One way to model such a diversity of situations can be the introduction of different kernels in the integrals in order to give more or less weight to the closer ranks. In any case, introducing competition by means of these kinds of environments can be useful to answer questions about evolutionary aspects of the growth rates under the continuously size-structured populations framework (see [1] for the case of discretely structured populations).

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