

## STEADY STATES IN HIERARCHICAL STRUCTURED POPULATIONS WITH DISTRIBUTED STATES AT BIRTH

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**ABSTRACT.** We investigate steady states of a quasilinear first order hyperbolic partial integro-differential equation. The model describes the evolution of a hierarchical structured population with distributed states at birth. Hierarchical size-structured models describe the dynamics of populations when individuals experience size-specific environment. This is the case for example in a population where individuals exhibit cannibalistic behavior and the chance to become prey (or to attack) depends on the individual's size. The other distinctive feature of the model is that individuals are recruited into the population at arbitrary size. This amounts to an infinite rank integral operator describing the recruitment process. First we establish conditions for the existence of a positive steady state of the model. Our method uses a fixed point result of nonlinear maps in conical shells of Banach spaces. Then we study stability properties of steady states for the special case of a separable growth rate using results from the theory of positive operators on Banach lattices.

**1. Introduction.** Classic population models often assume that individuals experience *scramble* competition. This means that all individuals in the population have equal chances in the competition for resources such as food, light, space etc., see e.g. [9, 18, 23, 24, 27]. In many species, however, competition for resources that determine individual mortality and fertility is based on some hierarchy in the population which is related to individuals size or to any other variable that characterizes physiological structure. Significant amount of interest has been paid to understand the dynamics of populations that exhibit *contest* competition. Structured population models are a useful tool to study intra-specific contest competition. Both (time-)discrete (see e.g. [20, 21]) and continuous (see e.g. [1, 2, 6, 7, 8, 14, 15]) models have been formulated and analysed to this end. Most of the nonlinear models in the literature incorporate environmental feedback through some form of density dependence in the vital rates. Our goal in this paper is to carry out a qualitative analysis of a continuous model which incorporates quite general nonlinearities.

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We study the following quasilinear partial integro-differential equation

$$\frac{\partial}{\partial t} p(s, t) + \frac{\partial}{\partial s} (\gamma(s, P(t)) p(s, t)) = -\mu(s, E(s, p)) p(s, t) + \int_0^m \beta(s, y, E(y, p)) p(y, t) dy, \quad (1.1)$$

$$\gamma(0, P(t)) p(0, t) = 0, \quad (1.2)$$

$$E(s, p) = \alpha \int_0^s w(r) p(r, t) dr + \int_s^m w(r) p(r, t) dr, \quad (1.3)$$

$$P(t) = \int_0^m \kappa(s) p(s, t) ds, \quad (1.4)$$

with the initial condition

$$p(s, 0) = p_0(s).$$

This model describes the long term dynamics of a population of a sufficiently large size living in a closed habitat. The function  $p = p(s, t)$  denotes the density of individuals of size (or other developmental stage)  $s$  at time  $t$ . It is assumed that individuals may have different sizes at birth and therefore  $\beta(s, y, \cdot)$  denotes the rate at which individuals of size  $y$  “produce” individuals of size  $s$ . Hence the non-local integral term in Equation (1.1) represents the recruitment of individuals into the population.  $\gamma$  denotes the size-specific growth rate, while  $\mu$  stands for the mortality rate. We assume that individual growth is also regulated by a weighted population size  $P$ , for example due to competition. Mortality however, depends on the size-specific environment  $E$ , for example due to cannibalism. The parameter  $\alpha$  is related to the strength of the hierarchy in the population. We note that if  $\alpha = 1$  our model reduces to the scramble competition model that in the special case  $\kappa \equiv w \equiv 1$  was considered in [12]. We make the following general assumptions on the model ingredients

$$\begin{aligned} \mu &\in C^1([0, m] \times [0, \infty)), & \beta &\in C^1([0, m] \times [0, m] \times [0, \infty)), \\ \gamma &\in C^2([0, m] \times [0, \infty)), & w, \kappa &\in L^\infty(0, m), \\ \beta, \alpha, w, \mu &\geq 0, & \gamma, \kappa &> 0. \end{aligned} \quad (1.5)$$

Notice that we make no requirement that  $\beta(s, y, E(y, p)) = 0$  if  $y < s$  although this seems natural from a biological point of view. In the remarkable paper [7], Calsina and Saldaña studied well-posedness of a very general size-structured model with distributed states at birth. They established global existence and uniqueness of solutions using results from the theory of nonlinear evolution equations. Model (1.1)-(1.4) is a special case of the general model treated in [7], however, in [7] qualitative questions were not addressed. In contrast to [7], our paper focuses on the existence and local asymptotic stability of equilibrium solutions of system (1.1)-(1.4) with particular regards to the effects of the distributed states at birth (previously we addressed simpler models without hierarchical structure in [12, 14, 15]). Earlier, in [19] Henson and Cushing studied continuous age-structured hierarchical models. They compared models with scramble versus contest competition for a limited resource. In particular the equilibrium levels for the two modes of competition were analyzed. Crucially however, the models in [19] incorporate vital rates that do not depend explicitly on the structuring variable.

In Section 2, we will establish conditions for the existence of positive steady states of our model. The question of the existence of non-trivial steady states is

difficult mainly for two reasons. Firstly, due to hierarchy in the population related to individual size, individual mortality and fertility depend on the size specific environment  $E$ . This environmental feedback yields an infinite dimensional nonlinearity in the model equations, in contrast to Gurtin-MacCamy type models [18], where the vital rates depend on a weighted total population size, or on a finite number of such variables. Secondly, as individuals may be recruited into the population at all possible sizes, a recruitment operator of infinite rank arises. This means that the steady state equation cannot be solved explicitly. In [12] we overcame this issue for a simpler model where the model ingredients only depended on the total population size by using results from the spectral theory of positive operators. Unfortunately this approach cannot be extended to the model considered here. Therefore we devise a different approach, based on fixed point results for nonlinear maps in conical shells of a Banach space, see [4, 10]. This approach was used before to treat age-structured models (also with diffusion), see [24, 26], where every individual enters the population at a single state, namely at age zero. The method is based on the construction of an appropriate nonlinear map that requires the implicit solution of the steady state equation. However, the solution of the steady state equation of our model is not available. Therefore we need to construct an appropriate sequence of recruitment processes of finite rank for which we can solve the corresponding steady state problems. Then we show that the steady states constructed from the fixed points of the sequence of the nonlinear maps, have actually a convergent subsequence and we show that the limit point is actually a steady state of the original problem (1.1)-(1.4).

In Section 3 we focus on the asymptotic behavior of solutions of the model. A positive quasicontraction semigroup describes the evolution of solutions of the system linearized at an equilibrium solution. We establish a regularity property of the governing linear semigroup in Proposition 3.7 that allows in principle to address stability questions of positive equilibrium solutions of (1.1)-(1.4). However, even the point spectrum of the linearized semigroup generator cannot be characterized explicitly via zeros of an associated characteristic function. This is because the eigenvalue equation cannot be solved explicitly due to the infinite dimensional nonlinearity in the original model and the very general recruitment process. We will overcome this issue by using compact positive perturbations of the semigroup generator and rank one perturbations of the general recruitment term. This allows us to arrive at stability/instability conditions for the steady states of our model.

**2. Existence of positive equilibrium solutions.** In this section we will discuss the existence of steady states of model (1.1)-(1.4). We define the nonlinear operator

$$\Psi : W^{1,1}(0, m) \rightarrow L^1(0, m)$$

by

$$\Psi(q) = \frac{\partial}{\partial s} (\gamma(s, Q)q(s)) + \mu(s, E(s, q))q(s) - \int_0^m \beta(s, y, E(y, q))q(y) dy, \quad (2.6)$$

where

$$Q = \int_0^m \kappa(s)q(s) ds.$$

It is clear that  $p_* \in W^{1,1}(0, m)$  is a steady state of (1.1)-(1.4) if and only if  $\Psi(p_*) = 0$  and  $p_*(0) = 0$ .

Our aim here is to apply a fixed point result, see e.g. Theorem 12.3 in [4] or Theorem A in [24]. Its proof uses the Leray-Schauder degree theory for compact perturbations of the identity in infinite dimensional Banach spaces.

**Theorem 2.1.** *Let  $(\mathcal{X}, \|\cdot\|_{\mathcal{X}})$  be a Banach space,  $\mathcal{K} \subset \mathcal{X}$  a closed convex cone and  $\mathcal{K}_r = \mathcal{K} \cap B_r(0)$ , where  $B_r(0)$  denotes the ball of radius  $r$  centered at the origin. Let  $\Phi : \mathcal{K}_r \rightarrow \mathcal{K}$  continuous such that  $\Phi(\mathcal{K}_r)$  is relatively compact. Assume that*

1.  $\Phi x \neq \lambda x$  for all  $\|x\|_{\mathcal{X}} = r, \lambda > 1$ .
2. There exists a  $\rho \in (0, r)$  and  $k \in \mathcal{K} \setminus \{0\}$  such that

$$x - \Phi x \neq \lambda k \quad \text{for all } \|x\|_{\mathcal{X}} = \rho, \lambda > 0.$$

Then  $\Phi$  has at least one fixed point  $x_*$  in the shell

$$\mathcal{S}_{\rho,r} = \{x \in \mathcal{K} : \rho \leq \|x\|_{\mathcal{X}} \leq r\}.$$

**2.1. The case of a separable fertility function.** First we show in Theorem 2.2 that for a finite rank fertility process the problem admits a positive steady state under biologically meaningful conditions on the model ingredients. Later we treat the general case in Theorem 2.3.

**Theorem 2.2.** *Assume that*

$$\beta(s, y, E(y)) = \sum_{j=1}^l \beta_j(s) \bar{\beta}_j(y, E(y)) \tag{2.7}$$

with continuous functions  $\beta, \bar{\beta}$  and there exists a  $j \in \{1, \dots, l\}$  such that

$$\int_0^m \bar{\beta}_j(s, 0) F_j(s, \mathbf{0}, 0) \, ds > 1, \tag{2.8}$$

where  $\mathbf{0}$  is the zero function and

$$F_j(s, E(s), P) = \int_0^s \exp \left\{ - \int_x^s \frac{\mu(r, E(r)) + \gamma_s(r, P)}{\gamma(r, P)} \, dr \right\} \frac{\beta_j(x)}{\gamma(x, P)} \, dx.$$

Let  $F$  be a bounded and measurable function that satisfies

$$F(s, H(s), P) \geq F_j(s, H(s), P)$$

for all  $j, s \in [0, m], H \in L^1_+(0, m)$  and  $P > 0$ , and  $c$  be a constant such that

$$\kappa(s) \geq c \sum_{k=1}^l \bar{\beta}_k(s, H(s)). \tag{2.9}$$

Suppose that there exists an  $R > 0$  such that for all  $(H, P) \in L^1_+(0, m) \times \mathbb{R}_+$  with  $\|H\|_{L^1} + P > R$  we have

$$\int_0^m \kappa(s) F(s, H(s), P) \, ds \leq c. \tag{2.10}$$

Then the model (1.1)-(1.4) admits a positive steady state  $p_*$ .

*Proof.* Let  $\mathcal{X} = L^1(0, m) \oplus l^1$  with norm  $\|\cdot\|_{\mathcal{X}} = \|\cdot\|_{L^1} + \|\cdot\|_{l^1}$ . We will use the notation  $x = (H, \mathbf{P})$ , where  $H \in L^1(0, m)$  and  $\mathbf{P} \in l^1$  or  $x = (H, P^0, \mathbf{P}')$  where  $P^0$  is just the first component of  $\mathbf{P}$  and  $\mathbf{P}' = (P^1, P^2, \dots)$ . We consider elements of  $\mathbb{R}^n$  to be in  $l^1$  by the trivial embedding. We denote by  $\mathcal{K} = (L^1(0, m) \oplus l^1)_+$  the positive cone of  $\mathcal{X}$  which is closed and convex and denote  $\mathcal{K}_r = \mathcal{K} \cap B_r(0)$ , where  $r$  has yet to be chosen. Without loss of generality we may assume that the indices have been assigned such that condition (2.8) holds for  $j = 1$ .

We note that for a fertility function  $\beta$  of the form (2.7) the non-trivial time independent solution of model (1.1)-(1.4) can be found (if it exists) as

$$p_*(s) = \sum_{j=1}^l P_*^j F_j(s, E_*(s), P_*^0), \tag{2.11}$$

where

$$\begin{aligned} P_*^j &= \int_0^m \bar{\beta}_j(s, E_*(s)) p_*(s) \, ds, \quad j \in \{1, \dots, l\}, \\ E_*(s) &= \alpha \int_0^s w(r) p_*(r) \, dr + \int_s^m w(r) p_*(r) \, dr, \\ P_*^0 &= \int_0^m \kappa(s) p_*(s) \, ds. \end{aligned} \tag{2.12}$$

We define a nonlinear map  $\Phi^l : \mathcal{K}_r \rightarrow \mathcal{K}$  by  $\Phi^l = (\Phi_1^l, \Phi_2^l)$ , where

$$\begin{aligned} \Phi_1^l(H, \mathbf{P})(s) &= \sum_{j=1}^l P^j \left( \alpha \int_0^s w(r) F_j(r, H(r), P^0) \, dr + \int_s^m w(r) F_j(r, H(r), P^0) \, dr \right), \\ \Phi_2^l(H, \mathbf{P}) &= \left( \sum_{j=1}^l P^j \int_0^m \kappa(s) F_j(s, H(s), P^0) \, ds, \right. \\ &\quad \left. \sum_{j=1}^l P^j \int_0^m \bar{\beta}_1(s, H(s)) F_j(s, H(s), P^0) \, ds, \dots, \right. \\ &\quad \left. \sum_{j=1}^l P^j \int_0^m \bar{\beta}_l(s, H(s)) F_j(s, H(s), P^0) \, ds, 0, \dots \right). \end{aligned}$$

Although at this moment we consider only a single fertility function  $\beta$  (namely the finite sum of separable functions from equation (2.7)), we use the superscript notation  $\Phi^l$  in anticipation of a sequence of such maps that we shall employ in the proof of Theorem 2.3 below. Note that  $\Phi_1^l(H, \mathbf{P}) \geq 0$  and since

$$(\Phi_1^l)'(H, \mathbf{P})(s) = \sum_{j=1}^l P^j (\alpha - 1) w(s) F_j(s, H(s), P^0),$$

also  $\Phi_1^l(H, \mathbf{P}) \in W^{1,1}(0, m)$ . Likewise  $\Phi_2^l(H, \mathbf{P}) \geq 0$  and the nonzero entries of  $\Phi_2^l(H, \mathbf{P})$  are in  $\mathbb{R}_+^{l+1}$ . Thus  $\Phi$  maps indeed into  $\mathcal{K}$  and has a relatively compact image. It can be seen that  $(E_*, \mathbf{P}_*) \in \mathcal{K}_r$  is a fixed point of the nonlinear map  $\Phi^l$  if and only if the function  $p_*$  defined via equations (2.11)-(2.12) is a steady state of problem (1.1)-(1.4).

Assume now that for  $(H, P^0, \mathbf{P}') \in \mathcal{K}_r$  such that

$$\|(H, P^0, \mathbf{P}')\|_{\mathcal{X}} = \|H\|_{L^1} + P^0 + \|\mathbf{P}'\|_{l^1} = r$$

and for some  $\lambda > 1$  we have

$$\Phi^l(H, P^0, \mathbf{P}') = \lambda(H, P^0, \mathbf{P}'),$$

that is

$$\Phi_1^l(H, P^0, \mathbf{P}') = \lambda H, \quad \Phi_2^l(H, P^0, \mathbf{P}') = \lambda(P^0, \mathbf{P}'). \tag{2.13}$$

The second equation in (2.13) can be written as

$$\lambda P^0 = \sum_{j=1}^l P^j \int_0^m \kappa(s) F_j(s, H(s), P^0) \, ds, \tag{2.14}$$

$$\lambda P^1 = \sum_{j=1}^l P^j \int_0^m \bar{\beta}_1(s, H(s)) F_j(s, H(s), P^0) \, ds, \tag{2.15}$$

...

$$\lambda P^l = \sum_{j=1}^l P^j \int_0^m \bar{\beta}_l(s, H(s)) F_j(s, H(s), P^0) \, ds. \tag{2.16}$$

It follows from equations (2.13)-(2.16) that we may assume that  $P^j \neq 0$  for  $j = 0, 1, 2, \dots, l$ .

From equations (2.15)-(2.16) we obtain

$$\lambda \|\mathbf{P}'\|_{l^1} = \sum_{k=1}^l \sum_{j=1}^l P^j \int_0^m \bar{\beta}_k(s, H(s)) F_j(s, H(s), P^0) \, ds. \tag{2.17}$$

Combining equations (2.14) and (2.17) we obtain

$$\|\mathbf{P}'\|_{l^1} = P^0 \left( \frac{\sum_{j=1}^l P_j \int_0^m \sum_{k=1}^l \bar{\beta}_k(s, H(s)) F_j(s, H(s), P^0) \, ds}{\sum_{j=1}^l P_j \int_0^m \kappa(s) F_j(s, H(s), P^0) \, ds} \right).$$

This, combined with inequality (2.9) implies that

$$c \|\mathbf{P}'\|_{l^1} \leq P^0. \tag{2.18}$$

However, by choosing  $r = \|H\|_{L^1} + P^0 + \|\mathbf{P}'\|_{l^1} \geq \|H\|_{L^1} + P^0 > R$  sufficiently large and using condition (2.10), we have from equation (2.14)

$$\begin{aligned} P^0 &< \sum_{j=1}^l P^j \int_0^m \kappa(s) F_j(s, H(s), P^0) \, ds \\ &\leq \|\mathbf{P}'\|_{l^1} \int_0^m \kappa(s) F(s, H(s), P^0) \, ds \leq c \|\mathbf{P}'\|_{l^1} \leq P^0, \end{aligned}$$

a contradiction. Thus condition (1) of Theorem 2.1 is established.

Let us now define  $k = (0, (1, \dots, 1, 0, \dots)) \in \mathcal{K} \setminus \{0\}$  with  $l + 1$  entries 1 and assume that for some  $\lambda > 0$  and  $\rho > 0$  we have for all  $(H, \mathbf{P})$  with  $\|(H, \mathbf{P})\|_{\mathcal{X}} = \rho$

$$(H, \mathbf{P}) - \Phi^l(H, \mathbf{P}) = \lambda k,$$

that is

$$H - \Phi_1^l(H, \mathbf{P}) = 0, \quad \mathbf{P} - \Phi_2^l(H, \mathbf{P}) = (\lambda, \dots, \lambda).$$

The latter equation can be written as

$$(\mathbf{I} - \mathbf{B}(H, P^0)) \cdot \mathbf{P} = (\lambda, \dots, \lambda), \tag{2.19}$$

where the  $(l + 1) \times (l + 1)$  matrix  $\mathbf{B}$  has elements  $B_{00} = 0$  and

$$B_{ii} = \int_0^m \bar{\beta}_i(s, H(s)) F_i(s, H(s), P^0) \, ds \quad \text{for } i = 1, \dots, l.$$

It follows from condition (2.8) and the continuity of  $\bar{\beta}_1$  and  $F_1$  that  $B_{11} > 1$  for all  $\|(H, P^0)\| = \rho$  for some small enough value  $\rho > 0$ . This renders the left hand side of (2.19) negative and yields a contradiction. Condition (2) of Theorem 2.1 is established and the proof is now completed.  $\square$

**2.2. General fertility function.** Every fertility function  $\beta$  of the required regularity  $C^1$  (in all its arguments, see (1.5)) can be written as a limit of partial sums of separable functions

$$\beta^l(s, y, E(y)) = \sum_{k=1}^l \beta_k^l(s) \bar{\beta}_k^l(y, E(y)), \tag{2.20}$$

with

$$\lim_{l \rightarrow \infty} \|\beta(\cdot, \cdot, E(\cdot)) - \beta^l(\cdot, \cdot, E(\cdot))\|_{L^\infty([0, m]^2)} = 0$$

for every  $E \in L^1(0, m)$ . This can be achieved by partitioning the interval  $[0, m]$  into  $l$  subintervals by  $y_k^l = k \frac{m}{l}$ ,  $k = 0, \dots, l$  and setting

$$\beta_{k+1}^l(s) = \beta(s, y_k^l, E(y_k^l)) \quad \text{and} \quad \bar{\beta}_{k+1}^l(y, E(y)) = \chi_{[y_{k-1}^l, y_k^l]}(y)$$

for  $k = 1, \dots, l$  where  $\chi_{[y_{k-1}^l, y_k^l]}$  denotes the indicator function of the respective interval. Then the partial sums converge in the supremum norm as the number of subintervals increases to infinity and there is a uniform bound of the derivatives in the  $s$ -direction

$$\|\beta_k^l\|_{C^1([0, m])} \leq M \tag{2.21}$$

for all  $k$ , uniformly for arbitrary  $E \in L^1$ . The latter is because of the boundedness of all derivatives of  $\beta$ .

**Theorem 2.3.** *Assume that for fixed model ingredients  $\mu, \gamma, \beta$  and  $\kappa$  there exists a bounded and measurable function  $b$  that satisfies*

$$b(s) \geq \beta(s, y, E) \quad \text{for every } s, y \in [0, m] \quad \text{and} \quad E \in L^1_+(0, m) \tag{2.22}$$

and there exists a  $R > 0$  such that for  $\|H\|_{L^1} + P^0 > R$  we have

$$\int_0^m \kappa(s) F_b(s, H(s), P^0) \, ds \leq c, \tag{2.23}$$

where

$$F_b(s, H(s), P^0) = \int_0^s \exp \left\{ - \int_x^s \frac{\mu(r, H(r)) + \gamma_s(r, P^0)}{\gamma(r, P^0)} \, dr \right\} \frac{b(x)}{\gamma(x, P^0)} \, dx,$$

and  $c$  satisfies

$$\kappa(s) \geq c b(s), \tag{2.24}$$

for every  $s \in [0, m]$ . Moreover assume that there exists a separable underestimator of the fertility,

$$0 \leq \beta_1(s) \bar{\beta}_1(y, E(y)) \leq \beta(s, y, E(y)) \tag{2.25}$$

for every  $s, y \in [0, m]$ ,  $E \in L^1_+(0, m)$  such that  $\bar{\beta}_1$  together with  $F_1$  satisfies

$$\int_0^m \bar{\beta}_1(s, \mathbf{0}) F_1(s, \mathbf{0}, 0) \, ds > 1. \tag{2.26}$$

Then model (1.1)-(1.4) admits a positive steady state  $p_* \in W^{1,1}(0, m)$ .

*Proof.* We begin by replacing  $\beta(s, y, E(y))$  by

$$\beta(s, y, E(y)) - \beta_1(s)\bar{\beta}_1(y, E(y)) \geq 0$$

from condition (2.25) and then decompose this remainder as indicated in equation (2.20). We also note that the decomposition of the  $\beta^l$  functions in (2.20) can be achieved in the way that there is a common first term for every  $l$ , i.e. we may write  $\beta_1(s)\bar{\beta}_1(y, E(y)) = \beta_1^l(s)\bar{\beta}_1^l(y, E(y))$  for every  $l$ . This gives a sequence of finite rank approximations

$$\beta^l(s, y, E(y)) = \beta_1(s)\bar{\beta}_1(y, E(y)) + \sum_{k=2}^l \beta_k^l(s)\bar{\beta}_k^l(y, E(y)).$$

Thus, by Theorem 2.2, every  $\Phi^l$  corresponding to a finite rank approximant  $\beta^l$  has a fixed point  $(E_*^l, \mathbf{P}_*^l)$  in the common shell

$$\mathcal{S}_{\rho,r} = \{x \in \mathcal{K} : \rho \leq \|x\|_{\mathcal{X}} \leq r\}.$$

Indeed, due to the uniform bound from inequalities (2.22) and (2.23), the outer radius  $r$  can be chosen uniformly. The common lower radius  $\rho$  can be guaranteed since all approximants  $\beta^l$  begin with a common first term for which condition (2.8) from Theorem 2.2 holds. By the additional gain in regularity due to  $\Phi_1^l$ , we have that  $E_*^l \in W^{1,1}(0, m)$ . By straightforward calculations,

$$\begin{aligned} F_j'(s, E_*^l(s), \mathbf{P}_*^l) &= \frac{\beta_j(s)}{\gamma(s, P_*^{0,l})} + \frac{\mu(s, E_*^l(s)) + \gamma_s(s, P_*^{0,l})}{\gamma(s, P_*^{0,l})} F_j(s, E_*^l(s), \mathbf{P}_*^l), \\ F_j''(s, E_*^l(s), \mathbf{P}_*^l) &= \frac{\beta_j'(s)}{\gamma(s, P_*^{0,l})} - \frac{\beta_j(s)\gamma_s(s, P_*^{0,l})}{\gamma^2(s, P_*^{0,l})} \\ &\quad + \frac{\mu_s(s, E_*^l(s)) + \mu_E(s, E_*^l(s))(E_*^l)'(s) + \gamma_{ss}(s, P_*^{0,l})}{\gamma(s, P_*^{0,l})} F_j(s, E_*^l(s), \mathbf{P}_*^l) \\ &\quad - \frac{\gamma_s(s, P_*^{0,l}) \left( \mu(s, E_*^l(s)) + \gamma_s(s, P_*^{0,l}) \right)}{\gamma^2(s, P_*^{0,l})} F_j(s, E_*^l(s), \mathbf{P}_*^l) \\ &\quad + \frac{\mu(s, E_*^l(s)) + \gamma_s(s, P_*^{0,l})}{\gamma(s, P_*^{0,l})} F_j'(s, E_*^l(s), \mathbf{P}_*^l) \end{aligned}$$

This shows that  $F_j(\cdot, E_*^l(\cdot), \mathbf{P}_*^l) \in W^{2,1}(0, m)$  for all  $l$  and  $j = 1, \dots, l$ , and moreover, that this family is uniformly bounded. For every  $l$  the fixed point yields a steady state of the approximate problem by

$$p_*^l(s) = \sum_{j=1}^l P_*^{j,l} F_j(s, E_*^l(s), P_*^{0,l}).$$

Since  $p_*^l$  is a linear combination of elements in  $W^{2,1}(0, m)$ , it is itself in  $W^{2,1}(0, m)$ . The uniform bound on the derivatives in (2.21) implies that

$$\|p_*^l\|_{W^{2,1}} = \|p_*^l\|_{L^1} + \left\| \frac{dp_*^l}{ds} \right\|_{L^1} + \left\| \frac{d^2p_*^l}{ds^2} \right\|_{L^1} \leq \tilde{M} \quad \text{for all } l \in \mathbb{N}.$$

This means that  $\{p_*^l\}_{l=1}^\infty$  is a bounded set in  $W^{2,1}(0, m)$  which is compactly embedded in  $W^{1,1}(0, m)$  (see e.g. Theorem 6.2 in [3]). Therefore the sequence  $p_*^l$  has a convergent subsequence, again denoted by  $p_*^l$ , with limit point  $p_*$  in  $W^{1,1}(0, m)$ .



This  $p_*$  is the natural candidate for a positive steady state of model (1.1)-(1.4). Next we show that

$$\lim_{l \rightarrow \infty} \|\Psi(p_*^l)\|_{L^1} = 0,$$

where  $\Psi$  is the nonlinear operator defined in (2.6). Let  $\Psi^l$  denote the nonlinear operator corresponding to the partial sum fertility function  $\beta^l$ . Then

$$\begin{aligned} & \|\Psi(p_*^l) - \Psi^l(p_*^l)\|_{L^1} \\ & \leq \int_0^m \left| \int_0^m [\beta(s, y, E_*^l(y)) - \beta^l(s, y, E_*^l(y))] p_*^l(y) dy \right| ds \\ & \leq \int_0^m \|\beta(s, \cdot, E_*^l(\cdot)) - \beta^l(s, \cdot, E_*^l(\cdot))\| p_*^l(\cdot) ds \\ & \leq \|p_*^l\|_{L^1} \int_0^m \|\beta(s, \cdot, E_*^l(\cdot)) - \beta^l(s, \cdot, E_*^l(\cdot))\|_{L^\infty} ds \\ & \leq K \|\beta(\cdot, \cdot, E_*^l(\cdot)) - \beta^l(\cdot, \cdot, E_*^l(\cdot))\|_{L^\infty}, \end{aligned}$$

for some positive constant  $K$ . Finally we have

$$\|\Psi(p_*)\|_{L^1} = \left\| \Psi \left( \lim_{l \rightarrow \infty} p_*^l \right) \right\|_{L^1} = \left\| \lim_{l \rightarrow \infty} \Psi(p_*^l) \right\|_{L^1} = \lim_{l \rightarrow \infty} \|\Psi(p_*^l)\|_{L^1} = 0,$$

where the second equality follows from the continuity of the operator  $\Psi$ . Thus  $p_*$  is the desired steady state. □

**Remark 2.4** We note that conditions (2.22)-(2.26) are natural and biologically relevant. They are similar to the ones obtained in [24] for the existence of a positive steady state of a nonlinear age-structured model. For our model the introduction of a net reproduction function (which will be an operator) will be somewhat cumbersome and biologically less straightforward, see the next section. However, it is still shown that conditions (2.22)-(2.26) require that the growth rate of the population is larger than one close to the zero steady state while the growth rate of the population is small (definitely less than 1) for large population sizes.

**3. Asymptotic behavior.** In this section we will investigate the asymptotic behavior of solutions. Our approach is based on a formal linearization around a steady state solution and on a careful spectral analysis of the linearized operator. More precisely, our goal is to establish conditions which guarantee that the growth bound  $\omega_0$  of the linearized semigroup is negative, respectively positive. We will show that the growth bound of the linearized semigroup can be completely characterized by the spectrum of its generator. However, as we noted before, the main difficulty is that the eigenvalues of the linearized semigroup generator and therefore the spectral bound cannot be characterized directly via eigenvalues, in the general case.

We note that the Principle of Linearized Stability has so far only been established for semilinear models, see e.g. [18, 24, 27], but not for general quasilinear equations, such as the one we treat in this paper. Therefore, for the remainder of the paper, we make the additional assumption that the growth rate is separable

$$\gamma(s, P) = \gamma_1(s)\gamma_2(P). \tag{3.27}$$

This is plausible from the biological point of view, as the growth rate is modulated by the total weighted population, equally for individuals of all sizes. Then the

quasilinear problem (1.1)-(1.4) can be written in the form

$$\frac{dp}{dt} = g(p)\mathbb{A}p + F(p), \quad p(0) = p_0, \tag{3.28}$$

where

$$g(p) := \gamma_2(P) = \gamma_2 \left( \int_0^m \kappa(s)p(s, t) \, ds \right), \quad \mathbb{A}p = \frac{\partial}{\partial s} (\gamma_1 p),$$

and the recruitment and mortality terms in equation (1.1) are incorporated in the nonlinear operator  $F$ . Grabosch and Heijmans in [17] introduced the transformation

$$\tau_p(t) = \int_0^t g(p(s)) \, ds$$

and defined

$$q(\tau) = p(t_p(\tau)), \quad \text{for } \tau \geq 0,$$

where  $t_p$  is the inverse function of  $\tau_p$ . It is then verified that  $q$  satisfies the semilinear equation

$$\frac{dq}{d\tau} = \mathbb{A}q(\tau) + B(q(\tau)), \quad q(0) = p_0, \tag{3.29}$$

with the same initial value as in (3.28), where the nonlinear operator  $B$  is defined via  $B(q) = F(q)/g(q)$ . This requires that  $g$  is a continuous, strictly positive and bounded function, as is guaranteed by our assumptions (1.5). In [17] Grabosch and Heijmans showed that

1. Solutions of problems (3.28) and (3.29) are in one-to-one correspondence with each other [17, Theorem 3.4].
2. Problems (3.28) and (3.29) have the same equilibrium solutions, and an equilibrium solution of (3.28) is stable if and only if it is stable for (3.29) [17, Theorem 5.1].

In what follows, we make the assumption of a separable growth rate (3.27), but keep the notation  $\gamma(s, P)$  to avoid cumbersome expressions.

**3.1. Linearization around steady states.** Given a stationary (time independent) solution  $p_*$  of system (1.1)-(1.4), we introduce the perturbation  $u = u(s, t)$  of  $p$  by making the ansatz  $p = u + p_*$  and we substitute this into equations (1.1)-(1.4). Then we are using Taylor series expansions of the vital rates of the following form

$$f(x, E) = f(x, E_*) + f_E(x, E_*)(E - E_*) + \text{“higher order terms”},$$

to arrive at

$$\begin{aligned} & u_t(s, t) + \left( (\gamma(s, P_*) + \gamma_P(s, P_*)U(t)) (u(s, t) + p_*(s)) \right)_s \\ &= -(\mu(s, E(s, p_*)) + \mu_E(s, E(s, p_*))E(s, u)) (u(s, t) + p_*(s)) \\ &+ \int_0^m (\beta(s, y, E(y, p_*)) + \beta_E(s, y, E(y, p_*))E(y, u)) (u(y, t) + p_*(y)) \, dy, \end{aligned} \tag{3.30}$$

where we have defined

$$U(t) = \int_0^m \kappa(s)u(s, t) \, ds.$$

Next we omit the nonlinear terms in equation (3.30) to arrive at the linearized problem

$$\begin{aligned}
 &u_t(s, t) + \gamma(s, P_*)u_s(s, t) + \gamma_s(s, P_*)u(s, t) + \gamma_{P_s}(s, P_*)p_*(s)U(t) \\
 &\quad + \gamma_P(s, P_*)p'_*(s)U(t) \\
 &= -\mu(s, E(s, p_*))u(s, t) - \mu_E(s, E(s, p_*))p_*(s)E(s, u) \\
 &\quad + \int_0^m \left( \beta(s, y, E(y, p_*))u(y, t) + \beta_E(s, y, E(y, p_*))p_*(y)E(y, u) \right) dy,
 \end{aligned} \tag{3.31}$$

with the boundary condition

$$\gamma(0, P_*)u(0, t) = 0. \tag{3.32}$$

Equations (3.31)–(3.32) are accompanied by the initial condition

$$u(s, 0) = u_0(s). \tag{3.33}$$

The linearized problem (3.31)–(3.33) is treated effectively in the framework of semi-group theory. To this end we cast the linearized system (3.31)–(3.33) in the form of an abstract Cauchy problem on the state space  $L^1(0, m)$  as follows:

$$\frac{d}{dt} u = (\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}) u, \quad u(s, 0) = u_0(s),$$

where

$$\mathcal{A}u = -\gamma(\cdot, P_*)u_s \text{ with } \text{Dom}(\mathcal{A}) = \{u \in W^{1,1}(0, m) \mid u(s=0) = 0\}, \tag{3.34}$$

$$\mathcal{B}u = -(\gamma_s(\cdot, P_*) + \mu(\cdot, E(\cdot, p_*)))u, \tag{3.35}$$

$$\begin{aligned}
 \mathcal{C}u &= -(\gamma_{P_s}(\cdot, P_*)p_*(\cdot) + \gamma_P(\cdot, P_*)p'_*(\cdot)) \int_0^m \kappa(y)u(y) dy \\
 &= -\rho_*(\cdot) \int_0^m \kappa(y)u(y) dy,
 \end{aligned} \tag{3.36}$$

$$\mathcal{D}u = -\mu_E(\cdot, E(\cdot, p_*))p_*(\cdot)E(\cdot, u), \tag{3.37}$$

$$\mathcal{F}u = \int_0^m \beta(\cdot, y, E(y, p_*))u(y) dy + \int_0^m \beta_E(\cdot, y, E(y, p_*))p_*(y)E(y, u) dy. \tag{3.38}$$

**Proposition 3.5.** *The operator  $\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}$  generates a strongly continuous quasicontractive semigroup  $\{\mathcal{T}(t)\}_{t \geq 0}$  of bounded linear operators on  $L^1(0, m)$ , which is positive if the operator  $\mathcal{C} + \mathcal{D} + \mathcal{F}$  is positive.*

We omit the proof of the above proposition as it can be established following similar results in [12, 14, 15, 16].

**3.2. Stability results for positive equilibria.** In this section we establish linear stability/instability results for a general steady state  $p_*$ . We will treat the extinction steady state in the next subsection in detail. When addressing stability questions the main difficulty is that, in general, the point spectrum of the semigroup generator cannot be characterized via zeros of an associated characteristic function. We will overcome this problem by using positive perturbation arguments.

**Theorem 3.6.** *Assume that*

$$\int_0^m \kappa(s) \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*))}{\gamma(x, P_*)} dx \right\} \frac{\rho_*(y)}{\gamma(y, P_*)} dy ds < -1. \tag{3.39}$$

Furthermore assume that

$$\rho_*(s) \leq 0, \quad s \in [0, m] \quad \text{and} \quad \exists \varepsilon > 0 \text{ such that } \rho_*(s) \neq 0 \text{ for a.e. } s \in [0, \varepsilon], \quad (3.40)$$

$$\mu_E(s, E(s, p_*)) \leq 0, \quad \beta_E(s, y, E(y, p_*)) \geq 0, \quad y, s \in [0, m]. \quad (3.41)$$

Then the steady state  $p_*$  of model (1.1)-(1.4) is linearly unstable.

*Proof.* First we note that  $\mathcal{A} + \mathcal{B} + \mathcal{C}$  generates a positive, irreducible and eventually compact semigroup if conditions (3.40) hold true. Eventual compactness is easily shown, see Proposition 3.7. To establish irreducibility we consider the resolvent equation

$$R(\lambda, \mathcal{A} + \mathcal{B} + \mathcal{C})h = u, \quad h \in \mathcal{X}^+.$$

The solution is obtained as:

$$\begin{aligned} u(s) = & \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*)) + \lambda}{\gamma(x, P_*)} dx \right\} \frac{h(y)}{\gamma(y, P_*)} dy \\ & - U \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*)) + \lambda}{\gamma(x, P_*)} dx \right\} \frac{\rho_*(y)}{\gamma(y, P_*)} dy, \end{aligned} \quad (3.42)$$

where

$$\begin{aligned} U = & \int_0^m \kappa(s) u(s) ds \\ = & \frac{\int_0^m \kappa(s) \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*)) + \lambda}{\gamma(x, P_*)} dx \right\} \frac{h(y)}{\gamma(y, P_*)} dy ds}{1 + \int_0^m \kappa(s) \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*)) + \lambda}{\gamma(x, P_*)} dx \right\} \frac{\rho_*(y)}{\gamma(y, P_*)} dy ds}. \end{aligned} \quad (3.43)$$

The second equality is obtained from (3.42) by multiplying by  $\kappa$  and integrating from 0 to  $m$ . Hence for  $\lambda$  large enough  $U > 0$  and  $u \gg 0$  follows from condition (3.40). The irreducibility and eventual compactness of the semigroup imply that the spectrum  $\sigma(\mathcal{A} + \mathcal{B} + \mathcal{C})$  is not empty, see e.g. Th. 3.7 in Sect. C-III in [5], hence the spectrum  $\sigma(\mathcal{A} + \mathcal{B} + \mathcal{C})$  contains at least one eigenvalue. Next we find the solution of the eigenvalue equation

$$(\mathcal{A} + \mathcal{B} + \mathcal{C})u = \lambda u$$

as

$$u(s) = -U \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*)) + \lambda}{\gamma(x, P_*)} dx \right\} \frac{\rho_*(y)}{\gamma(y, P_*)} dy. \quad (3.44)$$

Then we multiply the solution (3.44) by  $\kappa$  and integrate over  $[0, m]$  to obtain

$$\begin{aligned} U = & -U \int_0^m \kappa(s) \\ & \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*)) + \lambda}{\gamma(x, P_*)} dx \right\} \frac{\rho_*(y)}{\gamma(y, P_*)} dy ds. \end{aligned}$$

We note that, if  $U = 0$  then equation (3.44) shows that  $u(s) \equiv 0$ , hence we have a non-trivial eigenvector if and only if  $U \neq 0$  and  $\lambda$  satisfies the following characteristic equation

$$\begin{aligned} 1 = & K(\lambda) \stackrel{\text{def}}{=} \\ & \int_0^m \kappa(s) \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*)) + \lambda}{\gamma(x, P_*)} dx \right\} \frac{\rho_*(y)}{\gamma(y, P_*)} dy ds. \end{aligned} \quad (3.45)$$

It is easily shown that

$$\lim_{\lambda \rightarrow +\infty} K(\lambda) = 0,$$

therefore it follows from the assumption  $K(0) > 1$  (3.39), on the grounds of the Intermediate Value Theorem, that equation (3.45) has a positive (real) solution. Hence we have

$$0 < s(\mathcal{A} + \mathcal{B} + \mathcal{C}),$$

where  $s(\mathcal{A} + \mathcal{B} + \mathcal{C})$  stands for the spectral bound of the operator  $\mathcal{A} + \mathcal{B} + \mathcal{C}$ . The operators  $\mathcal{D}$  and  $\mathcal{F}$  are positive if conditions (3.41) hold true. We have for the spectral bound (see e.g. Corollary VI.1.11 in [11])

$$0 < s(\mathcal{A} + \mathcal{B} + \mathcal{C}) \leq s(\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}).$$

Since the growth bound of the semigroup is bounded below by the spectral bound of its generator, the proof is completed.  $\square$

We note that the instability conditions (3.41) imply that mortality is a non-increasing function of the environment and fertility is a non-decreasing function of the environment.

Next we establish conditions which guarantee that the equilibrium solution  $p_*$  is linearly asymptotically stable. To this end we establish first that the spectrum of the semigroup generator  $\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}$  consists of eigenvalues only and that the spectral mapping theorem holds true. Then the growth bound of the semigroup equals the spectral bound of its generator. These follow however from the following result (see e.g. Corollary IV.3.12 in [11]).

**Proposition 3.7.** *The semigroup  $\{\mathcal{T}(t)\}_{t \geq 0}$  generated by the operator  $\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}$  is eventually compact.*

*Proof.* We only sketch the proof here since analogous results for simpler problems can be found in [12, 14, 15, 16]. Due to the zero flux boundary condition and the finite maximal size, the operator  $\mathcal{A} + \mathcal{B}$  generates a nilpotent semigroup. The biological interpretation is that in the absence of recruitment the population dies out independently of the initial condition.  $\mathcal{C}$  is a bounded linear operator of rank one, hence it is compact. It only remains to establish that the bounded linear integral operators  $\mathcal{D}$  and  $\mathcal{F}$  are compact. These however, can be deduced using the Fréchet-Kolmogorov compactness criterion (see e.g. Chapter X in [28]) from the regularity assumptions we made on the model ingredients, see the proof of Theorem 12 in [12] for more details.  $\square$

The previous result guarantees that stability is determined by the leading eigenvalue of the semigroup generator  $\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}$ , unless the spectrum is empty. In that case one further needs to establish positivity of the semigroup which guarantees that the growth bound coincides with the spectral bound, which by definition equals minus infinity. However, as we noted before, the eigenvalue equation

$$(\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F} - \lambda \mathcal{I}) u = 0, \quad u(s = 0) = 0,$$

cannot be solved explicitly. This is due to the infinite dimensional nonlinearity in the original problem and to the very general recruitment term.

Compact perturbations do not change the essential spectrum of the semigroup generator. Therefore our approach to establish stability is to find a positive compact perturbation of the generator for which we can characterize the point spectrum via

zeros of an associated characteristic function. To this end, for a separable fertility function  $\beta$ , we introduce the following operators on  $L^1(0, m)$ ,

$$\begin{aligned} \bar{\mathcal{D}}u &= -\mu_E(\cdot, E(\cdot, p_*))p_*(\cdot) \int_0^m w(r)u(r) \, dr, \\ \bar{\mathcal{F}}_2u &= \beta_1(\cdot) \int_0^m \beta_{2_E}(y, E(y, p_*))p_*(y) \, dy \int_0^m w(r)u(r) \, dr. \end{aligned}$$

We formulate our main stability result in the following theorem.

**Theorem 3.8.** *Assume that there exists a function*

$$\tilde{\beta}(s, y, E(y, p_*)) = \beta_1(s)\beta_2(y, E(y, p_*))$$

such that

$$\beta(s, y, E(y, p_*)) \leq \tilde{\beta}(s, y, E(y, p_*)), \quad s, y \in [0, m]. \tag{3.46}$$

Furthermore assume that the following conditions hold true

$$\mu_E(s, E(s, p_*)) \leq 0, \quad \tilde{\beta}_E(s, y, E(y, p_*)) \geq 0, \quad s, y \in [0, m], \tag{3.47}$$

$$\gamma_{P_s}(s, P_*)p_*(s) + \gamma_P(s, P_*)p'_*(s) \leq 0, \quad s \in [0, m], \tag{3.48}$$

and the characteristic function  $K_{\tilde{\beta}}(\lambda)$  given by equation (3.54) corresponding to  $\tilde{\beta}$  and to the modified operators  $\bar{\mathcal{D}}$  and  $\bar{\mathcal{F}}_2$  does not have a zero with non-negative real part. Then the stationary solution  $p_*$  is linearly asymptotically stable.

*Proof.* We obtain the solution of the eigenvalue equation

$$(\mathcal{A} + \mathcal{B} + \mathcal{C} + \bar{\mathcal{D}} + \mathcal{F}_1 + \bar{\mathcal{F}}_2 - \lambda\mathcal{I})u = 0, \tag{3.49}$$

as

$$\begin{aligned} u(s) &= U_1 \int_0^s f_0^\lambda(s, y)f_1(y) \, dy \\ &\quad + U_2 \int_0^s f_0^\lambda(s, y)f_2(y) \, dy + U_3 \int_0^s f_0^\lambda(s, y)f_3(y) \, dy, \end{aligned} \tag{3.50}$$

where

$$\begin{aligned} U_1 &= \int_0^m \kappa(s)u(s) \, ds, \quad U_2 = \int_0^m w(s)u(s) \, ds, \\ U_3 &= \int_0^m \beta_2(s, E(s, p_*))u(s) \, ds, \\ f_0^\lambda(s, y) &= \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*)) + \lambda}{\gamma(x, P_*)} \, dx \right\}, \\ f_1(y) &= \frac{-\gamma_{P_s}(y, P_*)p_*(y) - \gamma_P(y, P_*)p'_*(y)}{\gamma(y, P_*)}, \quad f_3(y) = \frac{\beta_1(y)}{\gamma(y, P_*)}, \\ f_2(y) &= \frac{\beta_1(y) \int_0^m \beta_2(x, E(x, p_*))p_*(x) \, dx - \mu_E(y, E(y, p_*))p_*(y)}{\gamma(y, P_*)}. \end{aligned}$$

We multiply equation (3.50) by  $\kappa, w$  and by  $\beta_2$  and integrate from 0 to  $m$ , respectively to obtain

$$U_1(1 + a_{11}(\lambda)) + U_2a_{12}(\lambda) + U_3a_{33}(\lambda) = 0, \tag{3.51}$$

$$U_1a_{21}(\lambda) + U_2(a_{22}(\lambda) + 1) + U_3a_{23}(\lambda) = 0, \tag{3.52}$$

$$U_1a_{31}(\lambda) + U_2a_{32}(\lambda) + U_3(a_{33}(\lambda) + 1) = 0, \tag{3.53}$$

where for  $i = 1, 2, 3$ ,

$$\begin{aligned} a_{1i}(\lambda) &= \int_0^m \kappa(s) \int_0^s f_0^\lambda(s, y) f_i(y) \, dy \, ds, \\ a_{2i}(\lambda) &= \int_0^m w(s) \int_0^s f_0^\lambda(s, y) f_i(y) \, dy \, ds, \\ a_{3i}(\lambda) &= \int_0^m \beta_2(s, E(s, p_*)) \int_0^s f_0^\lambda(s, y) f_i(y) \, dy \, ds. \end{aligned}$$

If  $\lambda \in \sigma(\mathcal{A} + \mathcal{B} + \mathcal{C} + \overline{\mathcal{D}} + \mathcal{F}_1 + \overline{\mathcal{F}}_2)$  then the eigenvalue equation (3.49) admits a non-trivial solution  $u$  hence there exists a non-zero vector  $(U_1, U_2, U_3)$  which solves equations (3.51)-(3.53). To the contrary, if  $(U_1, U_2, U_3)$  is a non-zero solution of equations (3.51)-(3.53) for some  $\lambda \in \mathbb{C}$  then (3.50) yields a non-trivial solution  $u$ . This is because the only scenario for  $u$  to vanish would yield

$$\begin{aligned} -U_1 \int_0^s f_0^\lambda(s, y) f_1(y) \, dy &= U_2 \int_0^s f_0^\lambda(s, y) f_2(y) \, dy \\ &\quad + U_3 \int_0^s f_0^\lambda(s, y) f_3(y) \, dy, \end{aligned}$$

for every  $s \in [0, m]$ . This however, together with conditions (3.47)-(3.48) would yield  $U_1 = U_2 = U_3 = 0$ , a contradiction. Thus  $\lambda \in \mathbb{C}$  is an eigenvalue of  $\mathcal{A} + \mathcal{B} + \mathcal{C} + \overline{\mathcal{D}} + \mathcal{F}_1 + \overline{\mathcal{F}}_2$  if and only if it satisfies the characteristic equation

$$K_{\tilde{\beta}}(\lambda) \stackrel{\text{def}}{=} \det \begin{pmatrix} 1 + a_{11}(\lambda) & a_{12}(\lambda) & a_{13}(\lambda) \\ a_{21}(\lambda) & 1 + a_{22}(\lambda) & a_{23}(\lambda) \\ a_{31}(\lambda) & a_{32}(\lambda) & 1 + a_{33}(\lambda) \end{pmatrix} = 0. \tag{3.54}$$

Next we observe that conditions (3.47)-(3.48) guarantee that both  $\mathcal{C}$ ,  $\mathcal{D}$  and  $\mathcal{F}$  are positive operators. Therefore we conclude that  $\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}$  is a generator of a positive semigroup. Moreover, the operators  $(\overline{\mathcal{D}} - \mathcal{D})$ ,  $(\mathcal{F}_1^{\tilde{\beta}} - \mathcal{F}_1^\beta)$  and  $(\overline{\mathcal{F}}_2^{\tilde{\beta}} - \mathcal{F}_2^\beta)$  are all positive and bounded. We have

$$\begin{aligned} s(\mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}) &= s \left( \mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}_1^\beta + \mathcal{F}_2^\beta \right) \\ &\leq s \left( \mathcal{A} + \mathcal{B} + \mathcal{C} + \mathcal{D} + \mathcal{F}_1^\beta + \mathcal{F}_2^\beta + \overline{\mathcal{D}} - \mathcal{D} + \mathcal{F}_1^{\tilde{\beta}} - \mathcal{F}_1^\beta + \overline{\mathcal{F}}_2^{\tilde{\beta}} - \mathcal{F}_2^\beta \right) \\ &= s \left( \mathcal{A} + \mathcal{B} + \mathcal{C} + \overline{\mathcal{D}} + \mathcal{F}_1^{\tilde{\beta}} + \overline{\mathcal{F}}_2^{\tilde{\beta}} \right) < 0, \end{aligned}$$

and the proof is completed. □

**Example 3.9** The crucial assumption of the previous theorem is that the characteristic function  $K_{\tilde{\beta}}$  does not have a root with non-negative real part. Here we only present an example when this condition may be easily verified. In particular, let us assume that

$$\kappa \equiv c_1, \quad w \equiv c_2, \quad \beta_2 \equiv c_3$$

for some constants  $c_1, c_2, c_3 > 0$ . In this special case the characteristic equation  $K_{\tilde{\beta}}(\lambda) = 0$  takes the simple form

$$1 = \int_0^m \int_0^s f_0^\lambda(s, y) (c_1 f_1(y) + c_2 f_2(y) + c_3 f_3(y)) \, dy \, ds.$$

Therefore there exists a unique dominant real eigenvalue, which is negative, if

$$\int_0^m \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*))}{\gamma(x, P_*)} dx \right\} \times \left( \frac{\beta_1(y) (c_3 + c_2 \int_0^m \beta_2(s, E(s, p_*)) p_*(s) ds)}{\gamma(y, P_*)} - \frac{c_2 \mu_E(y, E(y, p_*)) + c_1 \gamma_{Ps}(y, P_*) p_*(y) + c_1 \gamma_P(y, P_*)}{\gamma(y, P_*)} \right) dy ds < 1.$$

The latter condition may be easily verified for fixed model ingredients.

**3.3. The extinction equilibrium.** In this subsection we establish a simple criterion for the stability/instability of the trivial steady state  $p_* \equiv 0$ . The stability of the trivial steady state is important from the biological point of view, as it can answer the question for example if a species can be introduced successfully into (or can invade) a new habitat. In case of the trivial steady state the eigenvalue problem can be written as

$$(\mathcal{A} + \mathcal{B} + \mathcal{F}_\beta - \lambda \mathcal{I}) u = 0, \quad u(s = 0) = 0, \tag{3.55}$$

where  $\lambda \in \mathbb{C}$ , the operators  $\mathcal{A}$  and  $\mathcal{B}$  are defined via (3.34)-(3.35) with  $p_* \equiv 0$  (and  $P_* = 0$ ) and

$$\mathcal{F}_\beta u = \int_0^m \beta(\cdot, y, \mathbf{0}) u(y) dy.$$

We recall that in case of simpler scramble competition models the so called net reproduction function played a crucial role in the stability analysis of equilibrium solutions, see e.g. [13]. In particular, we managed to relate our stability results to a biologically meaningful model ingredient, namely the net reproduction rate. In case of hierarchical contest competition models this is less straightforward as we have seen. Nevertheless at least for a separable fertility function

$$\beta(s, y, E(y, \cdot)) = \beta_1(s) \beta_2(y, E(y, \cdot)),$$

we may define a *net reproduction functional*

$$R : L^1_+(0, m) \rightarrow \mathbb{R}$$

of the standing population  $p$  as

$$\begin{aligned} R(p) &= \int_0^m \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P) + \mu(x, E(x, p))}{\gamma(x, P)} dx \right\} \frac{\beta_1(y) \beta_2(s, E(s, p))}{\gamma(y, P)} dy ds, \\ &= \int_0^m \frac{\beta_2(s, E(s, p))}{\gamma(s, P)} \int_0^s \beta_1(y) \exp \left\{ - \int_y^s \frac{\mu(x, E(x, p))}{\gamma(x, P)} dx \right\} dy ds, \end{aligned}$$

where  $P$  is the weighted population according to (1.4). The value of the functional  $R$  is the expected number of offspring to be produced by an individual in her lifetime. Individuals of size  $y$  are produced at a rate  $\beta_1$  and need to survive from size  $y$  to size  $s$  to reproduce. We also note that  $R(p_*) = 1$  is a necessary condition for the existence of a positive steady state  $p_*$  of our model. It is however not a sufficient condition in contrast to scramble competition models, i.e. when density dependence is incorporated via finite dimensional nonlinearities in the vital rates.



**Proposition 3.10.** *Assume that there exists a function  $\beta^l$  such that*

$$\beta^l(s, y) = \beta_1^l(s)\beta_2^l(y) \leq \beta(s, y, \mathbf{0})$$

*and  $R_{\beta^l}(\mathbf{0}) > 1$  (where  $R_{\beta^l}$  stands for the net reproduction functional corresponding to the fertility function  $\beta^l$ ). Then the trivial steady state is linearly unstable. On the other hand if there exists a function  $\beta^u$  with*

$$\beta^u(s, y) = \beta_1^u(s)\beta_2^u(y) \geq \beta(s, y, \mathbf{0})$$

*and  $R_{\beta^u}(\mathbf{0}) < 1$ , then the trivial steady state is linearly stable.*

*Proof.* The eigenvalue equation (3.55) has a nontrivial solution if and only if  $\lambda$  satisfies the characteristic equation

$$1 = K^l(\lambda) \stackrel{\text{def}}{=} \int_0^m \beta_2^l(s) \times \int_0^s \exp \left\{ - \int_y^s \frac{\gamma_s(x, P_*) + \mu(x, E(x, p_*))}{\gamma(x, P_*)} dx \right\} \frac{\beta_1^l(y)}{\gamma(y, P_*)} dy ds. \tag{3.56}$$

It can be shown that  $\lim_{\lambda \rightarrow +\infty} K^l(\lambda) = 0$ . Therefore, if  $R_{\beta^l}(\mathbf{0}) > 1$  holds true, then the characteristic equation (3.56) admits a positive solution  $\lambda$ . Since  $\mathcal{A} + \mathcal{B} + \mathcal{F}_{\beta^l}$  generates a positive semigroup, and the operator  $\mathcal{F}_\beta - \mathcal{F}_{\beta^l}$  is positive we have  $0 < s(\mathcal{A} + \mathcal{B} + \mathcal{F}_{\beta^l}) \leq s(\mathcal{A} + \mathcal{B} + \mathcal{F}_\beta)$  and the instability part follows. Similarly, if  $R_{\beta^u}(\mathbf{0}) < 1$  holds true, then the characteristic equation  $1 = K^u(\lambda)$  does not have a solution with non-negative real part. Therefore on the grounds of Proposition 3.7. we have

$$s(\mathcal{A} + \mathcal{B} + \mathcal{F}_\beta + \mathcal{F}_{\beta^u} - \mathcal{F}_\beta) \leq s(\mathcal{A} + \mathcal{B} + \mathcal{F}_{\beta^u}) < 0,$$

and the stability part follows. □

**4. Concluding remarks.** Hierarchical structured population models are important from the application point of view as they describe the evolution of populations in which individuals are experiencing size-specific environment. This is the case for example in a tree population or in a cannibalistic population. They pose a greater mathematical challenge though than scramble competition models. In the recent papers [14, 15] we started to investigate the asymptotic behavior of hierarchical structured partial differential equation models with one state at birth. Nevertheless, the question of the existence of positive equilibrium solutions for hierarchical models remained an open question up to our knowledge. In this work we formulated biologically relevant conditions for the existence of positive steady states of a very general model.

In the second part we focused on the stability of equilibria. As we have also seen earlier in [14, 15], the main difficulty to establish easily verifiable stability/instability conditions for positive steady states of hierarchical structured population models is that the point spectrum of the semigroup generator cannot be characterized explicitly via zeros of an associated characteristic function. In [14, 15] we devised a dissipativity calculation to show that the linearized semigroup has negative growth bound, and therefore the steady state is stable. The stability conditions we obtained in that way, though, were extremely restrictive. Therefore in this work we devised a new approach to establish stability by using results from the theory of compact and positive operators.

The separability assumption made in (3.27) is only required for the result of Grabosch and Heijmans [17] to be applicable, and not to prove any of the results concerning the linearized semigroup  $\mathcal{T}(t)$ . A Principle of Linearized Stability for fully nonlinear quasilinear hyperbolic equations remains a problem for future investigations (see also [22, 25, 27] for related results).

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