Hierarchical size-structured populations: The linearized semigroup approach

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Abstract

In the present paper we analyze the linear stability of a hierarchical size-structured population model where the vital rates (mortality, fertility and growth rate) depend both on size and a general functional of the population density (“environment”). We derive regularity properties of the governing linear semigroup, implying that linear stability is governed by a dominant real eigenvalue of the semigroup generator, which arises as a zero of an associated characteristic function. In the special case where neither the growth rate nor the mortality depend on the environment, we explicitly calculate the characteristic function and use it to formulate simple conditions for the linear stability of population equilibria. In the general case we derive a dissipativity condition for the linear semigroup, thereby characterizing exponential stability of the steady state.

Keywords: Hierarchical size-structured populations; Semigroup methods; Spectral analysis; Principle of linear stability

1. Introduction

In the last three decades nonlinear age- and size-structured population models have attracted a lot of interest both among theoretical biologists and applied mathematicians. Traditionally, structured population models have been formulated as partial differential equations for population densities. Starting with the seminal work \cite{16}, researchers have been developing and analyzing various

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physiologically structured population models. We refer here to the well-known monographs [5, 19, 22, 25].

Diekmann et al. have been developing a general mathematical framework for modeling structured populations, see for example [9, 10]. One of their most important recent results is that the qualitative behavior of nonlinear physiologically structured population models can be studied by means of linearization [7, 8]. In other words, they have proven for a very general class of physiologically structured population models that the nonlinear stability/instability of a population equilibrium is completely determined by its linear stability/instability. Such a fundamental result, often referred to as “the Principle of Linearized Stability”, has been shown previously for several concrete age- and size-structured models [10, 20, 23, 24, 25].

Following the lead of [23] and [25], we successfully applied linear semigroup methods to formulate biologically interpretable conditions for the linear stability/instability of equilibria of several structured population models [13, 14, 15]. In these problems the vital rates depend on size or age and on the total population size, in general. Hence it is assumed that any effect of intraspecific competition on individual behavior is primarily due to a change in population size and every individual in the population can influence the vital rates of other individuals, a scenario commonly referred to as “scramble competition”.

In other scenarios competition among individuals is based upon some hierarchy in the population which is often related to the size of individuals. In this case the nonlinearity (environmental feedback) in the model is incorporated through infinite dimensional interaction variables. A simple example for this situation is given by a forest consisting of tree individuals in which the height of a tree determines its rank in the population [21]. Taller individuals have higher efficiency when competing for resources such as light, while individuals of lower rank cannot affect the vital rates of individuals of higher rank. This scenario is the so called “contest competition”. Both discrete time and continuous hierarchical structured models have been developed, see [6] and the references therein.

Of interest in this work is the stability analysis of population equilibria by means of linearization of a continuous quasilinear size-structured model, recently discussed in [2]. In this model the density evolution of individuals of size \( s \) is assumed to be governed by the following quasilinear partial differential equation

\[
\frac{u_t(s, t)}{u(s, t)} + (\gamma(s, Q(s, t)) u(s, t))_s + \mu(s, Q(s, t)) u(s, t) = 0, \quad (1.1)
\]

defined for \( 0 \leq s \leq m < \infty \) and \( t > 0 \). The density of zero (or minimal) size individuals is given by the nonlocal boundary condition

\[
u(0, t) = \int_0^m \beta(s, Q(s, t)) u(s, t) \, ds, \quad t > 0. \quad (1.2)
\]

The quantity \( m \) denotes the maximum size of individuals. The initial condition takes the form

\[
u(s, 0) = u_0(s), \quad s \in [0, m]. \quad (1.3)
\]
Here $\beta$, $\mu$ and $\gamma$ denote the fertility, mortality and growth rate of individuals, respectively. We assume that these vital rates depend on the individual size $s$ and on the environment

$$Q(s, t) = \alpha \int_{0}^{s} w(\eta) u(\eta, t) \, d\eta + \int_{s}^{m} w(\eta) u(\eta, t) \, d\eta, \quad 0 \leq s \leq m, \quad t \geq 0.$$  \hfill (1.4)

The constant $\alpha$ is a parameter in $[0, 1]$ measuring the degree of hierarchy in the population, while the function $w$ represents a positive weight. For example in case of a tree population where taller individuals overshadow smaller individuals \cite{21} the vital rates of an individual of size $s$ are reasonably assumed to depend on the cumulative leaf area of individuals of size $s$ or larger, modeled by the function

$$Q(s, t) = \int_{s}^{m} w(\eta) u(\eta, t) \, d\eta. \hfill (1.5)$$

Here $w$ is an appropriately chosen weight function. Hence in this situation the parameter $\alpha$ would be 0. The case $\alpha = 1$ (which represents scramble competition) has been treated in detail in \cite{13}.

We impose the following regularity conditions on the model ingredients:

- $\mu = \mu(s, Q) \in C([0, m]; C^1[0, \infty)), \mu \geq 0$
- $\gamma = \gamma(s, Q) \in C^1([0, m]; C^4[0, \infty]) \cap C([0, m]; C^2[0, \infty)), \gamma > 0$
- $\beta = \beta(s, Q) \in C([0, m]; C^4[0, \infty)), \beta \geq 0$
- $w = w(s) \in C^1([0, m]), w > 0.$

These assumptions are tailored toward the linear analysis of this work. They might, however, not suffice to guarantee the existence and uniqueness of solutions of Eqs. (1.1)–(1.4). Well-posedness of structured partial differential equation models with infinite dimensional environmental feedback variables is in general an open question, although conditions for the global existence of weak solutions in the case discussed here are given in \cite{2}. It has recently been shown \cite{1, 21} that the population model (1.1)–(1.4) may exhibit a more complicated dynamical behavior than the simple size-structured model of scramble competition. In particular, in \cite{1} it was demonstrated both analytically and numerically that a singular solution of (1.1)–(1.4) containing a Dirac delta mass component can emerge if the growth rate $\gamma$ is not a decreasing function of the environment $Q$.

For a more realistic description of real populations in a specific setting, one will have to modify the assumptions on the vital rates above. For example, one would possibly demand that $\lim_{s \to m} \mu(s, \cdot) = \infty$, thus modeling a gradual rather than instantaneous reduction in the numbers of individuals reaching maximum size $m$. 
The size-structured model $\text{(1.1)-(1.4)}$ is often considered (see [1, 2]) with a boundary condition of the form

$$
\gamma(0, Q(0, t)) u(0, t) = C(t) + \int_0^m \beta(s, Q(s, t)) u(s, t) ds, \quad t > 0.
$$

(1.6)

In [1, 2] we have taken $C \equiv 0$ and incorporated the growth rate $\gamma(0, Q(0, t))$ on the left of (1.6) in the birth rate $\beta(s, Q(s, t))$ on the right of (1.2), assuming that zero size individuals grow instantaneously. This assumption seems reasonable, for example in case of a forest population. It is then clear that the two boundary conditions are equivalent (in the case $C \equiv 0$ treated here). We have observed, however, that (1.2) is better suited for analytical work [13, 14, 15]. As recent results indicate [12, 15], the introduction of a positive inflow $C$ may have a significant influence on the linearized dynamical behavior of (1.1)-(1.4). A comprehensive study of the effects of a positive inflow in hierarchical populations is left for future work.

The study of hierarchical models in the literature is largely based on a decoupling of the total population quantity from the governing equations and a transformation of the nonlocal partial differential equation (1.1) into a local one [3, 4, 21]. This technique allows to prove well-posedness and to study the asymptotic behavior of solutions by means of ODE methods. For Eqs. (1.1)-(1.4) this transformation fails since the vital rates depend on both size $s$ and on the environment $Q(s, t)$. Therefore it seems unavoidable to study the original partial differential equation (1.1) with the nonlocal integral boundary condition (1.2) directly. This approach is based on a linearization of the governing equations about steady state [12, 13, 14, 15, 23, 25]. While Sections 3 through 5 exploit spectral theoretic and structural properties of the governing linear semigroup extending related results in [13, 14, 15], Section 6 gives a new characterization of asymptotic stability of the semigroup in terms of a dissipativity criterion. This idea was previously introduced and employed in [17, 18] for elongational flow problems.

2. The linearized system

Eqs. (1.1)-(1.4) have obviously the trivial solution $u_\ast \equiv 0$. Realistically we also expect additional positive (continuously differentiable) solutions $u_\ast > 0$. In the following we formulate a necessary condition for the existence of a positive equilibrium solution of problem (1.1)-(1.4).

**Proposition 2.1** If $u_\ast$ is a positive stationary solution of problem (1.1)-(1.4), then the function $Q_\ast$, defined by

$$
Q_\ast(s) = \alpha \int_0^s w(\eta) u_\ast(\eta) d\eta + \int_s^m w(\eta) u_\ast(\eta) d\eta,
$$

(2.1)

satisfies the equation

$$
R(Q_\ast) = 1,
$$

(2.2)
where \( R : C([0, m]) \to \mathbb{R} \) is the inherent net reproduction rate
\[
R(Q) \overset{\text{def}}{=} \int_0^m \beta(s, Q(s)) \pi(s, Q) \, ds \quad (2.3)
\]
and the operator \( \pi \) is given for \( 0 \leq s \leq m \) and \( Q \in C([0, m]) \) by
\[
\pi(s, Q) \overset{\text{def}}{=} \frac{\gamma(0, Q(0))}{\gamma(s, Q(s))} \exp \left\{ - \int_0^s \frac{\mu(r, Q(r))}{\gamma(r, Q(r))} \, dr \right\}. \quad (2.4)
\]

**Proof.** For a positive stationary solution \( u_* \) let \( Q_* \) be given by (2.1). Since any stationary solution satisfies
\[
u_*(s) = u_*(0) \pi(s, Q_*), \quad (2.5)
\]
we obtain Eq. (2.2) when imposing the boundary condition (1.2). \( \square \)

Given any stationary solution \( u_* \) in \( C^1([0, m]) \), we linearize the governing equations by introducing the infinitesimal perturbation \( v = v(s, t) \) and making the ansatz \( u = v + u_* \). After inserting this expression in the governing equations and omitting all nonlinear terms, we obtain the linearized problem
\[
v_t(s, t) + \gamma_*(s) v_s(s, t) + \rho_*(s) v(s, t) + \sigma_*(s) V(s, t) = 0, \quad (2.6)
\]
\[
v(0, t) = \int_0^m \beta(s, Q_*(s)) v(s, t) \, ds + \int_0^m \beta Q(s, Q_*(s)) u_*(s) V(s, t) \, ds, \quad (2.7)
\]
where we have set
\[
V(s, t) = \alpha \int_0^s w(\eta) v(\eta, t) \, d\eta + \int_s^m w(\eta) v(\eta, t) \, d\eta, \quad (2.8)
\]
\[
\gamma_*(s) = \gamma(s, Q_*(s)), \quad (2.9)
\]
\[
\rho_*(s) = \mu(s, Q_*(s)) + \gamma_*(s, Q_*(s)) + 2(\alpha - 1) w(s) \gamma_Q(s, Q_*(s)) u_*(s), \quad (2.10)
\]
\[
\sigma_*(s) = \mu Q(s, Q_*(s)) u_*(s) + \gamma_Q(s, Q_*(s)) u_*(s) + \gamma Q(s, Q_*(s)) u'_*(s) + (\alpha - 1) w(s) \gamma_Q(s, Q_*(s)) u_*(s)^2. \quad (2.11)
\]

We denote the Lebesgue space \( L^1(0, m) \) with its usual norm \( \| \cdot \| \) by \( \mathcal{X} \) and introduce the bounded linear functional \( \Lambda \) on \( \mathcal{X} \) by
\[
\Lambda(v) = \int_0^m \beta(s, Q_*(s)) v(s) \, ds \quad (2.12)
\]
\[
+ \int_0^m \beta Q(s, Q_*(s)) u_*(s) \left( \alpha \int_0^s w(\eta) v(\eta, t) \, d\eta + \int_s^m w(\eta) v(\eta, t) \, d\eta \right) \, ds.
\]

Next we define the operators
\[
\mathcal{A} v = -\gamma(\cdot, Q_*) v_*, \quad \text{Dom}(\mathcal{A}) = \{ v \in W^{1,1}(0, m) \mid v(0) = \Lambda(v) \}, \quad (2.13)
\]
\[
\mathcal{B} v = -\rho_* v \quad \text{on} \mathcal{X}, \quad (2.14)
\]
\[
\mathcal{C} v = -\sigma_* \left( \alpha \int_0^s w(\eta) v(\eta, t) \, d\eta + \int_s^m w(\eta) v(\eta, t) \, d\eta \right) \quad \text{on} \mathcal{X}. \quad (2.15)
\]
Then the linearized system (2.6)–(2.7) can be cast in the form of an initial value problem for an ordinary differential equation on \( X \)

\[
\frac{d}{dt} v = (A + B + C) v, \tag{2.16}
\]
together with the initial condition

\[
v(0) = v_0. \tag{2.17}
\]

In analogy to previously discussed size-structured population models [13, 14, 15], we can invoke the Desch-Schappacher Perturbation Theorem [11] to obtain the following result.

**Proposition 2.2** The operator \( A + B + C \) generates a strongly continuous semigroup \( \{T(t)\}_{t \geq 0} \) of bounded linear operators on \( X \).

The proof is a minor modification of parallel results given in [13, 14, 15] and has therefore been omitted.

### 3. Spectral analysis and semigroup regularity

**Proposition 3.1** The spectrum of \( A + B + C \) can contain only isolated eigenvalues of finite multiplicity.

**Proof.** We prove that the resolvent operator of \( A + B + C \) is compact. Since \( B + C \) is a bounded perturbation of \( A \), it suffices to show that the resolvent operator of \( A \) is compact. To this end, given \( f \in \mathcal{X} \), we find a unique solution \( v \in \text{Dom}(A) \) of the equation

\[
\lambda v - A v = f \tag{3.1}
\]
in the form

\[
v(s) = e^{-\lambda \Gamma(s)} \left( A(v) + \int_0^s e^{\lambda \Gamma(r)} \frac{f(r)}{\gamma(r, Q_r(\eta))} \, dr \right) \tag{3.2}
\]
if \( \lambda \in \mathbb{R} \) is sufficiently large. Here we define

\[
\Gamma(s) \overset{\text{def}}{=} \int_0^s \frac{1}{\gamma_s(\eta)} \, d\eta. \tag{3.3}
\]

Consequently, for \( \lambda > 0 \) large enough, the resolvent operator \( (\lambda \mathcal{I} - A)^{-1} \) exists and is bounded, mapping \( \mathcal{X} = L^1(0, m) \) into \( W^{1,1}(0, m) \). Since \( W^{1,1}(0, m) \) is compactly embedded in \( L^1(0, m) \), the claim follows.
Theorem 3.2  The semigroup $\{T(t)\}_{t \geq 0}$, generated by the operator $A + B + C$, is eventually compact. Consequently, the Spectral Mapping Theorem holds true, i.e.

$$\sigma(T(t)) = \{0\} \cup \exp\{\sigma(A + B + C) t\}, \quad t > 0.$$  \hfill (3.4)

Moreover, the semigroup is spectrally determined, i.e. the growth rate $\omega(T)$ of the semigroup and the spectral bound $s(A + B + C)$ of its generator coincide.

Proof.  Since the operator $C$ is compact, it is enough to prove the claim for the operator $A + B$. The differential equation

$$\frac{d}{dt} v = (A + B) v$$

corresponds to the partial differential equation

$$v_t(s,t) + \gamma_*(s) v_s(s,t) + \rho_*(s) v(s,t) = 0$$  \hfill (3.6)

together with the boundary condition $2.7$. For $t_0 > 0$ let us introduce

$$\omega(s) = v(s,t(s)),$$  \hfill (3.7)

where

$$t(s) = t_0 + \Gamma(s).$$  \hfill (3.8)

Then $\omega$ satisfies the equation

$$\omega'(s) + \frac{\rho_*(s)}{\gamma_*(s)} \omega(s) = 0,$$  \hfill (3.9)

hence

$$\omega(s) = \Lambda(v(\cdot,t_0)) \pi(s,Q_*) \exp \left( (1 - \alpha) \int_0^s \frac{w(s) \gamma_Q(\eta,Q_*(\eta)) u_*(\eta)}{\gamma_*(\eta)} \, d\eta \right).$$  \hfill (3.10)

Thus for $t - \Gamma(s) > 0$ we have

$$v(s, t) = \Lambda(v(\cdot, t - \Gamma(s))) \pi(s,Q_*) \exp \left( (1 - \alpha) \int_0^s \frac{w(s) \gamma_Q(\eta,Q_*(\eta)) u_*(\eta)}{\gamma_*(\eta)} \, d\eta \right).$$  \hfill (3.11)

Therefore, noting the definition of $\Lambda$ in 2.12, we conclude that $v$ is continuous in $s$ and $t$ if $t > \Gamma(m) = \max_{0 \leq s \leq m} \Gamma(s)$. Consequently, Eq. (3.11) in combination with Eq. (3.6) implies that $v$ is continuously differentiable if $t > 2 \Gamma(m)$. Hence the semigroup generated by $A + B$ is differentiable for $t > 2 \Gamma(m)$. Finally, since $W^{1,1}(0,m)$ is compactly embedded in $L^1(0,m)$, the semigroup is compact for $t > 2 \Gamma(m)$. The validity of the Spectral Mapping Theorem and the claim about the spectral determinacy of the semigroup follow, see [11].

We conclude this section by formulating conditions for the positivity of the semigroup $\{T(t)\}_{t \geq 0}$. 


Theorem 3.3 Suppose that
\[ \sigma_* \leq 0 \quad \text{and} \quad (3.12) \]
\[ \beta(\cdot, Q_*) + w \left( \int_0^m \beta_Q(\eta, Q_*) u_*(\eta) \, d\eta + \alpha \int_0^m \beta_Q(\eta, Q_*) u_*(\eta) \, d\eta \right) \geq 0. \]
(3.13)

Then the semigroup \( \{ T(t) \}_{t \geq 0} \), generated by the operator \( A + B + C \), is positive.

Remark 3.4 Conditions (3.12), (3.13) are immediate generalizations of the corresponding positivity conditions given by Prüß in [23] for an age-structured scramble competition model. In general, if \( \beta_Q \equiv 0 \), condition (3.13) is trivially satisfied. Also, if the growth rate is independent of the environment (i.e. \( \gamma = \gamma(s) \)), condition (3.12) reduces to
\[ \mu_Q(s, Q_*) \leq 0, \quad s \in [0, \infty). \]
(3.14)

Hence in this case mortality is required to be a non-increasing function of the environment as well.

Proof of Theorem 3.3 Since \( C \) is a positive operator by condition (3.12), it suffices to prove the claim for the semigroup generated by \( A + B \). Hence we assume that \( v \) satisfies Eq. (3.6) such that the boundary condition (2.7) and the initial condition \( v = v_0 \in \text{Dom}(A) \) for \( t = 0 \) hold true. Let the function \( e_* \) be given by
\[ e_*(s) = \exp \left( (1 - \alpha) \int_0^s \frac{w(\eta) \gamma_Q(\eta, Q_*) u_*(\eta)}{\gamma_*(\eta)} \, d\eta \right). \]
(3.15)

Then the function \( \phi \), defined by
\[ \phi(s, t) = \frac{v(s, t)}{\pi(s, Q_*) e_*(s)}, \]
(3.16)
solves the problem
\[ \phi_t(s, t) + \gamma(s, Q_*) \phi_s(s, t) = 0, \]
(3.17)
\[ \phi(0, t) = \Lambda (\phi(\cdot, t) \pi(\cdot, Q_*) e_*), \]
(3.18)
\[ \phi(s, 0) = \frac{v_0(s)}{\pi(s, Q_*) e_*(s)} \overset{\text{def}}{=} \phi_0(s). \]
(3.19)

This boundary-initial value problem corresponds to the abstract initial value problem
\[ \frac{d}{dt} \phi = A_M \phi, \quad \phi(0) = \phi_0 \]
(3.20)
with the modified semigroup generator \( A_M \), defined by
\[ A_M \phi = - \gamma(\cdot, Q_*) \phi_s \quad \text{on the domain} \]
\[ \text{Dom}(A_M) = \{ \phi \in W^{1,1}(0, m) | \phi(0) = \Lambda (\phi \pi(\cdot, Q_*) e_*) \}. \]
(3.21)
For $\lambda \geq 0$ and $g \in L^1(0,m)$, the resolvent equation
\[ \lambda \phi - A_M \phi = g \] (3.22)
has the implicit solution
\[ \phi(s) = e^{-\lambda \Gamma(s)} \Lambda (\phi \pi(\cdot, Q_s) e_s) + \int_0^s e^{\lambda (\Gamma(r) - \Gamma(s))} \frac{g(r)}{\gamma(r, Q_s(r))} dr. \] (3.23)
Applying $\Lambda$, we deduce the equation
\[ \Lambda (\phi \pi(\cdot, Q_s) e_s) = \Lambda \left( \int_0^s e^{\lambda (\Gamma(r) - \Gamma(s))} \frac{g(r)}{\gamma(r, Q_s(r))} dr \pi(\cdot, Q_s) e_s \right) \] if $\lambda$ is large enough. Condition (3.13) guarantees that $\Lambda$ is a positive linear functional. Hence the solution $\phi$, given by Eq. (3.23), is nonnegative if $g$ is nonnegative and $\lambda$ is sufficiently large. It follows that the resolvent operator of $A_M$ (and consequently of $A+B$) is positive if $\lambda$ is large enough. This observation proves the claim.

The positivity of the semigroup has far-reaching consequences. In particular, we obtain the following result from the theory of positive semigroups [11].

**Corollary 3.5** Suppose that the semigroup \(\{T(t)\}_{t \geq 0}\), generated by the operator $A+B+C$, is positive. Then the spectral bound $s(A+B+C) \in [\mathbb{-\infty, \infty})$ satisfies
\[ s(A+B+C) = \max \{ \lambda \in \mathbb{R} | \lambda \text{ is eigenvalue of } A+B+C \}. \] (3.25)
Moreover, the spectrum of $A+B+C$ is nonempty if and only if the spectral bound is finite.

**4. The characteristic equation**

In light of Theorem 3.2, the growth of the governing semigroup is determined by the eigenvalues of its generator. Hence it is essential to determine the eigenvalues of $A+B+C$. The eigenvalue equation
\[ \lambda v - (A+B+C) v = 0 \] (4.1)
for $\lambda \in \mathbb{C}$ and nontrivial $v$ is equivalent to the system
\[ v'(s) \gamma_*(s) + v(s) (\lambda + \rho_*(s)) + V(s) \sigma_*(s) = 0, \] (4.2)
\[ v(0) = \int_0^m \beta(s, Q_*(s)) v(s) ds + \int_0^m \beta Q(s, Q_*(s)) u_*(s) V(s) ds, \] (4.3)
where
\[
V(s) = \alpha \int_0^s w(\eta) v(\eta) d\eta + \int_s^m w(\eta) v(\eta) d\eta \\
= (\alpha - 1) \int_0^s w(\eta) v(\eta) d\eta + \int_0^m w(\eta) v(\eta) d\eta.
\] (4.4)

For the remainder of this section let us assume that \( \alpha \in [0, 1) \). From (4.4) we obtain
\[
V'(s) = (\alpha - 1) w(s) v(s) \quad \text{and} \quad V''(s) = (\alpha - 1) (w'(s) v(s) + w(s) v'(s)).
\] (4.5)

Using the relations (4.5) we can rewrite system (4.2)–(4.3) in terms of \( V \) and its derivatives as follows
\[
V''(s) + \frac{\rho_*(s) + \lambda}{\gamma_*(s)} V'(s) + V(s) (\alpha - 1) \frac{\sigma_*(s)}{\gamma_*(s)} = 0.
\] (4.6)

Eq. (4.6) is accompanied by boundary conditions of the form
\[
\alpha V(0) = V(m),
\] (4.7)
\[
V'(0) = w(0) \int_0^m \frac{\beta(s, Q_*(s))}{w(s)} V'(s) ds \\
+ \int_0^m (\alpha - 1) \frac{\beta_Q(s, Q_*(s)) u_*(s)}{w(s)} V(s) ds.
\] (4.8)

For \( \lambda \in \mathbb{C} \), any solution \( V_\lambda(s) \) of the second order homogeneous ordinary differential equation (4.6) can be written as
\[
V_\lambda(s) = c_1 V_1(s, \lambda) + c_2 V_2(s, \lambda),
\] (4.9)

where \( V_1(s, \lambda) \) and \( V_2(s, \lambda) \) are any fixed, linearly independent solutions of Eq. (4.6) and \( c_1, c_2 \) are arbitrary constants. When imposing the boundary conditions (4.7)–(4.8), we obtain the conditions
\[
c_1 V_1'(0, \lambda) + c_2 V_2'(0, \lambda) = c_1 \int_0^m \frac{w(0)}{w(s)} \beta(s, Q_*(s)) V_1'(s, \lambda) ds \tag{4.10}
+ c_2 \int_0^m \frac{w(0)}{w(s)} \beta(s, Q_*(s)) V_2'(s, \lambda) ds \tag{4.11}
+ c_1 \int_0^m (\alpha - 1) w(0) \beta_Q(s, Q_*(s)) u_*(s) V_1(s, \lambda) ds \tag{4.12}
+ c_2 \int_0^m (\alpha - 1) w(0) \beta_Q(s, Q_*(s)) u_*(s) V_2(s, \lambda) ds \tag{4.13}
\]
or in short
\[
c_1 H_1(\lambda) + c_2 H_2(\lambda) = 0,
\] (4.14)

and
\[
c_1 \alpha V_1(0, \lambda) + c_2 \alpha V_2(0, \lambda) = c_1 V_1(m, \lambda) + c_2 V_2(m, \lambda),
\] (4.15)
in short
\[ c_1 J_1(\lambda) + c_2 J_2(\lambda) = 0. \]  (4.16)
Here the functions \( H_1, \ H_2, \ J_1, \) and \( J_2 \) represent the terms multiplying \( c_1, \)
\( c_2, \) respectively. The homogeneous system \((4.14), (4.10)\) admits a nontrivial
solution for \( c_1, c_2 \) if and only if \( \lambda \) satisfies the equation
\[ H_1(\lambda) J_2(\lambda) - H_2(\lambda) J_1(\lambda) = 0. \]  (4.17)
This equation is the characteristic equation of the linearized system \((2.6)-(2.7)\). Its zeros are the eigenvalues of the operator \( A+B+C, \) which completely describe
the spectrum of \( A+B+C. \)

The explicit information contained in the characteristic equation is, however,
rather limited since linearly independent solutions of the second order differential
equation \((4.6)\) are in general not directly available, unless one resorts to
numerical techniques. As we will see in the forthcoming section this problem
can, however, be overcome in special cases of the model ingredients.

5. A special case

In this section we treat the special case when the mortality and growth rate
are independent of the environment \( Q, \) i.e. \( \gamma_Q \equiv 0 \equiv \mu_Q. \) Hence \( \sigma_\ast \equiv 0 \) and \( e_\ast \equiv 1. \) In this situation we are able to determine the characteristic equation \((4.17)\)
explicitly and to formulate simple conditions for the linear stability/instability
of positive stationary solutions. In contrast to the preceding section we allow
\( \alpha \in [0,1]. \)

**Theorem 5.1** Suppose \( \sigma_\ast \equiv 0. \) Then a positive stationary solution \( u_\ast \) is lin-
early asymptotically stable if
\[ \beta_Q(\cdot, Q_\ast) \leq 0, \quad \beta_Q(\cdot, Q_\ast) \neq 0 \]  (5.1)
and the positivity condition \((3.13)\) holds true. If, however,
\[ \beta_Q(\cdot, Q_\ast) \geq 0, \quad \beta_Q(\cdot, Q_\ast) \neq 0, \]  (5.2)
then \( u_\ast \) is linearly unstable.

Note that the instability part of the theorem does not require the positivity
condition.

**Proof:** We assume first that \( 0 \leq \alpha < 1. \) Then the general solution of \((4.3)\) is
found as
\[ V(s) = V(0) + V'(0) \int_0^s \frac{w(r)}{w(0)} \Pi(\lambda, r) dr, \]  (5.3)
where we have set
\[ \Pi(\lambda, r) \overset{\text{def}}{=} \frac{\gamma_\ast(0)}{\gamma_\ast(s)} \exp \left\{ - \int_0^s \frac{\lambda + \mu_\ast(r)}{\gamma_\ast(r)} \, dr \right\}. \]  (5.4)
Imposing the boundary condition (4.7) on the solution (5.3), we obtain
\[ 0 = V(0) (1 - \alpha) + V'(0) \int_0^m \frac{w(s)}{w(0)} \Pi(\lambda, s) \, ds, \quad (5.5) \]
while the boundary condition (4.8) gives
\[ 0 = V(0) \left( \alpha w(0) (1 - \alpha) \int_0^m \beta(s, Q_*(s)) u_*(s) \, ds \right) \]
\[ + V'(0) \left( 1 - \int_0^m \beta(s, Q_*(s)) \Pi(\lambda, s) \, ds \right) \]
\[ + (1 - \alpha) \int_0^m \beta(s, Q_*(s)) u_*(s) \int_s^m w(r) \Pi(\lambda, r) \, dr \, ds \]
\[ + (1 - \alpha) \int_0^m \beta_Q(s, Q_*(s)) u_*(s) \int_s^m w(r) \Pi(\lambda, r) \, dr \, ds \]
\[ + \int_0^m \beta_Q(s, Q_*(s)) u_*(s) \int_0^m w(s) \Pi(\lambda, s) \, ds \overset{def}{=} K(\lambda). \quad (5.6) \]

The linear system (5.5)–(5.6) has a nontrivial solution \((V(0), V'(0))\) if and only if \(\lambda\) satisfies
\[ 1 = \int_0^m \beta(s, Q_*(s)) \Pi(\lambda, s) \, ds \]
\[ + (\alpha - 1) \int_0^m \beta_Q(s, Q_*(s)) u_*(s) \int_0^s w(r) \Pi(\lambda, r) \, dr \, ds \]
\[ + \int_0^m \beta_Q(s, Q_*(s)) u_*(s) \int_0^m w(s) \Pi(\lambda, s) \, ds \overset{def}{=} K(\lambda). \quad (5.7) \]

This equation corresponds to the characteristic equation (4.17). If, however, \(\alpha = 1\), \(V\), defined by (4.4), is constant. When we solve the problem (4.2)–(4.3) directly, we obtain again the condition
\[ K(\lambda) = 1, \quad (5.8) \]
where \(K\) is given by (5.7) with \(\alpha = 1\). Hence (5.7) is the characteristic equation for all \(0 \leq \alpha \leq 1\). For the stability part, our assumptions guarantee that the positivity conditions (3.12), (3.13) hold true. Therefore, to prove asymptotic stability, it suffices to show that the characteristic equation (5.7) has no nonnegative (real) solutions. To this end, we observe that
\[ K(0) = R(Q_*) + \int_0^m \beta_Q(s, Q_*(s)) u_*(s) \]
\[ \times \left( \alpha \int_0^s w(r) \pi(r, Q_*) \, dr + \int_s^m w(r) \pi(r, Q_*) \, dr \right) \, ds < 1 \quad (5.9) \]
b by condition (5.1). Moreover, the positivity condition (3.13) yields that
\[ K'(\lambda) = - \int_0^m \Pi(\lambda, s) \int_0^s \frac{1}{\gamma(r, Q_*(r))} dr \left( \beta(s, Q_*(s)) \right) \]
\[ + w(s) \int_0^s \beta_Q(r, Q_*(r)) u_*(r) \, dr \]
\[ + \alpha w(s) \int_s^m \beta_Q(r, Q_*(r)) u_*(r) \, dr \, ds \leq 0. \quad (5.10) \]
Consequently, $K$ is monotone decreasing for $\lambda \geq 0$. Hence the stability part is proven. The instability part of the theorem follows from the Intermediate Value Theorem since $K(0) > 1$ by (5.2) and $\lim_{\lambda \to \infty} K(\lambda) = 0$.

**Example 5.2** Let us consider an example where Theorem [5,1] yields asymptotic stability. We choose

$$m = 1, \quad \alpha = \frac{1}{2}, \quad w \equiv 1$$

(5.11)

and let

$$\gamma(s) = 1 - \frac{1}{2} s, \quad \mu \equiv 1,$$

(5.12)

$$\beta(s, Q) = \frac{480}{997} (1 + s) (3 - 2 Q) \quad \text{if} \quad Q \leq \frac{3}{4}, \quad 0 \leq s \leq 1,$$

(5.13)

where we assume that $\beta$ extends to a continuously differentiable, non-negative function on $[0, 1] \times [0, \infty)$. Then the corresponding problem has the stationary solution $u_*(s) = 1 - \frac{1}{2} s$ with

$$Q_*(s) = \frac{s^2}{8} - \frac{s}{2} + \frac{3}{4} \leq \frac{3}{4} \quad \text{for} \quad 0 \leq s \leq 1.$$  

(5.14)

It is readily seen that

$$\beta Q(s, Q_*(s)) = -\frac{960}{997} (1 + s) < 0, \quad 0 \leq s \leq 1$$

(5.15)

and that the positivity condition (3.13) reduces to

$$-\frac{s^3}{24} + \frac{s^2}{4} + \frac{3 s}{4} + \frac{5}{24} \geq 0, \quad 0 \leq s \leq 1.$$  

(5.16)

Since this inequality holds true, the stationary solution $u_*$ is linearly asymptotically stable.

### 6. Direct approach: dissipativity

Since in the general case of environment dependent vital rates the characteristic equation is not explicitly available, we shall pursue a different path to obtain asymptotic stability. This approach is based on dissipativity calculations in the underlying state space $\mathcal{X} = L^1(0, m)$ and proceeds parallel to similar developments for the linear semigroup of fiber spinning in [17, 18]. An added advantage of this technique is that we can discuss linear stability of the trivial stationary solution and that we can forego imposing positivity conditions on the semigroup. In addition we can include the case $\alpha = 1$ without technical difficulties. To our knowledge dissipativity estimates have so far not been used in the case of hierarchical size-structured population models.
Theorem 6.1 A stationary solution $u_*$ is linearly asymptotically stable if

$$
\mu(s, Q_*(s)) > w(s) \left((1 - \alpha) \gamma_Q(s, Q_*(s)) u_*(s) + ||\sigma_*||\right) \\
+ \gamma(0, Q_*(0)) \left[ \beta(s, Q_*(s)) + \alpha w(s) \int_s^m \beta_Q(r, Q_*(r)) u_*(r) \, dr \right] \\
+ w(s) \int_0^s \beta_Q(r, Q_*(r)) u_*(r) \, dr
$$

(6.1)

for $0 \leq s \leq m$.

As before the norm on $L^1(0, m)$ is denoted by $\| \cdot ||$.

**Proof.** We will show that, under the given condition, there exists $\kappa > 0$ such that the operator $A + B + C + \kappa I$ is dissipative. Consequently, the semigroup $\{ T(t) \}_{t \geq 0}$ generated by the operator $A + B + C$ obeys

$$
\| T(t) \| \leq e^{-\kappa t}, \quad t \geq 0,
$$

(6.2)

which proves the claim.

To obtain dissipativity, assume that, for given $h \in X$, $v \in \text{Dom}(A)$ is such that, for some $\lambda > 0$,

$$
v - \lambda (A + B + C + \kappa I) v = h.
$$

(6.3)

Then we have

$$
\| v \| = \int_0^m v(s) \, ds
$$

$$
= \int_0^m h(s) \, ds - \lambda \int_0^m \gamma(s, Q_*(s)) v_*(s) \, ds
$$

$$
- \lambda \int_0^m \rho_*(s) v(s) \, ds
$$

$$
- \lambda \int_0^m \sigma_*(s) \left( \alpha \int_s^m v(\eta) \, d\eta \right) \, ds
$$

$$
+ \int_s^m w(\eta) v(\eta) \, d\eta \right) \, ds + \lambda \kappa \int_0^m v(s) \, ds.
$$

Here we have used the definition $\text{sgn} 0 = 0$. The set of points in the interval $(0, m)$ where $v$ is nonzero is the countable union of disjoint open intervals $(a_i, b_i)$ on each of which either $v > 0$ or $v < 0$ holds true such that $v(a_i) = 0$ for all $i$ unless $a_i = 0$, and such that $v(b_i) = 0$ unless $b_i = m$. If $(a_i, b_i)$ is any such interval on which $v > 0$ we have after integration by parts

$$
\int_{a_i}^{b_i} v(s) \, ds \leq \int_{a_i}^{b_i} |h(s)| \, ds - \lambda \gamma(b_i, Q_*(b_i)) v(b_i) + \lambda \gamma(a_i, Q_*(a_i)) v(a_i)
$$

$$
+ \lambda \int_{a_i}^{b_i} (\kappa - \mu(s, Q_*(s)) - (\alpha - 1) w(s) \gamma_Q(s, Q_*(s)) u_*(s)) v(s) \, ds
$$

$$
+ \lambda \int_{a_i}^{b_i} |\sigma_*(s)| \, ds \int_0^m w(s) |v(s)| \, ds.
$$

(6.5)
Similarly, on any interval \((a_i, b_i)\) where \(v < 0\) we have

\[
\int_{a_i}^{b_i} |v(s)| \, ds \leq \int_{a_i}^{b_i} |h(s)| \, ds + \lambda \gamma(b_i, Q_*(b_i)) \, v(b_i) - \lambda \gamma(a_i, Q_*(a_i)) \, v(a_i) \\
+ \lambda \int_{a_i}^{b_i} (\kappa - \mu(s, Q_*(s)) - (\alpha - 1) \, w(s) \, \gamma_Q(s, Q_*(s)) \, u_*(s)) |v(s)| \, ds \quad (6.6) \\
+ \lambda \int_{a_i}^{b_i} |\sigma_*(s)| \, ds \int_{0}^{m} w(s) |v(s)| \, ds.
\]

Finally, noting that \(v(a_i) = 0 = v(b_j)\) unless \(a_i = 0, b_j = m\), we combine these two estimates to obtain

\[
||v|| \leq ||h|| + \lambda \gamma(0, Q_*(0)) |v(0)| + \lambda \int_{0}^{m} (\kappa - \mu(s, Q_*(s)) + w(s) ((1 - \alpha) \, \gamma_Q(s, Q_*(s)) \, u_*(s) + ||\sigma_*||)) |v(s)| \, ds. 
\]

Since

\[
|v(0)| = |\Lambda(v)| \leq \int_{0}^{m} \left| \beta(s, Q_*(s)) + \alpha \, w(s) \int_{0}^{m} \beta_Q(r, Q_*(r)) \, u_*(r) \, dr \right| \\
+ (1 - \alpha) \, w(s) \int_{0}^{m} \beta_Q(r, Q_*(r)) \, u_*(r) \, dr |v(s)| \, ds \quad (6.8)
\]

and since condition (6.1) is satisfied, we can choose \(\kappa > 0\) such that, for \(0 \leq s \leq m\),

\[
\kappa - \mu(s, Q_*(s)) + w(s) ((1 - \alpha) \, \gamma_Q(s, Q_*(s)) \, u_*(s) + ||\sigma_*||)) \\
+ \gamma(0, Q_*(0)) \left| \beta(s, Q_*(s)) + \alpha \, w(s) \int_{0}^{m} \beta_Q(r, Q_*(r)) \, u_*(r) \, dr \right| \\
+ (1 - \alpha) \, w(s) \int_{0}^{m} \beta_Q(r, Q_*(r)) \, u_*(r) \, dr \right| \leq 0. 
\]

For such \(\kappa\), we have the desired inequality

\[
||v|| \leq ||h|| \quad \text{for } \lambda > 0, \quad (6.10)
\]

thus establishing dissipativity. Hence we conclude that \(A + B + C + \kappa I\) generates a contraction semigroup.

\[\square\]

**Remark 6.2** Suppose \(u_*\) is a stationary solution such that condition (6.1) is
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satisfied with $\beta_Q \geq 0$. Then we have

$$R(Q) = \int_0^m \frac{\beta(s, Q_s(s)) \gamma(0, Q_s(0))}{\gamma(s, Q_s(s))} \exp\left(-\int_0^s \frac{\mu(r, Q_s(r))}{\gamma(r, Q_s(r))} dr\right) ds$$

$$\leq \int_0^m \frac{\mu(s, Q_s(s))}{\gamma(s, Q_s(s))} \exp\left(-\int_0^s \frac{\mu(r, Q_s(r))}{\gamma(r, Q_s(r))} dr\right) ds$$

$$= 1 - \exp\left(-\int_0^m \frac{\mu(r, Q_s(r))}{\gamma(r, Q_s(r))} dr\right) < 1.$$  \hspace{1cm} (6.11)

Hence in light of (2.2) we have to conclude that $u_\ast \equiv 0$.

**Remark 6.3** For the stability of the trivial equilibrium $u_\ast \equiv 0$ the criterion (6.1) reduces to

$$\mu(s, 0) > \gamma(0, 0) \beta(s, 0), \quad s \in [0, m].$$  \hspace{1cm} (6.13)

Note that (6.13) clearly implies $R(0) < 1$, which is the well-known stability criterion of the trivial steady state in scramble competition, see [19].

**Remark 6.4** In scramble competition ($\alpha = 1$) the stability criterion (6.1) for a stationary solution $u_\ast$ with total (weighted) population

$$P_\ast = \int_0^m w(\eta) u_\ast(\eta) d\eta$$  \hspace{1cm} (6.14)

reads

$$\mu(s, P_\ast) > w(s) ||\sigma|| + \left|\tilde{\beta}(s, P_\ast) + w(s) \int_0^m \tilde{\beta}_\rho(r, P_\ast) u_\ast(r) dr\right|, \quad 0 \leq s \leq m,$$  \hspace{1cm} (6.15)

where

$$\tilde{\beta}(s, P) = \gamma(0, P) \beta(s, P).$$  \hspace{1cm} (6.16)

**Example 6.5** We will give a nontrivial example of a stationary solution for which the stability criterion (6.1) holds true. We choose

$$m = 1, \quad \alpha = \frac{1}{2}, \quad w \equiv 1, \quad \gamma(s) = 1 - \frac{1}{2} s, \quad \mu \equiv 1$$  \hspace{1cm} (6.17)

and let $\beta \in C^1([0, 1] \times [0, \infty))$ be positive such that

$$\beta(s, Q) = \frac{160}{159} (1 + s) (2 - 2Q) \quad \text{if } Q \leq \frac{3}{4}, \quad 0 \leq s \leq 1.$$  \hspace{1cm} (6.18)

Then we have again the stationary solution $u_\ast(s) = 1 - \frac{1}{2} s$ with

$$Q_\ast(s) = \frac{s^2}{8} - \frac{s}{2} + \frac{3}{4} \leq \frac{3}{4} \quad \text{for } 0 \leq s \leq 1.$$  \hspace{1cm} (6.19)
Now, however, the positivity condition (3.13) is violated. Nonetheless we obtain
\[
\beta(s, Q_*(s)) + \frac{1}{2} \int_s^1 \beta_Q(r, Q_*(r)) u_*(r) \, dr + \int_0^s \beta_Q(r, Q_*(r)) u_*(r) \, dr
\]
\[
= \frac{160}{159} \left| \frac{s^3}{12} - \frac{s^2}{2} + \frac{7}{12} \right| < 1, \quad 0 \leq s \leq 1. 
\] (6.20)

Hence the stationary solution is linearly asymptotically stable by Theorem 6.1.

A straightforward perturbation argument can be used to extend this example to a more complicated situation with environment dependent mortality and growth rate.

7. Conclusion

In this work we have analyzed the linear asymptotic stability of equilibrium solutions of a nonlinear hierarchical size-structured population model. We have extended our previous mathematical approach in [13, 14, 15] for the case of scramble competition models to the hierarchical case. As conjectured in [10] for general physiologically structured models, we note that the linear asymptotic stability of stationary solutions is determined by zeros of a characteristic function. When the linear dynamical behavior is governed by a positive semigroup, the characteristic function has a dominant real root, unless the spectrum of the semigroup generator is empty. As we have seen in Section 4, however, this function is not explicitly available (except in special cases). Nevertheless, we managed to characterize the spectrum of the linearized operator implicitly, by deducing an eigenvalue problem for a second order differential operator. This characterization allows in principle to further investigate stability questions by numerical techniques in case of concrete model ingredients.

To overcome the severe limitations caused by the spectral characterizations of asymptotic stability, we have given a direct dissipativity condition in terms of the model ingredients in the relevant state space, guaranteeing the exponential decay of the governing linear semigroup. This elementary, though important criterion allows us to expand linear stability studies beyond the setting of positive semigroups and dominant eigenvalues.

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