Competitive exclusion and coexistence for a quasilinear size-structured population model

Azmy S. Ackleh *, Keng Deng, Xubo Wang

Department of Mathematics, University of Louisiana at Lafayette, Lafayette, LA 70504-1010, United States

Abstract

We present a quasilinear size-structured model which describes the dynamics of a population with n competing ecotypes. We assume that the vital rates of each subpopulation depend on the total population due to competition. We provide conditions on the individual rates which guarantee competitive exclusion in the case of closed reproduction (offspring always belongs to the same ecotype as the parent). In particular, our results suggest that the ratio of the reproduction and mortality rates is a good measure to determine the winning ecotype. Meanwhile, we show that in the case of open reproduction all ecotypes coexist.

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1. Introduction

The competitive exclusion principle asserts that no two populations competing for a common resource can live indefinitely in the same ecological niche. The validity of this principle has been investigated for many mathematical models which include both structured and non-structured populations (e.g., [2–4,12–14,17–24]).

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* Corresponding author. Tel.: +1 337 482 6709; fax: +1 337 482 5346.
  E-mail address: ackleh@louisiana.edu (A.S. Ackleh).

On the side of non-structured population models the literature contains many results. Below we briefly discuss a few of them. In [4,20,24] the authors investigate a competitive Lotka–Volterra system of equations and provide conditions on the parameters which guarantee that all but one of the species are driven to extinction. In [2] a generalized logistic model was developed. This model is composed of a continuum of subpopulations each with its own growth and mortality rates. Using the theory of weak convergence of probability measures the authors show that the competitive exclusion principle is valid for their model. In [3], a predator–prey Lotka–Volterra model which consists of many predator–prey subpopulations was studied. Therein, the authors show that all subpopulations become extinct except for the predator–prey pair which optimizes the growth to mortality ratio. In [19] the author studies the global stability of a boundary equilibrium (that corresponds to the extinction of one competing species) for a general three-dimensional competition model with two competing predators. The global stability is achieved by the construction of an appropriate Lyapunov function, which is a modification of those introduced by others.

In [10] the authors consider an n-pathogen, single host model. They show that pathogen strains with differing levels of virulence die out asymptotically except for those that optimize the basic reproduction number. In [1] the authors study an n-pathogen, single host model with variable population size. They prove that if the model parameters satisfy certain inequalities, then competition between n pathogens for a single host leads to exclusion of all pathogens except the one with the largest basic reproduction number. In addition, they give an example which shows that if these inequalities are not satisfied, then coexistence may occur. In [13] the authors study a two-sex, susceptible–infective–susceptible sexually transmitted disease model with two competing strains. Therein, they investigate the existence and stability of the boundary equilibria that characterize the competitive exclusion of these two strains; they also investigate the existence and stability of the positive coexistence equilibrium, which characterizes the possibility of coexistence of the two strains. They obtain sufficient and necessary conditions for the existence and global stability of these equilibria.

For structured populations considerably less work has been done due to the complexity of these models. In [23] competitive exclusion is proved for a discrete-time, size-structured, non-linear matrix model of m competing species in a chemostat. The winner is the population that is able to grow at the lowest nutrient concentration. In [17] age and age-size structured population models composed of n ecotypes were studied. The authors show that a good measure of 'ecotype fitness' is the product of the reproduction and survivorship functions.

Our paper is organized as follows. In Section 2 we present the population model. In Section 3 we establish existence and uniqueness results for the model. In Section 4 under the closed reproduction we provide conditions on the individuals rates which guarantee competitive exclusion, while under the open reproduction we show that all ecotypes survive. Further discussion and some numerical results are given in Section 5.

2. The population model

We consider a species with n competing ecotypes. For $i = 1, 2, \ldots, n$, we describe the dynamics of the subpopulation consisting of individuals of the ith ecotype with the following individual size-structured model of McKendrick–von Foerster type

$$(u_i)_t + g_i(P(t))(u_i)_x + m_i(P(t))u_i = 0 \quad 0 < x < \infty, \quad t > 0,$$

$$g_i(P(t))u_i(0,t) = \sum_{j=1}^{n} \int_0^{\infty} \gamma_{i,j}\beta_j(P(t))u_j(x,t)\mathrm{d}x \quad t > 0, \tag{1}$$

$$u_i(x,0) = u_{i0}(x) \quad 0 \leqslant x < \infty.$$

Here $u_i(x,t)$, $i = 1,2,\ldots n$, is the density of individuals of the ith ecotype having size x at time t, and $P(t) = \sum_{i=1}^{n} \int_0^{\infty} u_i(x,t)\mathrm{d}x$ is the total number of individuals in the population at time t. The functions g_i, m_i, and β_i denote the growth rate, the mortality rate, and the reproduction rate of an individual in the ith subpopulation, respectively. These individual rates depend on the total number of individuals in the population. The constant parameter $0 \leqslant \gamma_{i,j} \leqslant 1$ represents the probability that an individual of the jth ecotype will reproduce an individual of the ith ecotype. Clearly, $\sum_{j=1}^{n} \gamma_{i,j} = \sum_{i=1}^{n} \gamma_{i,j} = 1$, $1 \leqslant i$, $j \leqslant n$. In this paper we focus on the asymptotic behavior of the population in two cases. The first case is that all ecotypes are closed under reproduction in which offspring always belongs to the same ecotype as the parent, i.e., $\gamma_{i,i} = 1$ and $\gamma_{i,j} = 0$ for $i \neq j$. The second case is that ecotypes are open under reproduction in which individuals of ecotype i may reproduce individuals of ecotype j.

Linear models of type (1) have been used to describe the dynamics of mosquitofish populations in rice fields [6]. Simulation studies therein demonstrate that solutions to such models could lead to population densities that exhibit dispersion and bimodality as field data suggested in [9]. Such dispersion and bimodality cannot result from the classical size-structured model (i.e., all individuals are assumed to be of the same ecotype) except under some biologically unrealistic conditions (see [7]). This indicates that the consideration of several ecotypes is important if such size-structured models are to be used as prediction tools.

Rigorous theoretical developments of inverse problems associated with linear models of type (1) were given in [7,15,16]. In [8] such inverse methodology was used for estimating the distribution of individual growth rates based on aggregate population data. Therein, a good fit of the model to field data was presented. A survey of results and other references for such models can be found in [5].

3. Existence and uniqueness results

Throughout the discussion we assume that the parameters in (1) satisfy the following:

(H1) $g_i(P)$ is strictly positive and continuously differentiable for $0 < P < \infty$.

(H2) $m_i(P)$ is non-negative and continuously differentiable for $0 \leqslant P < \infty$.

(H3) $\beta_i(P)$ is continuously differentiable and uniformly bounded for $0 \leqslant P < \infty$ with $0 \leqslant \beta_i \leqslant \beta_M$.

(H4) $u_{i0} \in L^1(0,\infty)$ and $u_{i0} \geqslant 0$.

In the spirit of [11], we use the contraction mapping argument to discuss the existence-uniqueness of solutions to problem (1). We begin with the definition of the solution.

Definition 1. A non-negative function $u(x,t) = (u_1(x,t), u_2(x,t), \ldots, u_n(x,t))$ on $[0,\infty) \times [0,T]$, with $u(\cdot, t)$ integrable is a solution of (1) if $P(t) := \sum_{i=1}^{n} \int_0^\infty u_i(x,t) \mathrm{d}x$ is a continuous function on [0,T] and for $i = 1,2, \ldots, n, u_i(x,t)$ satisfies $(1)_2$, $(1)_3$, and the equation

$$Du_i(x,t) = -m_i(P(t))u_i(x,t) \quad 0 < x < \infty, \quad 0 < t < T \tag{2}$$

with

$$Du_i(x,t) = \lim_{h \to 0} \frac{u_i(X_i(t+h;x,t), t+h) - u_i(x,t)}{h}, \tag{3}$$

where $X_i(t; x_0, t_0)$ is the solution of the equation for the characteristic curves given by

$$\begin{cases} \frac{\mathrm{d}}{\mathrm{d}t} x(t) = g_i(P(t)), \\ x(t_0) = x_0. \end{cases} \tag{4}$$

From (H1) it follows that the function X_i is strictly increasing. Hence, a unique inverse function $\tau_i(x; x_0, t_0)$ exists. Let $z_i(t) = X_i(t;0,0)$ where $(z_i(t), t)$ represents the characteristic curve passing through (0,0) and dividing the (x,t)-plane into two parts.

Let $B_i(t) := \sum_{j=1}^{n} \int_0^\infty \gamma_{i,j}\beta_j(P(t))u_j(x,t)\mathrm{d}x$, the inflow of newborns in the ith subpopulation at time t. Using the method of characteristics, we reduce problem (1) to a system of coupled equations for $P(t)$ and $B_i(t)$.

Integrating (2) along the characteristics, we have

$$u_i(x,t) = \frac{B_i(\tau_i(0;x,t))}{g_i(P(\tau_i(0;x,t)))} \exp\left(-\int_{\tau_i(0;x,t)}^{t} m_i(P(s))\mathrm{d}s\right) \quad x < z_i(t),$$

$$u_i(x,t) = u_{i0}(X_i(0;x,t)) \exp\left(-\int_0^t m_i(P(s))\mathrm{d}s\right) \quad x \geqslant z_i(t). \tag{5}$$

Then integrating (5) with respect to x and summing over the indices $i = 1,2, \ldots, n$, we obtain an integral equation for $P(t)$

$$\begin{aligned}
P(t) &= \sum_{i=1}^{n} \left[\int_0^{z_i(t)} \frac{B_i(\tau_i(0;x,t))}{g_i(P(\tau_i(0;x,t)))} \exp\left(-\int_{\tau_i(0;x,t)}^{t} m_i(P(s))\mathrm{d}s\right)\mathrm{d}x \right. \\
&\quad \left. + \int_{z_i(t)}^{\infty} u_{i0}(X_i(0;x,t)) \exp\left(-\int_0^t m_i(P(s))\mathrm{d}s\right)\mathrm{d}x \right] \\
&= \sum_{i=1}^{n} \left[\int_0^t B_i(\eta)\mathrm{e}^{-\int_\eta^t m_i(P(s))\mathrm{d}s}\mathrm{d}\eta + \int_0^\infty u_{i0}(\xi)\mathrm{e}^{-\int_0^t m_i(P(s))\mathrm{d}s}\mathrm{d}\xi \right].
\end{aligned} \tag{6}$$

Similarly, substituting (5) in the definition of $B_i(t)$, we obtain an integral equation for $B_i(t)$, $i = 1,2, \ldots, n$,

$$B_i(t) = \sum_{j=1}^{n} \left[\int_0^t \gamma_{i,j}\beta_j(P(t))B_j(\eta)\mathrm{e}^{-\int_\eta^t m_j(P(s))\mathrm{d}s}\mathrm{d}\eta + \int_0^\infty \gamma_{i,j}\beta_j(P(t))\mu_{j0}(\xi)\mathrm{e}^{-\int_0^t m_j(P(s))\mathrm{d}s}\mathrm{d}\xi \right]. \tag{7}$$

Clearly, if $P(t)$ and $B_i(t)$ are non-negative continuous solutions of (6) and (7), then $u(x,t)$ defined by (5) is a solution of (1). Since we have established a correspondence between (1) and (6)–(7), to obtain the existence and uniqueness results for problem (1), we only need to study the solvability of the system of integral equations (6) and (7). To this end, for $K > \|u_0\|_{L^1} = \sum_{i=1}^{n} \int_0^{\infty} u_{i0}(x)\mathrm{d}x$, let $S_{T,K} = \{f(t) \in C[0,T] \mid f(0) = \|u_0\|_{L^1}, 0 \leqslant f(t) \leqslant K\}$. For each $P \in S_{T,K}$, let $B_i(t) \in C[0,T]$ be the unique non-negative solution of the linear Volterra integral equation (7), and we define the operator $\mathscr{P} : S_{T,K} \to C[0,T]$ in such a way that $\mathscr{P}(P)(t)$ is the right-hand side of (6) for these $P(t)$ and $B_i(t)$.

Lemma 2. *Suppose that hypotheses* (H1)–(H4) *hold. Then there exists a value* $T > 0$ *for which* $\mathscr{P}$ *has a unique fixed point.*

Proof. We first show that $\mathscr{P}$ maps $S_{T,K}$ into itself. To this end, we obtain a function to bound $B_i(t)$. By (7) and the hypotheses (H2), (H3), we have

$$B_i(t) \leqslant \beta_M \sum_{j=1}^{n} \int_0^t B_j(\eta)\mathrm{d}\eta + \beta_M \|u_0\|_{L^1}.$$

Thus,

$$\sum_{j=1}^{n} B_j(t) \leqslant n\beta_M \int_0^t \sum_{j=1}^{n} B_j(\eta)\mathrm{d}\eta + n\beta_M \|u_0\|_{L^1},$$

which, by Gronwall's inequality implies

$$\sum_{j=1}^{n} B_j(t) \leqslant n\beta_M \|u_0\|_{L^1} \mathrm{e}^{n\beta_M T}. \tag{8}$$

A combination of (6) and (8) then yields

$$\mathscr{P}(P)(t) \leqslant \int_0^t \sum_{j=1}^{n} B_j(\eta)\mathrm{d}\eta + \|u_0\|_{L^1} \leqslant n\beta_M \|u_0\|_{L^1} \int_0^t \mathrm{e}^{n\beta_M \eta}\mathrm{d}\eta + \|u_0\|_{L^1} \leqslant \mathrm{e}^{n\beta_M T} \|u_0\|_{L^1} \leqslant K$$

provided T is very small.

We next show that $\mathscr{P}$ is contractive. For any $P, \hat{P} \in S_{T,K}$, letting B_i and $\widehat{B}_i$ be the solutions of (7) for P and $\hat{P}$, respectively, we have

$$|\mathscr{P}(P)(t) - \mathscr{P}(\hat{P})(t)| = \left| \sum_{j=1}^{n} \int_0^t B_j(\eta)\mathrm{e}^{-\int_\eta^t m_j(P(s))\mathrm{d}s}\mathrm{d}\eta - \sum_{j=1}^{n} \int_0^t \widehat{B}_j(\eta)\mathrm{e}^{-\int_\eta^t m_j(\hat{P}(s))\mathrm{d}s}\mathrm{d}\eta \right.$$
$$\left. + \sum_{j=1}^{n} \int_0^\infty u_{j0}(\xi)\left[\mathrm{e}^{-\int_0^t m_j(P(s))\mathrm{d}s} - \mathrm{e}^{-\int_0^t m_j(\hat{P}(s))\mathrm{d}s}\right]\mathrm{d}\xi \right|$$
$$\leqslant \sum_{j=1}^{n} \int_0^t \left|B_j(\eta) - \widehat{B}_j(\eta)\right|\mathrm{d}\eta + \sum_{j=1}^{n} \int_0^t \widehat{B}_j(\eta) \int_\eta^t \left|m_j(P(s))\right.$$
$$\left. - m_j(\hat{P}(s))\right|\mathrm{d}s\mathrm{d}\eta + \sum_{j=1}^{n} \int_0^\infty u_{j0}(\xi) \int_0^t \left|m_j(P(s)) - m_j(\hat{P}(s))\right|\mathrm{d}s\mathrm{d}\xi.$$
$$\tag{9}$$

We now estimate each integral in the last expression of (9). Let $|F_i(t)| = |B_i(t) - \widehat{B}_i(t)|$. Then from (7) and (8), we have

$$
\begin{aligned}
|F_i(t)| \leqslant \sum_{j=1}^{n} \Bigg| & \int_0^t \gamma_{i,j} \beta_j(P(t)) B_j(\eta) e^{-\int_\eta^t m_j(P(s))ds} d\eta - \int_0^t \gamma_{i,j} \beta_j(P(t)) \widehat{B}_j(\eta) e^{-\int_\eta^t m_j(P(s))ds} d\eta \\
& + \int_0^t \gamma_{i,j} \beta_j(P(t)) \widehat{B}_j(\eta) e^{-\int_\eta^t m_j(P(s))ds} d\eta - \int_0^t \gamma_{i,j} \beta_j(P(t)) \widehat{B}_j(\eta) e^{-\int_\eta^t m_j(\hat{P}(s))ds} d\eta \\
& + \int_0^t \gamma_{i,j} \beta_j(P(t)) \widehat{B}_j(\eta) e^{-\int_\eta^t m_j(\hat{P}(s))ds} d\eta - \int_0^t \gamma_{i,j} \beta_j(\hat{P}(t)) \widehat{B}_j(\eta) e^{-\int_\eta^t m_j(\hat{P}(s))ds} d\eta \Bigg| \\
& + \sum_{j=1}^{n} \left[\int_0^\infty \gamma_{i,j} \left| \beta_j(P(t)) e^{-\int_0^t m_j(P(s))ds} - \beta_j(\hat{P}(t)) e^{-\int_0^t m_j(\hat{P}(s))ds} \right| u_{j0}(\xi) d\xi \right] \\
\leqslant \sum_{j=1}^{n} & \beta_M \int_0^t \left| B_j(\eta) - \widehat{B}_j(\eta) \right| d\eta + \sum_{j=1}^{n} \beta_M \int_0^t \widehat{B}_j(\eta) \int_\eta^t \left| m_j(P(s)) - m_j(\hat{P}(s)) \right| ds\, d\eta \\
& + \sum_{j=1}^{n} \int_0^t \widehat{B}_j(\eta) \left| \beta_j(P(t)) - \beta_j(\hat{P}(t)) \right| d\eta \\
& + \sum_{j=1}^{n} \int_0^\infty \left| \beta_j(P(t)) e^{-\int_0^t m_j(P(s))ds} - \beta_j(\hat{P}(t)) e^{-\int_0^t m_j(\hat{P}(s))ds} \right| u_{j0}(\xi) d\xi
\end{aligned}
$$

or equivalently,

$$
|F_i(t)| \leqslant \sum_{j=1}^{n} \beta_M \int_0^t |F_j(\eta)|\, d\eta + G_i(t). \tag{10}
$$

Here

$$
\begin{aligned}
G_i(t) = & \sum_{j=1}^{n} \beta_M \int_0^t \widehat{B}_j(\eta) \int_\eta^t \left| m_j(P(s)) - m_j(\hat{P}(s)) \right| ds\, d\eta \\
& + \sum_{j=1}^{n} \int_0^t \widehat{B}_j(\eta) \left| \beta_j(P(t)) - \beta_j(\hat{P}(t)) \right| d\eta \\
& + \sum_{j=1}^{n} \int_0^\infty \left| \beta_j(P(t)) e^{-\int_0^t m_j(P(s))ds} - \beta_j(\hat{P}(t)) e^{-\int_0^t m_j(\hat{P}(s))ds} \right| u_{j0}(\xi) d\xi \\
\leqslant & \sum_{j=1}^{n} \beta_M \int_0^t \widehat{B}_j(\eta) \int_\eta^t \left| m_j(P(s)) - m_j(\hat{P}(s)) \right| ds\, d\eta + \beta_K |P(t) - \hat{P}(t)| \sum_{j=1}^{n} \int_0^t \widehat{B}_j(\eta) d\eta \\
& + \sum_{j=1}^{n} \int_0^\infty \left[\beta_M \int_0^t \left| m_j(P(s)) - m_j(\hat{P}(s)) \right| ds + \left| \beta_j(P(t)) - \beta_j(\hat{P}(t)) \right| \right] u_{j0}(\xi) d\xi \\
\leqslant & (\beta_M m_K T + \beta_K) \|P - \hat{P}\|_\infty \sum_{j=1}^{n} \int_0^t \widehat{B}_j(\eta) d\eta + (\beta_M m_K T + \beta_K) \|P - \hat{P}\|_\infty \|u_0\|_{L^1} \\
\leqslant & (\beta_M m_K T + \beta_K) e^{n\beta_M T} \|u_0\|_{L^1} \|P - \hat{P}\|_\infty := J(T) \|P - \hat{P}\|_\infty,
\end{aligned}
$$

where $\beta_K = \sup_{P \in [0,\widehat{K}], 1 \leqslant i \leqslant n} \mid \beta'_i(P) \mid$ and $m_{\widehat{K}} = \sup_{P \in [0,\widehat{K}], 1 \leqslant i \leqslant n} \mid m'_i(P) \mid$. Thus, from (10) we obtain

$$\mid F_i(t) \mid \leqslant \sum_{j=1}^{n} \beta_M \int_0^t \mid F_j(\eta) \mid \mathrm{d}\eta + J(T)\|P - \hat{P}\|_{\infty}.$$

Summing the above inequality over the indices $i = 1, 2, \ldots, n$, we find

$$\sum_{i=1}^{n} \mid F_i(t) \mid \leqslant n\beta_M \int_0^t \sum_{j=1}^{n} \mid F_j(\eta) \mid \mathrm{d}\eta + nJ(T)\|P - \hat{P}\|_{\infty},$$

which, by Gronwall's inequality leads to

$$\sum_{i=1}^{n} \mid F_i(t) \mid \leqslant nJ(T)\mathrm{e}^{n\beta_M T}\|P - \hat{P}\|_{\infty}.$$

Hence, we have

$$\sum_{j=1}^{n} \int_0^t \left| B_j(\eta) - \widehat{B}_j(\eta) \right| \mathrm{d}\eta \leqslant nJ(T)\mathrm{e}^{n\beta_M T}T\|P - \hat{P}\|_{\infty}.$$

On the other hand, we find that

$$\sum_{j=1}^{n} \int_0^t \widehat{B}_j(\eta) \int_\eta^t \left| m_j(P(s)) - m_j(\hat{P}(s)) \right| \mathrm{d}s\mathrm{d}\eta \leqslant m_K T\|P - \hat{P}\|_{\infty} \int_0^t \sum_{j=1}^{n} \widehat{B}_j(\eta)\mathrm{d}\eta$$

$$\leqslant m_K T\|u_0\|_{L^1}\mathrm{e}^{n\beta_M T}\|P - \hat{P}\|_{\infty}$$

and

$$\sum_{j=1}^{n} \int_0^\infty u_{j0}(\xi) \int_0^t \left| m_j(P(s)) - m_j(\hat{P}(s)) \right| \mathrm{d}s\mathrm{d}\xi \leqslant m_K T\|u_0\|_{L^1}\|P - \hat{P}\|_{\infty}.$$

Therefore, $\mathscr{P}$ is contractive provided that T is sufficiently small. The proof is thus completed. $\square$

From the unique existence of the solution $P(t)$ and $B_i(t)$ of system (6)–(7) it follows that the solution of problem (1) must be unique because each $u_i(x, t)$ given by (5) is uniquely determined by $P(t)$ and $B_i(t)$. Thus we have the following local existence result.

Theorem 3. *Suppose that hypotheses (H1)–(H4) hold. Then there exists a value $T > 0$ such that problem (1) has a unique solution up to time T.*

In order to establish the global existence result for problem (1), we introduce an upper bound on $P(t)$ for $t \in [0, T]$.

Lemma 4. *Let $u(x, t)$ be a solution of (1) up to time T. Then $P(t)$ satisfies the following bound*:

$$P(t) \leqslant \|u_0\|_{L^1}\mathrm{e}^{\beta_M T} \text{ for } t \in [0, T]. \tag{11}$$

Proof. Let $P_i(t) = \int_0^\infty u_i(x, t)\mathrm{d}x$ and $P(t) = \sum_{i=1}^{n} P_i(t)$. Integrating (5) with respect to x, we obtain an integral equation for $P_i(t), i = 1, 2, \ldots, n$,

$$P_i(t) = \int_0^t B_i(\eta) e^{-\int_\eta^t m_i(P(s))ds} d\eta + \int_0^\infty u_{i0}(\xi) e^{-\int_0^t m_i(P(s))ds} d\xi. \tag{12}$$

Then differentiating (12) with respect to t, we have

$$P_i'(t) = \sum_{j=1}^n \gamma_{i,j} \beta_j(P) P_j - m_i(P) P_i. \tag{13}$$

Thus,

$$P'(t) = \sum_{i=1}^n \left(\sum_{j=1}^n \gamma_{j,i} \beta_i(P) - m_i(P) \right) P_i = \sum_{i=1}^n (\beta_i(P) - m_i(P)) P_i \leqslant \sum_{i=1}^n \beta_i(P) P_i \leqslant \beta_M P(t).$$

Integrating the above relation over $(0, t)$ yields (11). $\square$

Theorem 5. *Suppose that hypotheses* (H1)–(H4) *hold, then problem* (1) *has a unique solution for all positive time.*

The proof is essentially the same as that of Theorem 3 in [11], and hence is omitted.

4. Asymptotic behavior

Throughout this section, we assume an additional condition on the reproduction and the mortality rates.

(H5) $\beta_i(P)$ is non-increasing and $m_i(P)$ is increasing for $0 \leqslant P < \infty$, and there exists P_i^* such that $\beta_i(P_i^*) = m_i(P_i^*)$, $i = 1, 2, \ldots, n$.

In order to study the asymptotic behavior of the population, we consider the following system of coupled ordinary differential equations:

$$P_i'(t) = \sum_{j=1}^n \gamma_{i,j} \beta_j(P) P_j - m_i(P) P_i, \quad P_i(0) > 0, \quad i = 1, 2, \ldots, n. \tag{14}$$

We first show that the population $P(t)$ is uniformly bounded.

Lemma 6. *Let* $\overline{P} = \max_{1 \leqslant i \leqslant n} P_i^*$ *and* $\underline{P} = \min_{1 \leqslant i \leqslant n} P_i^*$. *For any* $0 < \varepsilon < 1$, *define* $I_\varepsilon = [\underline{P}(1 - \varepsilon), \overline{P}(1 + \varepsilon)]$. *Then there exists a finite time* t_ε^* *such that* $P \in I_\varepsilon$ *for* $t \geqslant t_\varepsilon^*$.

Proof. Summing (14) over the indices $i = 1, 2, \ldots, n$, we have

$$P'(t) = \sum_{i=1}^n \left(\sum_{j=1}^n \gamma_{j,i} \beta_i(P) - m_i(P) \right) P_i = \sum_{i=1}^n (\beta_i(P) - m_i(P)) P_i. \tag{15}$$

If $P > \overline{P}(1 + \varepsilon)$, then $\beta_i(P) - m_i(P) \leqslant -\tilde{\theta}_\varepsilon$ with $\tilde{\theta}_\varepsilon > 0$ for $i = 1, 2, \ldots, n$. By (15), $P' \leqslant -\tilde{\theta}_\varepsilon P$, i.e., P is strictly decreasing in t. Hence, there exists a value $\tilde{t}_\varepsilon$ such that $P \leqslant \overline{P}(1 + \varepsilon)$ for $t \geqslant \tilde{t}_\varepsilon$.

On the other hand, if $P < \underline{P}(1-\varepsilon)$, then $\beta_i(P) - m_i(P) \geqslant \hat{\theta}_\varepsilon$ with $\hat{\theta}_\varepsilon > 0$ for $i = 1, 2, \ldots, n$. By (15), $P' \geqslant \hat{\theta}_\varepsilon P$, i.e., P is strictly increasing in t. Hence, there exists a value $\hat{t}_\varepsilon$ such that $P \geqslant \underline{P}(1 - \varepsilon)$ for $t \geqslant \hat{t}_\varepsilon$.

Let $t_\varepsilon^* = \max\{\tilde{t}_\varepsilon, \hat{t}_\varepsilon\}$. Then $\underline{P}(1 - \varepsilon) \leqslant P(t) \leqslant \overline{P}(1 + \varepsilon)$ for all $t \geqslant t_\varepsilon^*$. $\square$

4.1. Closed reproduction case

In this case, we assume that reproduction is closed under subpopulations, that is, individuals in the ith subpopulation only reproduce individuals in the ith subpopulation. Hence $\gamma_{i,i} = 1, \gamma_{i,j} = 0, i \neq j, i, j = 1, 2, \ldots, n$, and (14) takes the form

$$P_i' = (\beta_i(P) - m_i(P))P_i, \quad P_i(0) > 0, \qquad i = 1, 2, \ldots, n. \tag{16}$$

We now introduce a condition on the ratio of the reproduction and mortality rates.

(H6) $\frac{\beta_1(P)}{m_1(P)} > \frac{\beta_i(P)}{m_i(P)}, \quad i = 2, \ldots, n$, for any $P \in I_0 = [\underline{P}, \overline{P}]$.

The next result shows that under (H6) the subpopulations $P_2, \ldots, P_n$ become extinct as $t \to \infty$.

Lemma 7. *Suppose that hypothesis (H6) holds. Then the solution of (16) satisfies that for each $i = 2, \ldots, n, P_i(t) \to 0$ as $t \to \infty$.*

Proof. We first note that by the continuity of β_i and m_i, there exists an $\bar{\varepsilon}(0 < \bar{\varepsilon} < 1)$ such that (H6) holds for $P \in I_{\bar{\varepsilon}}$. In particular, (H6) holds for $P = P_1^*$, which implies $\overline{P} = P_1^* > P_i^*$, $i = 2, \ldots, n$. To show that for $i = 2, \ldots, n, P_i(t) \to 0$ as $t \to \infty$, it suffices to show that for $i = 2, \ldots, n, \frac{P_i^{\sigma_i}}{P_1} \to 0$ as $t \to \infty$ for some positive constant σ_i. To this end, choose $0 < \varepsilon < \bar{\varepsilon}$ sufficiently small so that for any $P \in I_\varepsilon \subset I_{\bar{\varepsilon}}$ we have

$$(\sigma_i m_i(P) - m_1(P))\left(\frac{\beta_1(P)}{m_1(P)} - 1\right) \leqslant \frac{1}{2}\sigma_i m_i(P)\left(\frac{\beta_1(P)}{m_1(P)} - \frac{\beta_i(P)}{m_i(P)}\right),$$

where $\sigma_i = \min_{P \in I_{\bar{\varepsilon}}} \frac{m_1(P)}{m_i(P)}$. Set $\Phi_i(t) = \frac{P_i^{\sigma_i}(t)}{P_1(t)}$. Φ_i satisfies that for $t \geqslant t_\epsilon^*$

$$\Phi_i' = \frac{\sigma_i P_i^{\sigma_i-1} P_i' P_1 - P_i^{\sigma_i} P_1'}{P_1^2} = \frac{\sigma_i P_i^{\sigma_i}(\beta_i(P) - m_i(P))P_1 - P_i^{\sigma_i}(\beta_1(P) - m_1(P))P_1}{P_1^2}$$

$$= [\sigma_i(\beta_i(P) - m_i(P)) - (\beta_1(P) - m_1(P))]\Phi_i$$

$$= \left[\sigma_i m_i(P)\left(\frac{\beta_i(P)}{m_i(P)} - 1\right) - m_1(P)\left(\frac{\beta_1(P)}{m_1(P)} - 1\right)\right]\Phi_i$$

$$= \left[(\sigma_i m_i(P) - m_1(P))\left(\frac{\beta_1(P)}{m_1(P)} - 1\right) - \sigma_i m_i(P)\left(\frac{\beta_1(P)}{m_1(P)} - \frac{\beta_i(P)}{m_i(P)}\right)\right]\Phi_i$$

$$\leqslant -\frac{1}{2}\sigma_i m_i(P)\left(\frac{\beta_1(P)}{m_1(P)} - \frac{\beta_i(P)}{m_i(P)}\right)\Phi_i \leqslant -\lambda_i \Phi_i \tag{17}$$

with positive λ_i. Integrating (17) from t_ε^* to t then yields

$$\Phi_i(t) \leqslant \Phi_i(t_\varepsilon^*)e^{-\lambda_i(t-t_\varepsilon^*)}, \tag{18}$$

where $\Phi_i(t_\varepsilon^*) = \frac{P_i^{\sigma_i}(t_\varepsilon^*)}{P_1(t_\varepsilon^*)} > 0$. Hence, $\Phi_i(t) \to 0$ as $t \to \infty$. $\square$

We now show that P_1 converges to a positive equilibrium, and hence is the winning ecotype. To this end, we fix ε as chosen in the proof of the above theorem.

Theorem 8. *Suppose that hypothesis* (H6) *holds. Then* $P_1(t) \to P_1^*$ *as* $t \to \infty$.

Proof. Consider the following initial value problem:

$$\begin{cases} y' = (\beta_1(y) - m_1(y))y, & t_\varepsilon^* < t < \infty, \\ y(t_\varepsilon^*) = P_1(t_\varepsilon^*). \end{cases}$$

Clearly, $y(t) \to P_1^*$ as $t \to \infty$. Furthermore, since $P_1' \leqslant (\beta_1(P_1) - m_1(P_1))P_1$, by comparison $y(t) \geqslant P_1(t)$ for all $t \geqslant t_\varepsilon^*$. On the other hand, we have

$$\frac{\mathrm{d}}{\mathrm{d}t} \ln\left(\frac{P_1}{y}\right) = \frac{P_1'}{P_1} - \frac{y'}{y} = (\beta_1(P) - m_1(P)) - (\beta_1(y) - m_1(y))$$

$$= (\beta_1(P_1) - m_1(P_1)) - (\beta_1(y) - m_1(y)) + (\beta_1'(\zeta) - m_1'(\zeta)) \sum_{j=2}^{n} P_j$$

$$= \left(\beta_1'(\hat{\zeta}) - m_1'(\hat{\zeta})\right)(P_1 - y) + (\beta_1'(\zeta) - m_1'(\zeta)) \sum_{j=2}^{n} P_j, \tag{19}$$

where ζ is between P and P_1 and $\hat{\zeta}$ is between P_1 and y.

Since $\left(m_1'(\zeta) - \beta_1'(\zeta)\right) \geqslant c > 0$ for $t \geqslant t_\varepsilon^*$, rewriting (19) we find

$$y - P_1 \leqslant \frac{1}{c}\left(\frac{\mathrm{d}}{\mathrm{d}t} \ln\left(\frac{P_1}{y}\right) + (m_1'(\hat{\zeta}) - \beta_1'(\hat{\zeta})) \sum_{j=2}^{n} P_j\right). \tag{20}$$

Integrating (20) from t_ε^* to t, we then obtain

$$\int_{t_\varepsilon^*}^{t} (y(\eta) - P_1(\eta))\mathrm{d}\eta \leqslant \frac{1}{c}\left(\ln\left(\frac{P_1(t)}{y(t)}\right) + \sum_{j=2}^{n} \int_{t_\varepsilon^*}^{t} (m_1'(\zeta) - \beta_1'(\zeta))P_j(\eta)\mathrm{d}\eta\right) \leqslant M < \infty,$$

where M is independent of t, since $P_1(t)$ and $y_1(t)$ are both bounded by positive constants, and by (18) for $j = 2, \ldots, n$, $\int_{t_\varepsilon^*}^{t} P_j(t)\mathrm{d}t < \infty$. This implies that $\int_{t_\varepsilon^*}^{t} (y(t) - P_1(t))\mathrm{d}t < \infty$. Furthermore, it is easily seen that $(y(t) - P_1(t))'$ is bounded on $[t_\varepsilon^*, \infty)$. Hence, $y(t) - P_1(t) \to 0$ as $t \to \infty$, that is, $P_1(t) \to P_1^*$ as $t \to \infty$.　□

4.2. Open reproduction case

In this case, we assume that reproduction is open under subpopulations, that is, individuals in the ith subpopulation may also reproduce individuals in the jth subpopulation. We will show that if the graph associated with the matrix $[\gamma_{i,j}]$ is strongly connected (the matrix $[\gamma_{i,j}]$ is irreducible), then all ecotypes of the population coexist. To this end, for the convenience of the reader, we assume the following:

(H7) $\gamma_{1,2} > 0$, $\gamma_{2,3} > 0$, $\ldots \gamma_{n-1,n} > 0$, and $\gamma_{n,1} > 0$. Otherwise, $\gamma_{i,j} \geqslant 0$, $1 \leqslant i, j \leqslant n$.

The assumption (H7) implies that the matrix $[\gamma_{i,j}]$ is irreducible, and our following argument can be easily modified to apply in the case where (H7) is replaced by any other assumption that leads to strongly connected graph associated with the matrix $[\gamma_{i,j}]$.

We now show that under (H7) all ecotypes coexist for all times.

Theorem 9. *Suppose that hypothesis* (*H*7) *holds. Then there exists a positive constant c such that* $\lim \inf_{t\to\infty} P_i(t) \geqslant c$ *for* $i = 1, 2, \ldots, n$.

Proof. To obtain the claimed lower bound, it suffices to show that there exists a $T_1^* > 0$ such that $P_i \geqslant c$ for $t \geqslant T_1^*$, $i = 1, 2, \ldots, n$. For simplicity, let $I = I_{1/2} = [\underline{P}/2, 3\overline{P}/2]$ and $T_0^* = t_{1/2}^*$. We first define $\Psi_1(t) = P_1(t)$. Taking (14) into account, we find that for $t \geqslant T_0^*$, Ψ_1 satisfies

$$\Psi_1' = \sum_{j=1}^n \gamma_{1,j}\beta_j(P)P_j - m_1(P)P_1 \geqslant \gamma_{1,2}\beta_2(P)P_2 - m_1(P)P_1 \geqslant c_1(P_2 + \Psi_1) - d_1\Psi_1, \tag{21}$$

where $c_1 = \min\{\gamma_{1,2}\min_{P \in I} \beta_2(P), \min_{P \in I} m_1(P)\}$ and $d_1 = 2 \max_{P \in I} m_1(P)$. Then let $\Psi_2(t) = P_2 + \Psi_1$. Ψ_2 satisfies

$$\Psi_2' = \sum_{j=1}^n \gamma_{2,j}\beta_j(P)P_j + \Psi_1' - m_2(P)P_2 \geqslant \gamma_{2,3}\beta_3(P)P_3 + c_1\Psi_2 - d_1\Psi_1 - m_2(P)P_2$$

$$\geqslant c_2(P_3 + \Psi_2) - d_2\Psi_2. \tag{22}$$

Now let $\Psi_3(t) = P_3 + \Psi_2$. In a similar manner, we can see that Ψ_3 satisfies

$$\Psi_3' \geqslant c_3(P_4 + \Psi_3) - d_3\Psi_3. \tag{23}$$

Thus, we can define a sequence $\{\Psi_i(t)\}_{i=1}^n$ such that for $t \geqslant T_0^*$, $i = 1, 2, \ldots, n-1$,

$$\Psi_i' \geqslant c_i\Psi_{i+1} - d_i\Psi_i \tag{24}$$

and

$$\Psi_n = P_n + \Psi_{n-1} = P \geqslant \underline{P}, \tag{25}$$

where $c_i = \min\{c_{i-1}, \gamma_{i,i+1}\min_{P\in I} \beta_{i+1}(P)\}$ and $d_i = \max\{d_{i-1}\max_{P\in I} m_i(P)\}$, $i = 2, \ldots, n-1$.

In view of (24) and (25), we have

$$\Psi_{n-1} \geqslant \tilde{c}_{n-1} - d_{n-1}\Psi_{n-1}.$$

Integrating the above inequality from T_0^* to t, we find

$$\Psi_{n-1}' \geqslant \frac{\tilde{c}_{n-1}}{d_{n-1}}\left(1 - e^{-d_{n-1}(t-T_0^*)}\right),$$

which implies that for $t \geqslant 2T_0^*$, $\Psi_{n-1} \geqslant \hat{c}_{n-1}$. Then by means of (24), we find that for $t \geqslant 3T_0^*$, $\Psi_{n-2} \geqslant \hat{c}_{n-2}$. Continuing in such a way, finally we obtain that for $t \geqslant nT_0^*$, $\Psi_1 \geqslant \hat{c}_1$, that is $P_1 \geqslant \hat{c}_1$. We then make use of (14) to find that for $t \geqslant nT_0^*$,

$$P_n' \geqslant \gamma_{n,1}\beta_1(P)P_1 - m_n(P)P_n \geqslant \delta_n - d_nP_n, \tag{26}$$

which, upon integration over (nT_0^*, t) yields that for $t \geqslant (n+1)T_0^*$, $P_n \geqslant \hat{\delta}_n$. Repeating this process in a backward manner, one can see that there exists a positive constant c such that $P_i \geqslant c$ for $t \geqslant T_1^* = 2nT_0^*$, $i = 1, 2, \ldots, n$. Thus, the proof is completed. $\square$

5. Further discussion and numerical results

In the closed reproduction case, from Section 4.1 it is clear that subpopulations with smaller ratios $\beta_i(P)/m_i(P)$ will go to extinction. This leads to the following question: What happens if two subpopulations have the same largest ratio? We will show that in this case both subpopulations should survive. To this end, since all other subpopulations having smaller ratio will go to extinction, we will focus on the following subsystem consisting of two subpopulations with the largest ratio $\beta_1(P)/m_1(P) = \beta_2(P)/m_2(P)$

$$P_i' = (\beta_i(P) - m_i(P))P_i, \quad P_i(0) > 0, \quad i = 1, 2. \tag{27}$$

Because the ratios are equal, $P_1^* = P_2^* (= P^*)$. If $P_1(0) + P_2(0) = P(0) < P^*$, then $P_i' > 0$, which means that both P_1 and P_2 will increase in t, and hence for $t \geqslant 0, P_i(0) \leqslant P_i(t) \leqslant P^*, i = 1,2$. If $P_1(0) + P_2(0) = P(0) = P^*$, then $P_1 = P_1(0)$ and $P_2 = P_2(0)$ for $t \geqslant 0$. Finally, if $P_1(0) + P_2(0) = P(0) > P^*$, it is easily seen that $P^* \leqslant P(t) \leqslant P(0)$ for $t \geqslant 0$. To show that in this case lim inf$_{t\to\infty}P_i(t) > 0$ for $i = 1,2$ as well, we argue as follows: From the proof of Lemma 7 we see that for any arbitrary positive constant σ_2 and for $P^* \leqslant P(t) \leqslant P(0)$

$$\Phi_2'(t) \leqslant (\sigma_2 m_2(P) - m_1(P))\left(\frac{\beta_1(P)}{m_1(P)} - 1\right).$$

Choose σ_2 large enough such that $\sigma_2 m_2(P) - m_1(P) \geqslant 0$ for $P \in [P^*, P(0)]$. Then $\Phi_2'(t) \leqslant 0$, which yields $P_2^{\sigma_i}(t)/P_1(t) \leqslant \Phi_2(0)$. Hence if lim inf$_{t\to\infty}P_1(t) = 0$, then lim inf$_{t\to\infty}P_2(t) = 0$. Using similar argument, it follows that if lim inf$_{t\to\infty}P_2(t) = 0$, then lim inf$_{t\to\infty}P_1(t) = 0$. Since $P^* \leqslant P(t) \leqslant P(0)$, we obtain lim inf$_{t\to\infty}P_i(t) > 0, i = 1,2$, and therefore both subpopulations should survive.

Although we have shown that in the case of two equal largest ratios, both subpopulations survive, the exact asymptotic behavior of this two-ecotype system remains complicated and may depend on the initial conditions $P_i(0)$, $i = 1,2$. For example, suppose that $\beta_1(P) = \beta_2(P) = 1$ and $m_1(P) = m_2(P) = P$, then system (27) reduces to the following system:

$$P_i' = (1 - P)P_i, \quad P_i(0) > 0, \quad i = 1, 2.$$

Note that the equilibrium of this system satisfies $\hat{P}_1 + \hat{P}_2 = \hat{P} = 1$. Hence, there is an infinite number of equilibrium points with $0 \leqslant \hat{P}_1 \leqslant 1$ being arbitrary and $\hat{P}_2 = 1 - \hat{P}_1$. Adding the two equations, one can easily find that P satisfies a logistic dynamics and $P \to 1$ as $t \to \infty$. Furthermore, dividing the two equations, one has $dP_1/dP_2 = P_1/P_2$, and therefore $P_1/P_2 = P_1(0)/P_2(0)$. From this one can see that $P_1 \to P_1(0)/P(0)$ and $P_2 \to P_2(0)/P(0)$ as $t \to \infty$.

In the open reproduction case, if the kth ($1 \leqslant k \leqslant n$) node in the graph associated with the matrix $[\gamma_{i,j}]$ is not connected to any other node, that is, $\gamma_{k,k} = 1$ and $\gamma_{k,j} = 1$ for $j = 1, \ldots, k-1, k+1, \ldots, n$, then the kth subpopulation may become extinct. To show this,

noticing $\sum_{i=1}^{n} \gamma_{i,k} = 1$, it follows that $\gamma_{i,k}=0$ for $i = 1, \ldots, k-1, k+1, \ldots, n$. Let $\tilde{P} = \sum_{i=1}^{k-1} P_i + \sum_{i=k+1}^{n} P_i$. Summing (14) over the indices $i = 1, \ldots, k-1, k+1, \ldots, n$, we find

$$\tilde{P}' = \sum_{\substack{i=1 \\ i \neq k}}^{n} \left(\sum_{\substack{j=1 \\ i \neq k}}^{n} \gamma_{j,i} \beta_i(P) - m_i(P) \right) P_i = \sum_{\substack{i=1 \\ i \neq k}}^{n} (\beta_i(P) - m_i(P)) P_i \geqslant (\underline{\beta}(P) - \bar{m}(P)) \tilde{P}, \qquad (28)$$

where $\underline{\beta} = \min\{\beta_1 \ldots, \beta_{k-1}, \beta_{k+1}, \ldots, \beta_n\}$ and $\bar{m} = \max\{m_1, \ldots, m_{k-1}, m_{k+1}, \cdots, m_n\}$.

As before, we impose an assumption on the ratio of the reproduction and mortality rates.

(H8) For any $P \in I_0 = [\underline{P}, \overline{P}], \frac{\underline{\beta}(P)}{\bar{m}(P)} > \frac{\beta_k(P)}{m_k(P)}$ and $\underline{\beta}(P) \geqslant \bar{m}(P)$.

As in the proof of Lemma 7, we choose $\varepsilon(0 < \varepsilon < \bar{\varepsilon})$ small enough so that for any $P \in I_\varepsilon \subset I_{\bar{\varepsilon}}$

$$(\sigma m_k(P) - \bar{m}(P)) \left(\frac{\underline{\beta}(P)}{\bar{m}(P)} - 1 \right) \leqslant \frac{1}{2} \sigma m_k(P) \left(\frac{\underline{\beta}(P)}{\bar{m}(P)} - \frac{\beta_k(P)}{m_k(P)} \right),$$

where $\sigma = \min_{P \in I_{\bar{\varepsilon}}} \frac{\bar{m}(P)}{m_k(P)}$. We then introduce an auxiliary function $\Phi(t) = \frac{P_k^\sigma(t)}{\tilde{P}(t)}$. Φ satisfies that for $t \geqslant t_\varepsilon^*$,

$$\begin{aligned}
\Phi' &= \frac{\sigma P_k^{\sigma-1} P_k' \tilde{P} - P_k^\sigma \tilde{P}'}{\tilde{P}^2} \leqslant \frac{\sigma P_k^\sigma (\beta_k(P) - m_k(P)) \tilde{P} - P_k^\sigma (\underline{\beta}(P) - \bar{m}(P)) \tilde{P}}{\tilde{P}^2} \\
&= [\sigma(\beta_k(P) - m_k(P)) - (\underline{\beta}(P) - \bar{m}(P))] \Phi \\
&= \left[\sigma m_k(P) \left(\frac{\beta_k(P)}{m_k(P)} - 1 \right) - \bar{m}(P) \left(\frac{\underline{\beta}(P)}{\bar{m}(P)} - 1 \right) \right] \Phi \\
&= \left[(\sigma m_k(P) - \bar{m}(P)) \left(\frac{\underline{\beta}(P)}{\bar{m}(P)} - 1 \right) - \sigma m_k(P) \left(\frac{\underline{\beta}(P)}{\bar{m}(P)} - \frac{\beta_k(P)}{m_k(P)} \right) \right] \Phi \\
&\leqslant -\frac{1}{2} \sigma m_k(P) \left(\frac{\underline{\beta}(P)}{\bar{m}(P)} - \frac{\beta_k(P)}{m_k(P)} \right) \Phi \leqslant -\lambda \Phi \qquad (29)
\end{aligned}$$

with $\lambda > 0$. Integrating (29) from t_ε^* to t then yields

$$\Phi(t) \leqslant \Phi(t_\varepsilon^*) e^{-\lambda(t - t_\varepsilon^*)},$$

which implies $\Phi(t) \to 0$, and hence $P_k(t) \to 0$ as $t \to \infty$. Clearly, if the remaining $n-1$ ecotypes satisfy (H7) (with n replaced by $n-1$), then using previous arguments one can see that they coexist. Thus we have the following result.

Theorem 10. *If the kth subpopulation satisfies $\gamma_{k,k} = 1, \gamma_{k,j} = 0$ for $j = 1, \ldots, k-1, k+1, \ldots, n$ and hypothesis (H8) holds, then it will eventually become extinct. Moreover, if the other $n-1$ ecotypes satisfy (H7), they will coexist.*

The next numerical example illustrates that assumption (H8) is sufficient but not necessary for the extinction of the kth subpopulation. In this example we let $n = 3, \beta_1 = 2.7, \beta_2 = 2.4$ and $\beta_3 = 2.1$. We choose the mortality functions as $m_1 = 0.054P$, $m_2 = 0.096P$ and $m_3 = 0.07P$, while the probabilities $\gamma_{i,j}$ are selected as $\gamma_{1,1} = 0.4, \gamma_{1,2} = 0.6, \ \gamma_{1,3} = 0, \gamma_{2,1} = 0.6, \gamma_{2,2} = 0.4, \gamma_{2,3} = 0,$

$\gamma_{3,1} = 0, \gamma_{3,2} = 0$ and $\gamma_{3,3} = 1$. In Fig. 1 we present the solution to this system of differential equations with the initial conditions $P_1(0) = P_2(0) = 0.5$ and $P_3(0) = 1$. The figure shows that P_3 becomes extinct although it can be easily verified that hypothesis (H8) does not hold for this example.
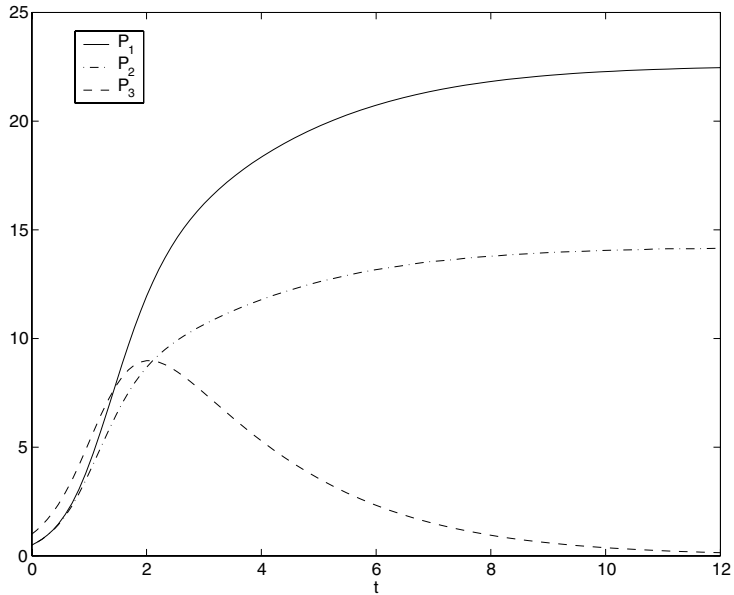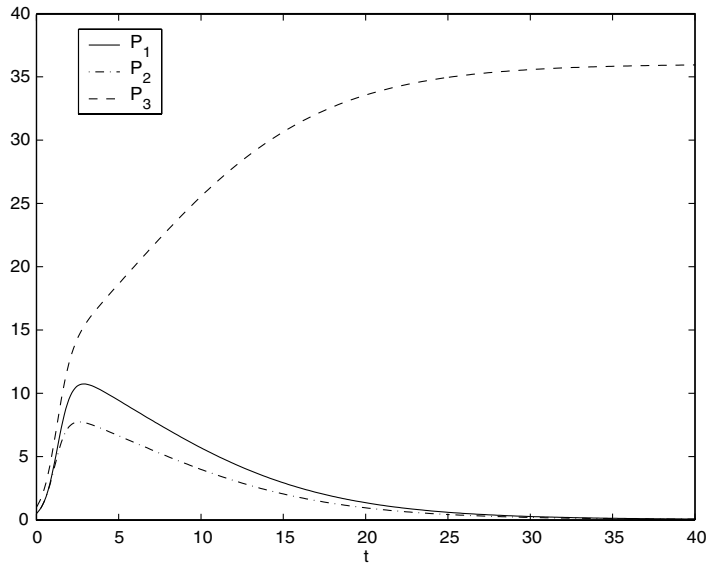

Fig. 1. Extinction of P_3.

Fig. 2. Survival of P_3 and extinction of P_1 and P_2.

Our last numerical example indicates that if (H8) is not satisfied, then the kth subpopulation may possibly survive while the subpopulations $P_1, \ldots, P_{k-1}, P_{k+1}, \ldots, P_n$ can become extinct. In this example we still let $n = 3, \beta_1 = 2.7, \beta_2 = 2.4$ and $\beta_3 = 2.1$. We choose the mortality functions as $m_1 = 0.054P, m_2 = 0.1091P$ and $m_3 = 0.0583P$, while the probabilities $\gamma_{i,j}$ are selected as $\gamma_{1,1} = 0.1, \gamma_{1,2} = 0.9, \gamma_{1,3} = 0, \ \gamma_{2,1} = 0.9, \gamma_{2,2} = 0.1, \gamma_{2,3} = 0, \gamma_{3,1} = 0, \gamma_{3,2} = 0$ and $\gamma_{3,3} = 1$. In Fig. 2 we present the numerical results for the initial conditions $P_1(0) = P_2(0) = 0.5$ and $P_3(0) = 1$. The figure shows that P_3 survives while P_1 and P_2 die out. It is worth pointing out that even though P_1 dies out, $\frac{\beta_1}{m_1} > \frac{\beta_3}{m_3}$ for this choice of functions.

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