

Analysis of a lottery competition model with limited nutrient availability

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How a plant species utilizes a limited nutrient is important for its survival. The purpose of this work is to examine how nutrient utilization mechanisms (for seed production) affect the coexistence of competing plant species. We construct a revised lottery model that uses one of three possible kinds of nutrient utilization functions. In all cases the models suggest that two species can coexist under certain circumstances, but that three species cannot coexist, at least when the nutrient utilization functions are continuous functions of nutrient uptake. However, in the discontinuous case three species can coexist in a state of sustained oscillations. The results suggest that one need pay close attention to the differences in the nutrient utilization mechanisms among competing plant species in order to ascertain the competitive outcome.

Keywords: Lottery models; Population dynamics; Difference equations; Stability; Periodic orbits; Competition; Coexistence; Competitive exclusion

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1. Introduction

One of the important issues in ecology is to understand how a variety of species coexist [1]. In this paper, we restrict ourselves to plant species and consider the relationship between species coexistence and nutrient utilization mechanisms for the production of seeds. Plant species utilize inorganic material from soil for seed production. This is because of their need for kinds of nutrients that cannot be generated by photosynthesis [2]. After a nutrient is taken up, a plant species must decide how to utilize it for seed production. The decision is a critical one for seeds, since their germination depends on the amount of nutrient received. Therefore, the amount of nutrient allotted to the production of seeds by the adult plant is critical for the survival of the seeds.

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For a lottery model, let us denote the fraction of the sites occupied by adults of species i as P_i . The time unit is one year and the immature period is shorter than a year. There are n plant species in a single habitat. We assume each plant produces seed each year. Additionally, every year adult plants are removed at some rate, and these removals create vacant space that we assume is immediately occupied by individuals randomly chosen from the seed pool. The standard lottery model [3, 4] is given by the following non-autonomous difference equation

$$P_i(t+1) = (1 - \delta_i(t))P_i(t) + S(P_1(t), \dots, P_n(t)) \frac{\beta_i(t)P_i(t)}{\sum_{j=1}^n \beta_j(t)P_j(t)}, i = 1, \dots, n,$$

where t denotes a nonnegative integer. $\delta_i = \delta_i(t)$ is the mortality rate of adult individuals of species i , so $0 \leq \delta_i \leq 1$, and the vacant space created by the mortality of adults is $S(P_1, \dots, P_n) = 1 - \sum_{j=1}^n (1 - \delta_j(t))P_j$. $\beta_i = \beta_i(t) > 0$ is the per capita rate of seed production by adults of species i and the total amount of seeds produced by species i is $\beta_i(t)P_i(t)$. The initial condition satisfies $P_i(0) > 0, i = 1, \dots, n$ and $\sum_{j=1}^n P_j(0) = 1$. Note that every solution satisfies $\sum_{j=1}^n P_j(t) = 1$ for all $t = 1, 2, \dots$.

We find that the first term of the right-hand side of the standard lottery model above gives the fraction of sites at time t that are occupied by surviving adults at $t + 1$. The second term gives the fraction of sites occupied by new adults. This fraction is the fraction of vacant sites created by mortality in that year and the amount of the seeds produced during the year. Note that the successful settlement of each plant i depends on the fraction $\beta_i P_i / \sum_{j=1}^n \beta_j P_j$ of new plant.

In the above model, it is implicitly assumed that nutrients are always sufficiently available for all plant species. The studies of Chesson and Warner [3] and Chesson [2] show that the temporal fluctuation of the natality rates $\beta_i(t)$ promotes coexistence of species, but the temporal fluctuation of the mortality rates $\delta_i(t)$ does not. Furthermore, coexistence cannot be achieved for almost every pair of the parameters β_i and δ_i as long as they are constant. Additionally, in the above model with the constant parameters, the unique survival species can be determined by the ratio β_i/δ_i . Only plant k with the largest β_k/δ_k ($k = 1, \dots, n$) will survive.

The effects of temporal fluctuations in the recruitment process have been extensively analyzed for lottery models (e.g. see [5, 6]). Lottery models also provide a basis for understanding the coexistence of multiple species in terrestrial systems [7]. Additionally, Dewi and Chesson [8] studied a lottery model with a stage structure and Comins and Noble [9] studied the model with heterogeneous patches. The recent works of Muko and Iwasa [10, 11] considered another mechanism that promotes coexistence in the standard lottery model, namely, spatial heterogeneity. Their model includes multiple habitats, each of which has different mortality and natality rates of the species. Their study shows that the spatial heterogeneity of mortality rates promotes coexistence of species, but that spatial heterogeneity of natality rates does not [10]. From these two studies, we see that the spatial heterogeneity can promote coexistence in a lottery model. Although many researchers have studied lottery models that include a spatial factor, we know of no studies that include the dynamics and effect of limited nutrient availability.

In this study, we revise the basic lottery model by including the dynamics of a nutrient of limited availability utilized by competing plant species and its effect on coexistence. The organization of this paper is as follows. First, we modify the original lottery model to take into account effects due to the limited availability of a nutrient. Then we propose several types of reproduction functions for the revised model. Finally, we consider the effect of limited availability of nutrients on the plant diversity.

Note that Type I is obtained from Type II for $l_i = 0$. We consider Type I function to analyze the qualitative differences on dynamical behaviors between the models with Type I and Type II.

Type I

$$\beta_i(\alpha_i) = c_i\alpha_i,$$

Type II

$$\beta_i(\alpha_i) = \begin{cases} c_i(\alpha_i - l_i) & (l_i \leq \alpha_i) \\ 0 & (0 < \alpha_i < l_i), \end{cases}$$

Type III

$$\beta_i(\alpha_i) = \begin{cases} c_i\alpha_i & (l_i \leq \alpha_i) \\ 0 & (0 < \alpha_i < l_i). \end{cases}$$

Graphs of all types appear in figure 1. Here $c_i > 0$ is composed of two factors: the conversion rate from nutrient consumed by adults to seeds and the constant fraction of nutrient consumed by adults that is distributed to seeds. $l_i > 0$ is a positive constant expressing the nutrient threshold. For Type II and Type III, $\beta_i(\alpha_i) = 0$ for $0 < \alpha_i < l_i$. This corresponds to the situation where, although adult individuals reproduce seeds, there is not enough nutrient for seeds to germinate.

Let us consider system (1). We define $\Omega := \{(P_1, \dots, P_n, x) \in \mathbf{R}^{n+1} \mid P_1 \geq 0, \dots, P_n \geq 0, \sum_{j=1}^n P_j = 1, x > 0\}$. We first show that Ω is forward invariant.

LEMMA 1 *If $(P_1(0), \dots, P_n(0), x(0)) \in \Omega$, then $(P_1(t), \dots, P_n(t), x(t)) \in \Omega$ for all $t \geq 0$.*

Proof Let $(P_1(t), \dots, P_n(t), x(t)) \in \Omega$. Then it follows from (1) that $\sum_{j=1}^n P_j(t+1) = 1$. Since $\beta_i(\alpha_i(x))$ and $S(P_1, P_2, \dots, P_n)$ are nonnegative, $P_i(t+1) \geq 0$ holds for all $i = 1, 2, \dots, n$. Finally, we prove that $x(t+1) > 0$. In fact, by using $\max_{x \geq 0} (m_i/(a_i + x)) =$

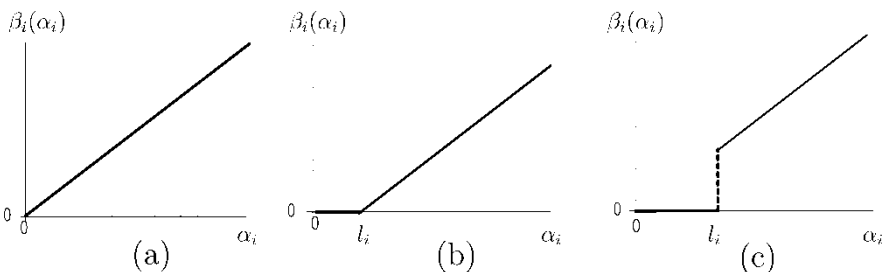


Figure 1. The graph of reproduction function of seeds (β_i) with respect to absorbed nutrient $\alpha_i(x)$. (a), (b) and (c) correspond to Type I, Type II and Type III, respectively.

m_i/a_i , we have the following inequalities:

$$\begin{aligned} x(t+1) &= x(t) - \sum_{j=1}^n \alpha_j(x(t))P_j(t)q + s \\ &\geq x(t) - \sum_{j=1}^n \frac{m_j}{a_j}x(t)P_j(t)q + s \\ &\geq x(t)\left(1 - \sum_{j=1}^n P_j(t)\right)q + s \\ &= s. \end{aligned}$$

Here we used $m_i/a_i \leq 1$ for $i = 1, \dots, n$. This completes the proof. ■

LEMMA 2 *Every solution of system (1) with the initial condition $(P_1(0), \dots, P_n(0), x(0)) \in \Omega$ is bounded.*

Proof From Lemma 1, if $(P_1(0), \dots, P_n(0), x(0)) \in \Omega$, then $(P_1(t), \dots, P_n(t), x(t)) \in \Omega$ for all $t \geq 0$. So, it is sufficient only to show that $x(t)$ is bounded above. If $(P_1(t), \dots, P_n(t), x(t)) \in \Omega$, then $(x(t) - \sum_{j=1}^n \alpha_j(x(t))P_j(t))q + s \leq qx(t) + s$ holds. Therefore, we have

$$x(t+1) \leq qx(t) + s.$$

If we reduce both sides of the inequality by $s/(1-q)$, we obtain

$$\begin{aligned} x(t+1) - \frac{s}{1-q} &\leq qx(t) + s - \frac{s}{1-q} \\ &= q \left(x(t) - \frac{s}{1-q} \right) \\ &\leq q^{t+1} \left(x(0) - \frac{s}{1-q} \right). \end{aligned}$$

This implies the boundedness of $x(t)$. Note that $0 < q < 1$. This completes the proof. ■

These lemmas imply that the occupation rate P_i always satisfies $0 \leq P_i \leq 1$ and the amount of nutrient is always positive and bounded. These lemmas are reasonable in nature, that is, the fraction of occupation by species i is naturally positive and less than 1. Furthermore, the amount of nutrient x is always positive. Note that there is never any vacant space because $\sum_{j=1}^n P_j(t) = 1$. This is qualitatively different from the model without nutrient dynamics and only density dependence.

Additionally, we find the following lemma about an interior equilibrium.

LEMMA 3 *If (1) has a positive equilibrium $(P_1^*, \dots, P_n^*, x^*)$, then the following conditions hold:*

$$\frac{\beta_i(\alpha_i(x^*))}{\delta_i} = \frac{\beta_j(\alpha_j(x^*))}{\delta_j}, 1 \leq i \neq j \leq n. \tag{3}$$

Lemma 3 shows that at most two species can coexist in general under the influence of nourishment and three or more species cannot coexist at the positive equilibrium in general.

This is because condition (3) cannot be satisfied in general for $n > 3$. We consider the case with two or three species (i.e. $n = 2$ or $n = 3$) in section 3. For the three-species case, we give only the simulation results. Hereafter we always assume that species 1 belongs to Type I. Note that this assumption ensures that $\sum_{j=1}^n \beta_j(\alpha_j(x))P_j \neq 0$ on Ω whenever $P_1 \neq 0$. That is, the total amount of seeds cannot be zero.

3. The stability analysis for the revised lottery model

3.1 System with Type I species

First we consider the case $n = 2$ with both species of Type I. In this case, system (1) reduces to

$$\begin{cases} P_1(t+1) = (1 - \delta_1)P_1(t) + \left\{ 1 - \sum_{j=1}^2 (1 - \delta_j)P_j(t) \right\} \frac{\beta_1(\alpha_1(x(t)))P_1(t)}{\sum_{j=1}^2 \beta_j(\alpha_j(x(t)))P_j(t)} \\ P_2(t+1) = (1 - \delta_2)P_2(t) + \left\{ 1 - \sum_{j=1}^2 (1 - \delta_j)P_j(t) \right\} \frac{\beta_2(\alpha_2(x(t)))P_2(t)}{\sum_{j=1}^2 \beta_j(\alpha_j(x(t)))P_j(t)} \\ x(t+1) = x(t) - \sum_{j=1}^2 \alpha_j(x(t))P_j(t)q + s, \end{cases} \quad (4)$$

where $\beta_i(\alpha_i(x)) = c_i\alpha_i(x)$, $i = 1, 2$. Hereafter we assume $\Gamma = c_2m_2\delta_1/(c_1m_1\delta_2) > 1$ without loss of generality.

There are three types of equilibria in system (4) as follows:

1. boundary equilibrium: $E_1^I(1, 0, \hat{x}_1^I)$, $\hat{x}_1^I > 0$,
2. boundary equilibrium: $E_2^I(0, 1, \hat{x}_2^I)$, $\hat{x}_2^I > 0$,
3. interior equilibrium: $E_+^I(P_{1+}^I, P_{2+}^I, x_+^I)$, $P_{1+}^I > 0, P_{2+}^I > 0, x_+^I > 0$,

where $\hat{x}_i^I, P_{1+}^I, P_{2+}^I, x_+^I$ are given by

$$\hat{x}_i^I = \frac{s - (1 - q)a_i - m_iq + \sqrt{(s - (1 - q)a_i - m_iq)^2 + 4sa_i(1 - q)}}{2(1 - q)}$$

$$P_{1+}^I = \frac{\alpha_2(x_+^I)q - (s - (1 - q)x_+^I)}{(\alpha_2(x_+^I) - \alpha_1(x_+^I))q}, \quad P_{2+}^I = \frac{(s - (1 - q)x_+^I) - \alpha_1(x_+^I)q}{(\alpha_2(x_+^I) - \alpha_1(x_+^I))q}, \quad x_+^I = \frac{a_2 - a_1\Gamma}{\Gamma - 1}.$$

Table 1 summarizes the feasibility and local asymptotic stability conditions of the equilibria. We straightforwardly obtain conditions for the feasibility of the interior equilibrium from the formulas above. The conditions that ensure $x_+^I > 0$ are given by $a_2/a_1 > \Gamma > 1$. Furthermore, the conditions that ensure $P_{i+}^I > 0$ for both i are $\alpha_1(x_+^I)q \geq s - (1 - q)x_+^I \geq \alpha_2(x_+^I)q$ (where the upper inequalities are to be taken together and the lower inequalities are to be taken together). From the definitions of the equilibrium points, these inequalities are equivalent to the inequalities $\hat{x}_2^I \geq x_+^I \geq \hat{x}_1^I$, as the following lemma shows.

LEMMA 4 *Suppose that $x_+^I > 0$. Then the following relationship holds:*

$$\alpha_1(x_+^I)q \geq s - (1 - q)x_+^I \geq \alpha_2(x_+^I)q \iff \hat{x}_2^I \geq x_+^I \geq \hat{x}_1^I.$$

Table 1. The feasibility and stability conditions of equilibria for system (4).

Equilibrium point	Feasibility conditions	Stability conditions
E_1^I	always	$\hat{x}_1^I < x_+^I$
E_2^I	always	$\hat{x}_2^I > x_+^I$
E_+^I	$a_2/a_1 > \Gamma > 1$ $\hat{x}_1^I \geq x_+^I \geq \hat{x}_2^I$	$\hat{x}_1^I > x_+^I > \hat{x}_2^I$

Proof We will prove $\alpha_1(x_+^I)q > s - (1 - q)x_+^I > \alpha_2(x_+^I)q \iff \hat{x}_2^I > x_+^I > \hat{x}_1^I$. The remaining case can be proved similarly.

(\implies) Suppose that $\alpha_1(x_+^I)q > s - (1 - q)x_+^I > \alpha_2(x_+^I)q$ is true. Then, from the definition of \hat{x}_1^I , we have following inequalities:

$$s - (1 - q)\hat{x}_1^I - \alpha_1(\hat{x}_1^I)q = 0 > s - (1 - q)x_+^I - \alpha_1(x_+^I)q.$$

$$x_+^I > \hat{x}_1^I.$$

Note that the function $f(x) = s - (1 - q)x - \alpha_i(x)q$ is decreasing with respect to x . Similarly we have $x_+^I < \hat{x}_2^I$. The proof of the sufficiency is completed.

(\impliedby) Suppose that $\hat{x}_2^I > x_+^I > \hat{x}_1^I$. A similar argument to that the sufficiency condition establishes the desired inequality $\alpha_1(x_+^I)q > s - (1 - q)x_+^I > \alpha_2(x_+^I)q$. ■

Lemma 4 provides the feasibility condition given in table 1 for the equilibrium E_+^I . We also find in table 1 that there exists a *bistable state* where both E_1^I and E_2^I are stable ($\hat{x}_1^I < x_+^I < \hat{x}_2^I$). It turns out that if the system is *bistable*, then equilibrium E_+^I is positive and unstable while,

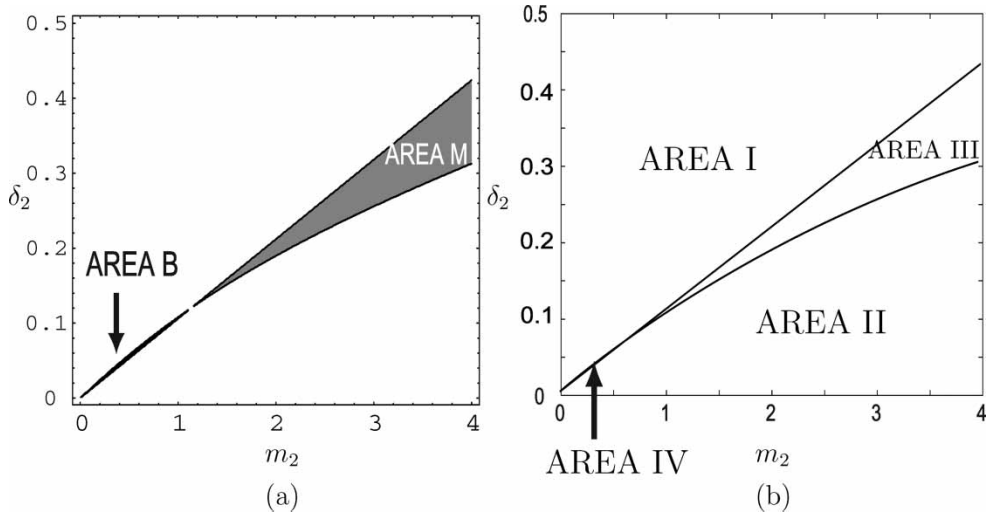


Figure 2. The (δ_2, m_2) plane for system (1) with two Type I species. (a) In AREA B, we have the bistable state and the interior equilibrium is unstable. AREA M gives the mutually invasinable state and the interior equilibrium is stable. (b) This graph shows the dynamical property of (1) during $t = 9 \times 10^3 - 10 \times 10^3$. In AREA I (resp. AREA II), only species 1 (resp. species 2) survives. In AREA III, two species coexist at an interior equilibrium point. In AREA IV, the survival species depend on the initial values of the species $(P_1(0), P_2(0), x(0))$. The parameters are $m_2 \in [0, 4]$ and $\delta_2 \in [0, 0.5]$, $\delta_1 = 0.12$, $m_1 = 0.6$, $a_1 = 1$, $a_2 = 4.7$, $l_1 = l_2 = 0$, $q = 0.8$, $s = 1$, $c_1 = c_2 = 2.0$. The initial condition for (b) is $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$.

on the other hand, if the system is *mutually invisable* (both E_1^I and E_2^I are unstable) then E_+^I is stable. We summarize these results in the following theorems, whose proofs appear in Appendix B.

THEOREM 1 *If system (4) is bistable, then an interior equilibrium is unstable.*

THEOREM 2 *If system (4) is mutually invisable, then an interior equilibrium is stable.*

We show some simulation results for two species with Type I seed production functions (figures 2 and 3). From these simulations, we can confirm that two species coexist when the system is mutually invisable. This result is also illustrated for three species in figure 4.

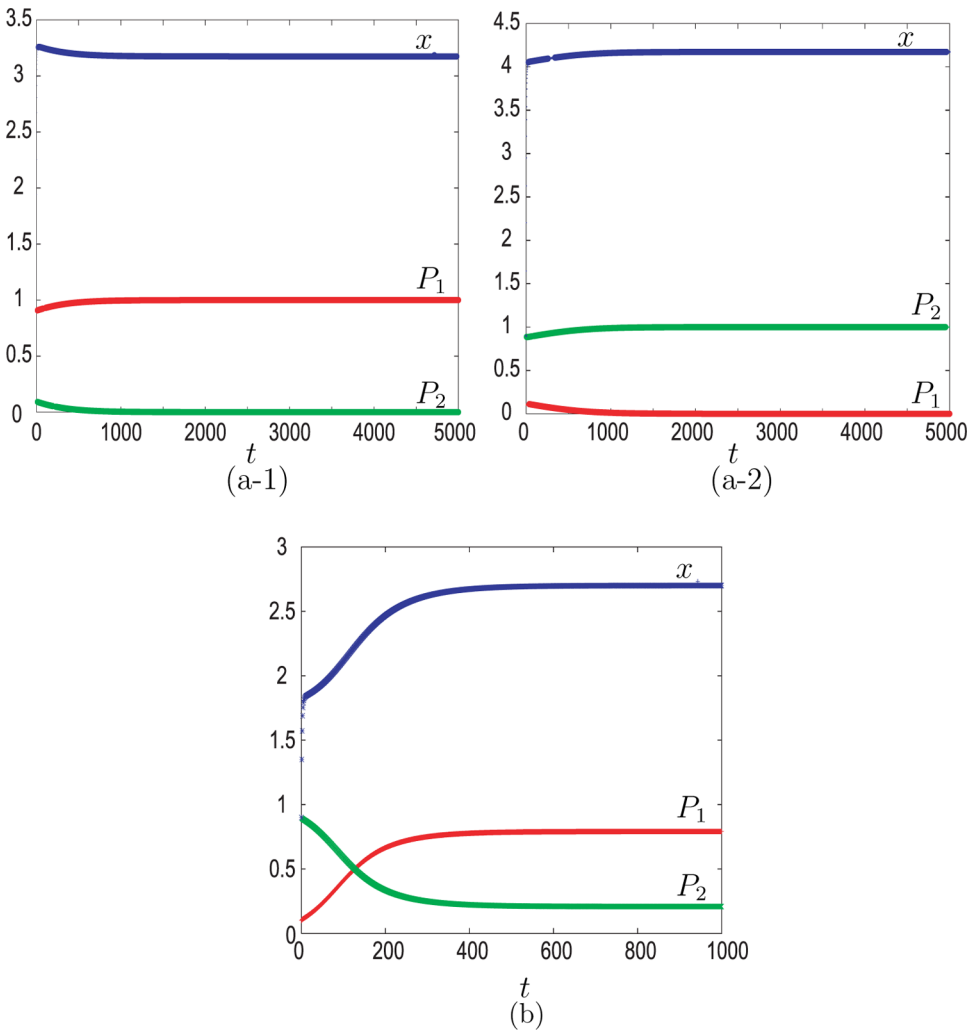


Figure 3. The temporal sequence of P_1 , P_2 and x for system (1) with two Type I species. (a-1) and (a-2): The parameters in AREA B in figure 2(a) are chosen and only species 1 or 2 survives depending on initial conditions (*bistable state*). (b) The parameter in AREA M in figure 2(a) is chosen and two species coexist (*invisable state*). The parameters are the same as figure 2 except for (a-1) $m_2 = 0.44$, $\delta_2 = 0.05$, $(P_1(0), P_2(0), x(0)) = (0.9, 0.1, 0.9)$, (a-2) $m_2 = 0.44$, $\delta_2 = 0.05$, $(P_1(0), P_2(0), x(0)) = (0.1, 0.9, 0.9)$, (b) $m_2 = 3$, $\delta_2 = 0.3$, $(P_1(0), P_2(0), x(0)) = (0.2, 0.6, 3)$.

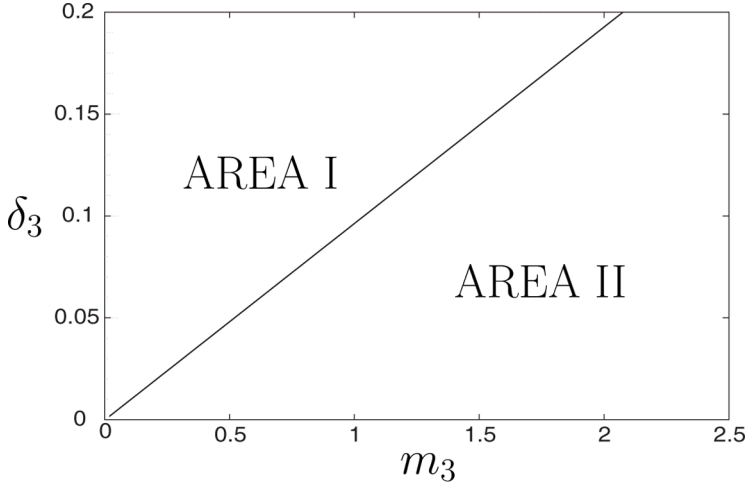


Figure 4. The (δ_3, m_3) plane for system (1) with three Type I species. In AREA I, species 1 and 2 coexist. In AREA II, only species 3 survives. The parameters are $m_3 \in [0, 2.5]$, $\delta_1 = 0.12$, $\delta_2 = 0.3$, $\delta_3 \in [0, 0.2]$, $m_1 = 0.6$, $m_2 = 3$, $a_1 = 1$, $a_2 = 4.7$, $a_3 = 5$ $l_1 = l_2 = l_3 = 0$, $q = 0.8$, $s = 1$, $c_1 = c_2 = c_3 = 2.0$. The initial condition is $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$.

3.2 System with Type II species

We will consider system (1) with Type II for species 2 and keep the species 1 belonging to Type I. Further we assume that $\delta_2 \neq 0$. Similar to the model considered in section 3.1 there are three types of equilibria for system (4):

1. boundary equilibrium: $E_1^{II}(1, 0, \hat{x}_1^{II}), \hat{x}_1^{II} > 0$;
2. boundary equilibrium: $E_2^{II}(0, 1, \hat{x}_2^{II}), \hat{x}_2^{II} > 0$;
3. interior equilibrium: $E_{\pm}^{II}(P_{1\pm}^{II}, P_{2\pm}^{II}, x_{\pm}^{II}), P_{1\pm}^{II} > 0, P_{2\pm}^{II} > 0, x_{\pm}^{II} > 0$;

where $\hat{x}_i^{II}, P_{1\pm}^{II}, P_{2\pm}^{II}, x_{\pm}^{II}$ are given by

$$\hat{x}_i^{II} = \frac{s - (1 - q)a_i - m_i q + \sqrt{(s - (1 - q)a_i - m_i q)^2 + 4sa_i(1 - q)}}{2(1 - q)}$$

$$P_{1\pm}^{II} = \frac{\alpha_2(x_{\pm}^{II})q - (s - (1 - q)x_{\pm}^{II})}{(\alpha_2(x_{\pm}^{II}) - \alpha_1(x_{\pm}^{II}))q}, P_{2\pm}^{II} = \frac{(s - (1 - q)x_{\pm}^{II}) - \alpha_1(x_{\pm}^{II})q}{(\alpha_2(x_{\pm}^{II}) - \alpha_1(x_{\pm}^{II}))q},$$

$$x_{\pm}^{II} = \frac{-A \pm \sqrt{A^2 + 4b_2a_1a_2(\Gamma - 1 - b_2)}}{2(\Gamma - 1 - b_2)},$$

where $\Gamma = c_2m_2\delta_1/(c_1m_1\delta_2) > 1$, $b_2 = \Gamma l_2/m_2$, $A = a_1\Gamma - a_2 - b_2(a_1 + a_2)$. Note that $x_+^{II} = x_-^{II} = x_+^I$ when $l_2 = 0$. The feasibility and stability conditions are summarized in table 2.

If $l_2 = 0$ holds, the first feasibility condition (i) of an interior equilibrium given in table 2 is reduced to the one given in table 1. Note that under $\Gamma > 1$ and $l_2 = 0$, $x_{\pm}^{II} > 0$ implies $-(a_1\Gamma - a_2) \pm |a_1\Gamma - a_2| > 0$. This inequality holds if and only if $a_1\Gamma - a_2 < 0$. Hence we have $a_2/a_1 > \Gamma > 1$. Note that condition (ii) is impossible when $l_2 = 0$, since we assumed $\Gamma > 1$.

Table 2. The feasibility and stability conditions for (1) with Type II. Here $B_{\pm} = a_1 - ((a_1 + a_2)x_{\pm}^{II} + 2a_1a_2)l_2/x_{\pm}^{II}m_2$, $b_2 = \Gamma l_2/m_2$, $H(x) = (\Gamma - 1 - b_2)x^2 + Ax - b_2a_1a_2$.

Equilibrium point	Feasibility conditions	Stability conditions
E_1^{II}	$(m_2 - l_2)\hat{x}_1^{II} > a_2l_2$	$H(\hat{x}_1^{II}) < 0$
	$(m_2 - l_2)\hat{x}_1^{II} \leq a_2l_2$	always
E_2^{II}	$(m_2 - l_2)\hat{x}_2^{II} > a_2l_2$	$H(\hat{x}_2^{II}) > 0$
$E_{b\pm}^{II}$	(i) $\Gamma > 1 + b_2$, $(m_2 - l_2)x_{\pm}^{II} > a_2l_2$ $\hat{x}_1^{II} \geq x_{+}^{II} \geq \hat{x}_2^{II}$	$\alpha_2(x_{\pm}^{II}) - \alpha_1(x_{\pm}^{II}) \geq 0$ $B_{\pm}\Gamma - a_2 \leq 0$ $\frac{c_1\alpha_1(x_{\pm}^{II})}{\delta_1c_2\alpha_2(x_{\pm}^{II})} > 1 > \frac{\delta_1\alpha_2(x_{\pm}^{II})}{\alpha_2(x_{\pm}^{II}) - l_2}$
	or	
	(ii) $\Gamma < 1 + b_2$, $(m_2 - l_2)x_{\pm}^{II} > a_2l_2$ $A^2 + 4\frac{l_2\Gamma}{m_2}a_1a_2\left(\Gamma - \Gamma\frac{l_2}{m_2} - 1\right) > 0$ $A > 0$, $\hat{x}_1^{II} \geq x_{\pm}^{II} \geq \hat{x}_2^{II}$ $(m_2 - l_2)x_{+}^{II} \leq a_2l_2$	unstable

Note from Lemma 3 that x_{+}^{II} is a positive solution of

$$H(x) = (\Gamma - 1 - b_2)x^2 + Ax - b_2a_1a_2 = 0$$

satisfying $\alpha_2(x) > l_2$. It is easy to check that such a solution exists if (i) $\Gamma > 1 + b_2$, $H(\bar{x}) < 0$, where \bar{x} is a solution to $\alpha_2(\bar{x}) = l_2$ (i.e. $\bar{x} = a_2l_2/(m_2 - l_2)$). Also two solutions x_{\pm}^{II} exist if (ii) $\Gamma < 1 + b_2$, $A > 0$, $A^2 + 4(\Gamma - 1 - b_2)b_2a_1a_2 > 0$, $H(\bar{x}) < 0$, $\bar{x} < A/2(1 + b_2 - \Gamma)$.

To ensure that $P_i^{II} > 0$ ($i = 1, 2$), we need

$$\hat{x}_1^{II} \leq x_{\pm}^{II} \leq \hat{x}_2^{II}$$

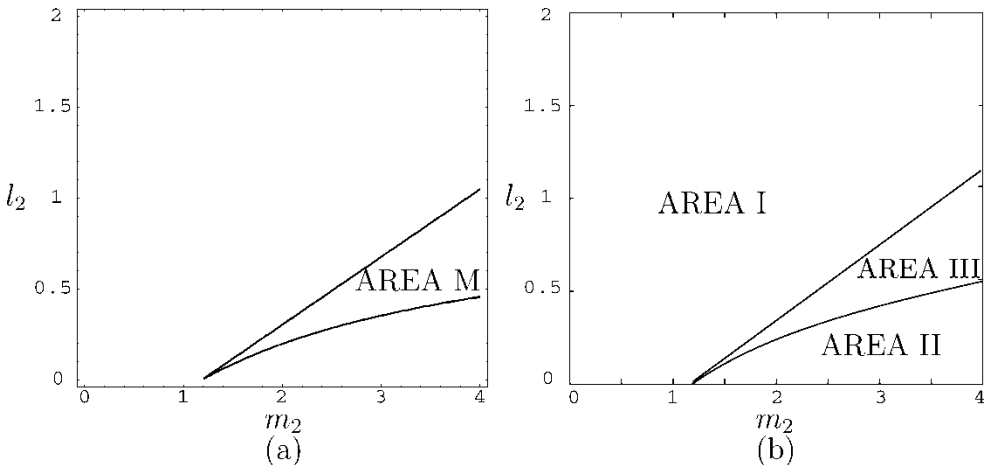


Figure 5. The (m_2, l_2) plane for system (1) with Type II plant 2 ($n = 2$). (a) The AREA M shows the its shape mutually invisable state. Furthermore, an interior equilibrium exists and is stable there. (b) This graph shows the dynamical property of (1) during $t \in [19.9 \times 10^3, 20 \times 10^3]$. In AREA I (resp. AREA II), only species 1 (resp. species 2) survives. In AREA III, two species coexist without a sustained oscillation. The parameters are $m_2 \in [0, 4.8]$, $l_2 \in [0, 2]$, $\delta_1 = \delta_2 = 0.12$, $m_1 = 0.6$, $a_1 = 1$, $a_2 = 4.7$, $l_1 = 0$, $q = 0.8$, $s = 1$, $c_1 = c_2 = 2.0$. The initial condition for (b) is $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$.

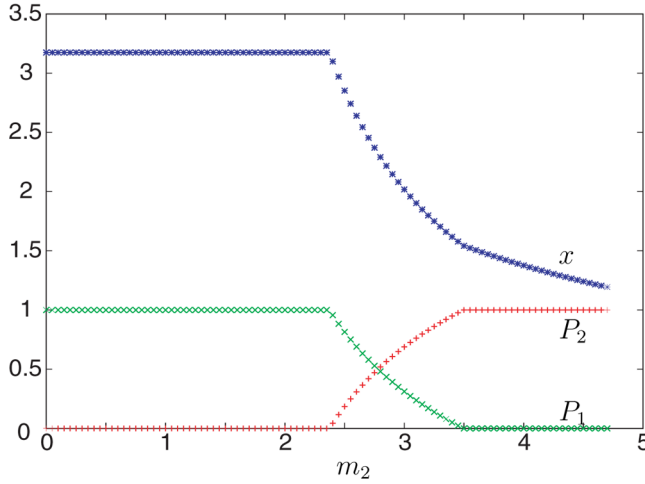


Figure 6. The bifurcation diagram for system (1) with Type II species 2 ($n = 2$). This graph plots eventual points with respect to m_2 during $t \in [19.9 \times 10^3, 20 \times 10^3]$ for the solution. The same parameters are taken as figure 5 except for $l_2 = 0.5$. The initial condition is $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$.

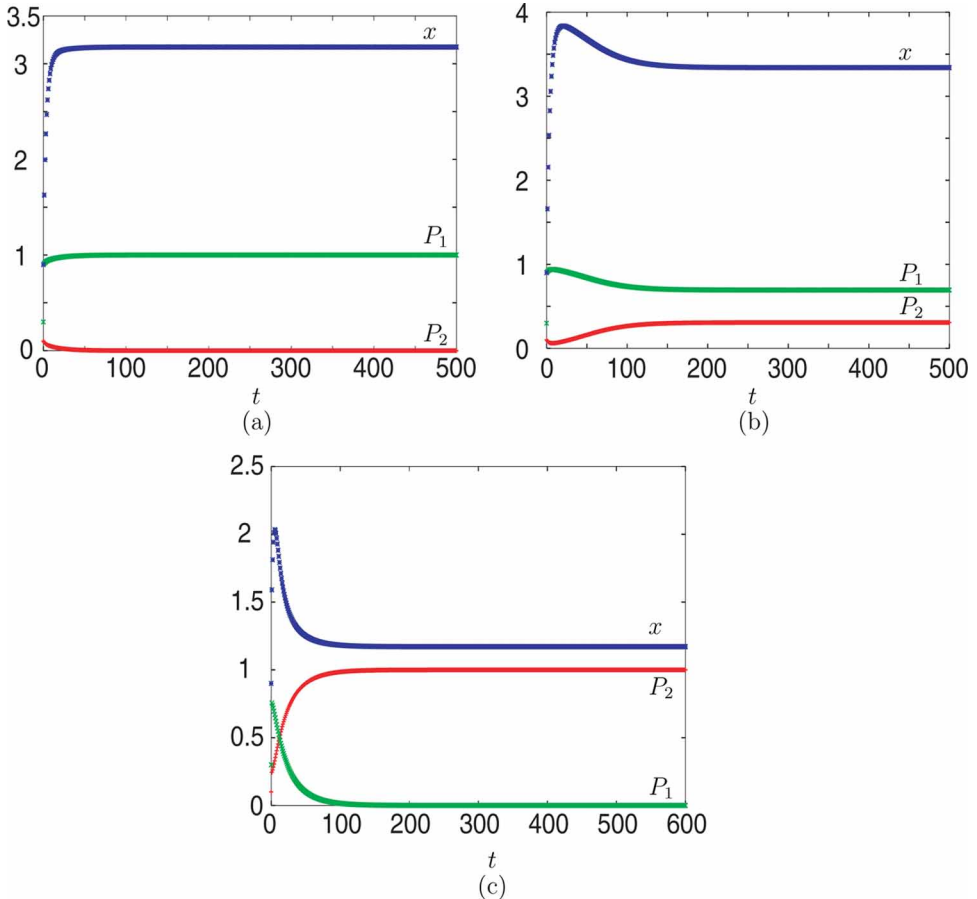


Figure 7. The temporal sequence of P_1 , P_2 and x for system (1) with Type II plant 2 ($n = 2$). The initial condition is $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$. The parameter values are the same as figure 6 except for (a) $m_2 = 1.9$, (b) $m_2 = 2.9$, (c) $m_2 = 4.8$.

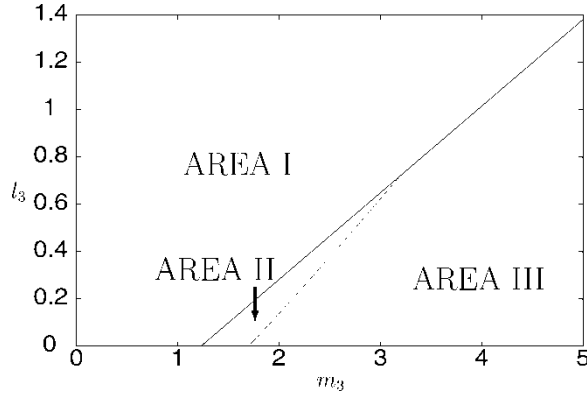


Figure 8. The (m_3, l_3) parameter plane for system (1) with Type II plants 2 and 3 ($n = 3$). In AREA I species 1 and 2 coexist. In AREA II species 1 and 3 coexist. In AREA III, only species 3 survives. The parameters are $m_3 \in [0, 5]$, $l_3 \in [0, 1.4]$, $m_1 = 0.6$, $m_2 = 1.5$, $a_1 = 1$, $a_2 = 4.7$, $a_3 = 5$, $l_1 = 0$, $l_2 = 0.7$, $\delta_1 = \delta_2 = \delta_3 = 0.12$, $c_1 = c_2 = c_3 = 2$, $q = 0.8$, $s = 1$. The initial condition is $(P_1(0), P_2(0), P_3(0), x(0)) = (0.3, 0.4, 0.2, 0.9)$.

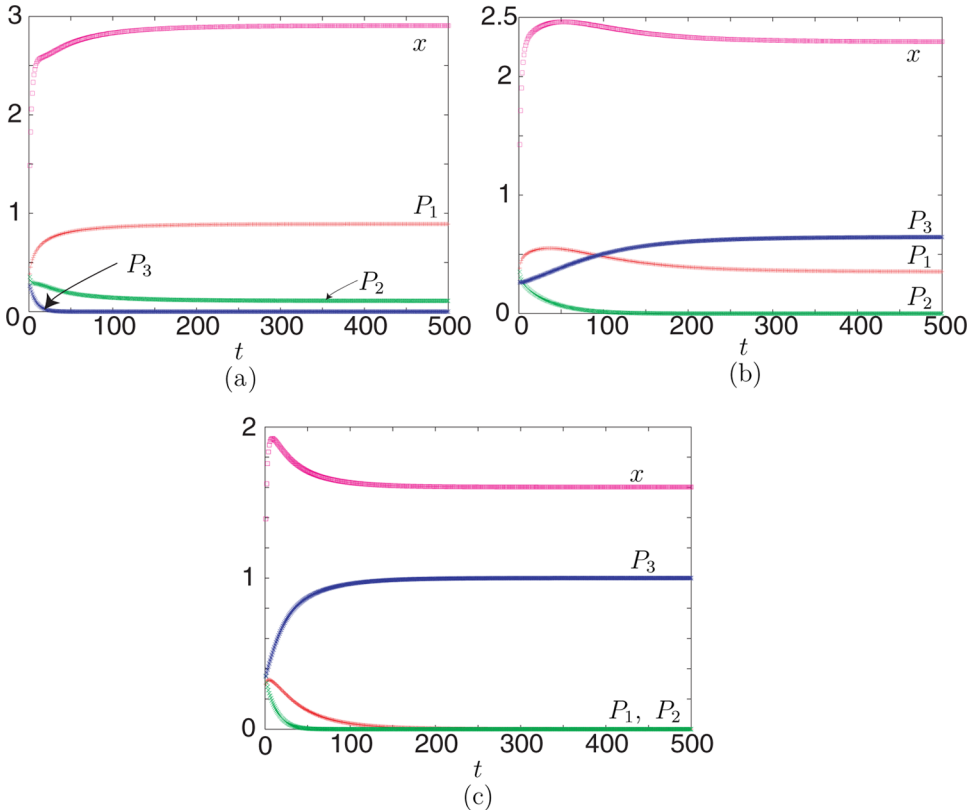


Figure 9. The temporal sequence of P_1, P_2, P_3 and x for system (1) with Type II species 2 and 3 ($n = 3$). The initial condition is $(P_1(0), P_2(0), P_3(0), x(0)) = (0.3, 0.4, 0.2, 0.9)$. The parameter values are the same as figure 8 except for (a) $(m_3, l_3) = (1, 0.4)$:AREA I, (b) $(m_3, l_3) = (2.6, 0.4)$:AREA II, (c) $(m_3, l_3) = (3.5, 0.4)$:AREA III.

for both cases. This gives the feasibility condition of interior equilibria in table 2. The stability conditions are shown in Appendix C.

Remark The stability conditions given in table 2 with $l_2 = 0$ correspond to those of table 1.

The simulation results for $n = 2$ (β_1 is Type I, β_2 is Type II) are given in figures 5–7. The simulation results for $n = 3$ (β_1 is Type I, β_2 and β_3 are Type II) are given in figures 8 and 9.

3.3 System with Type III species

We consider system (1) with Type III for species 2. This system has the same property on the stability as system (1) with Type I species, except for the feasibility conditions on the equilibrium points $E_1^{III}(1, 0, \hat{x}_1^{III})$, $E_2^{III}(0, 1, \hat{x}_2^{III})$ and $E_+^{III}(P_{1+}^{III}, P_{2+}^{III}, x_+^{III})$ (see table 3).

The simulation results for $n = 2$ (β_1 is Type I, β_2 is Type III) are given in figures 10–12 and for $n = 3$ (β_1 is Type I, β_2 and β_3 are Type III) are given in figures 14 and 15.

Table 3. The feasibility and stability conditions for (1) with Type III.

Equilibrium point	Feasibility conditions	Stability conditions
E_1^{III}	$(m_2 - l_2)\hat{x}_1^{III} > a_2l_2$ $(m_2 - l_2)\hat{x}_1^{III} \leq a_2l_2$	$\hat{x}_1^{III} < x_+^{III}$ always
E_2^{III}	$(m_2 - l_2)\hat{x}_2^{III} > a_2l_2$	$\hat{x}_2^{III} > x_+^{III}$
E_+^{III}	$(m_2 - l_2)x_+^{III} > a_2l_2$ $\frac{a_2}{a_1} > \Gamma > 1$ $\hat{x}_1^{III} \geq x_+^{III} \geq \hat{x}_2^{III}$ $(m_2 - l_2)x_+^{III} \leq a_2l_2$	$\hat{x}_1^{III} > x_+^{III} > \hat{x}_2^{III}$ unstable

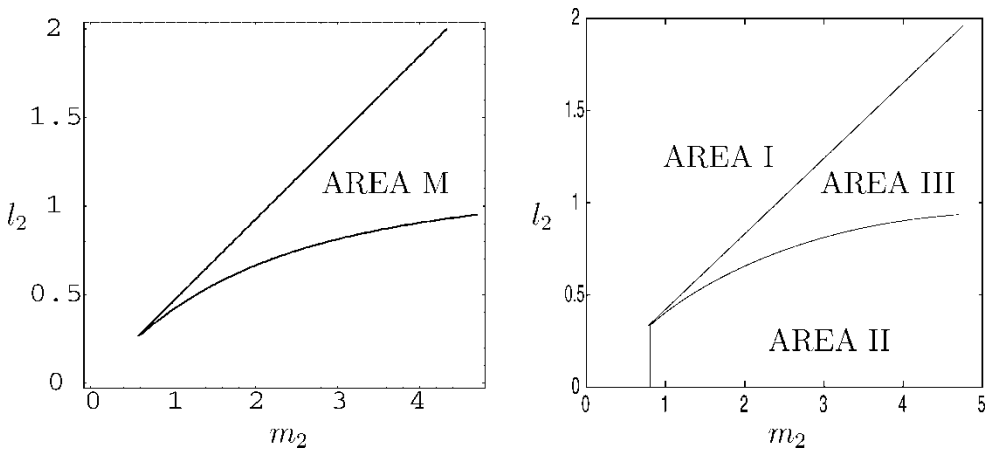


Figure 10. The (m_2, l_2) parameter plane for system (1) with Type III species 2 ($n = 2$). (a) The AREA M shows the region where E_+^{III} exists and is unstable ($\alpha_2(\hat{x}_1^{III}) > l_2$). (b) In AREA I, only species 1 survives. In AREA II, only species 2 survives. In AREA III, species 1 and 2 coexist with a sustained oscillation. The parameters are $m_2 \in [0, 4.7]$, $l_2 \in [0, 2.0]$, $\delta_1 = \delta_2 = 0.12$, $m_1 = 0.6$, $a_1 = 1$, $a_2 = 4.7$, $l_1 = 0$, $q = 0.8$, $s = 1$, $c_1 = c_2 = 2.0$. The initial condition for (b) is $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$.

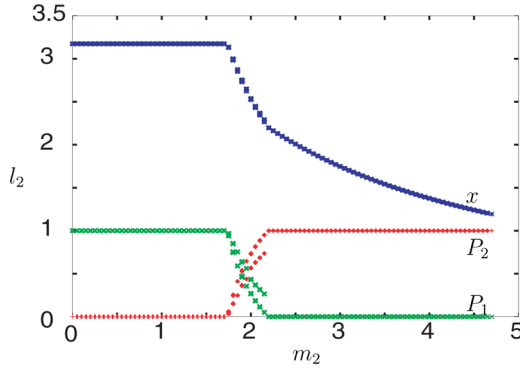


Figure 11. The bifurcation diagram for system (1) with Type III species 2 ($n = 2$). This graph plots eventual points with respect to m_2 during $t \in [19.9 \times 10^3, 20 \times 10^3]$ for the solution of system (1). The parameters are the same as figure 10 except for $l_2 = 0.7$. The initial condition is $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$.

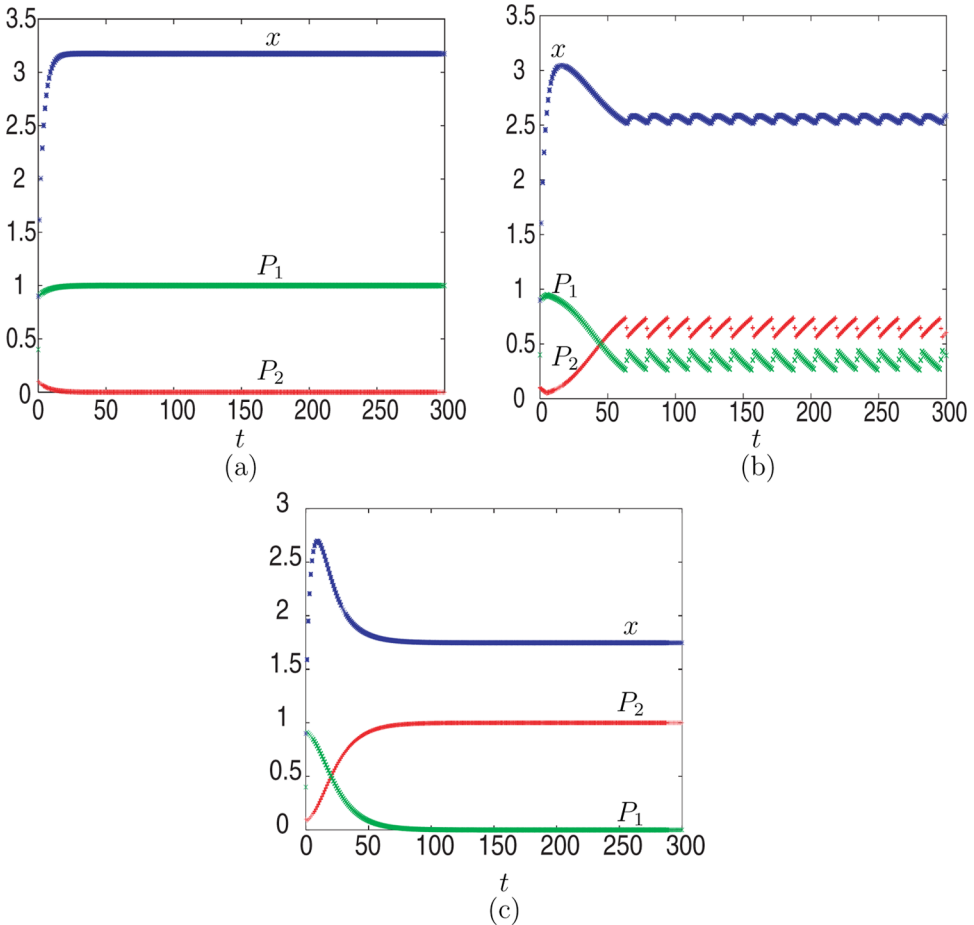


Figure 12. The temporal sequences of P_1 , P_2 and x for system (1) with Type III species 2 ($n = 2$). The initial condition is $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$. The parameters are the same as figure 11 except for (a) $m_2 = 1$, (b) $m_2 = 2$, (c) $m_2 = 3$.

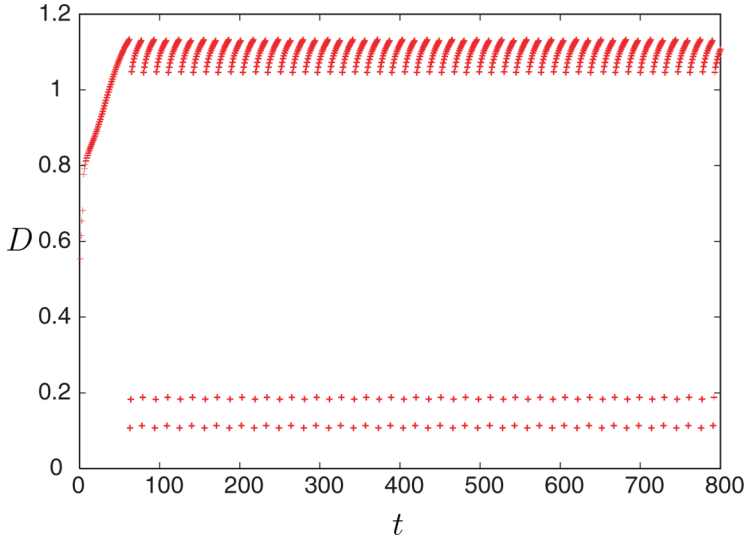


Figure 13. The temporal sequence of $D = \sum_{j=1}^2 \beta_j(\alpha_j(x))P_j - \{1 - \sum_{j=1}^2 (1 - \delta_j)P_j\}$ with initial condition $(P_1(0), P_2(0), x(0)) = (0.3, 0.1, 0.9)$ for system (1) with Type III species 2 ($n = 2$). The parameters are the same as figure 12(b).

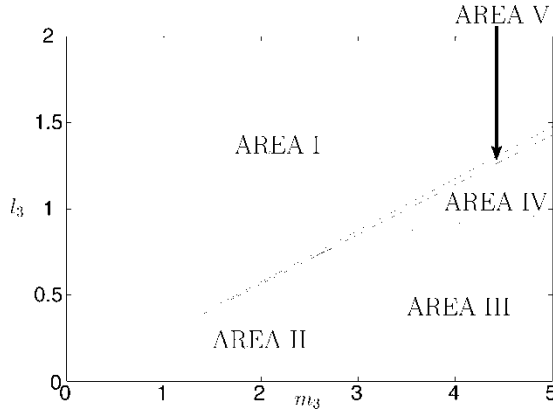


Figure 14. The (m_3, l_3) parameter plane for system (1) with Type III species 2 and 3 ($n = 3$). In AREA I, species 1 and 2 coexist with sustained oscillations. In AREA II, species 2 and 3 coexist with sustained oscillations. In AREA III, only species 3 survives. In AREA IV, species 1 and 3 coexist with sustained oscillations. In AREA V, three species coexist with sustained oscillations. The parameters are $m_3 \in [0, 5], l_3 \in [0, 2], m_1 = 0.6, m_2 = 3, a_1 = 1, a_2 = 4.7, a_3 = 5, l_1 = 0, l_2 = 0.9, \delta_1 = \delta_2 = \delta_3 = 0.12, c_1 = c_2 = c_3 = 2, q = 0.8, s = 1$. The initial condition is $(P_1(0), P_2(0), P_3(0), x(0)) = (0.3, 0.4, 0.2, 0.9)$.

4. Discussion

In this paper, we have investigated the effect of various types of functions β_i describing the utilization of nutrient for seed production by competing plant species. The differences among these functions dramatically change the population dynamics and the conditions for the species coexistence.

For all types of reproduction function β_i considered in this paper (Types I–III), we find that two species can coexist on a single limiting nutrient under certain conditions (see AREA III in

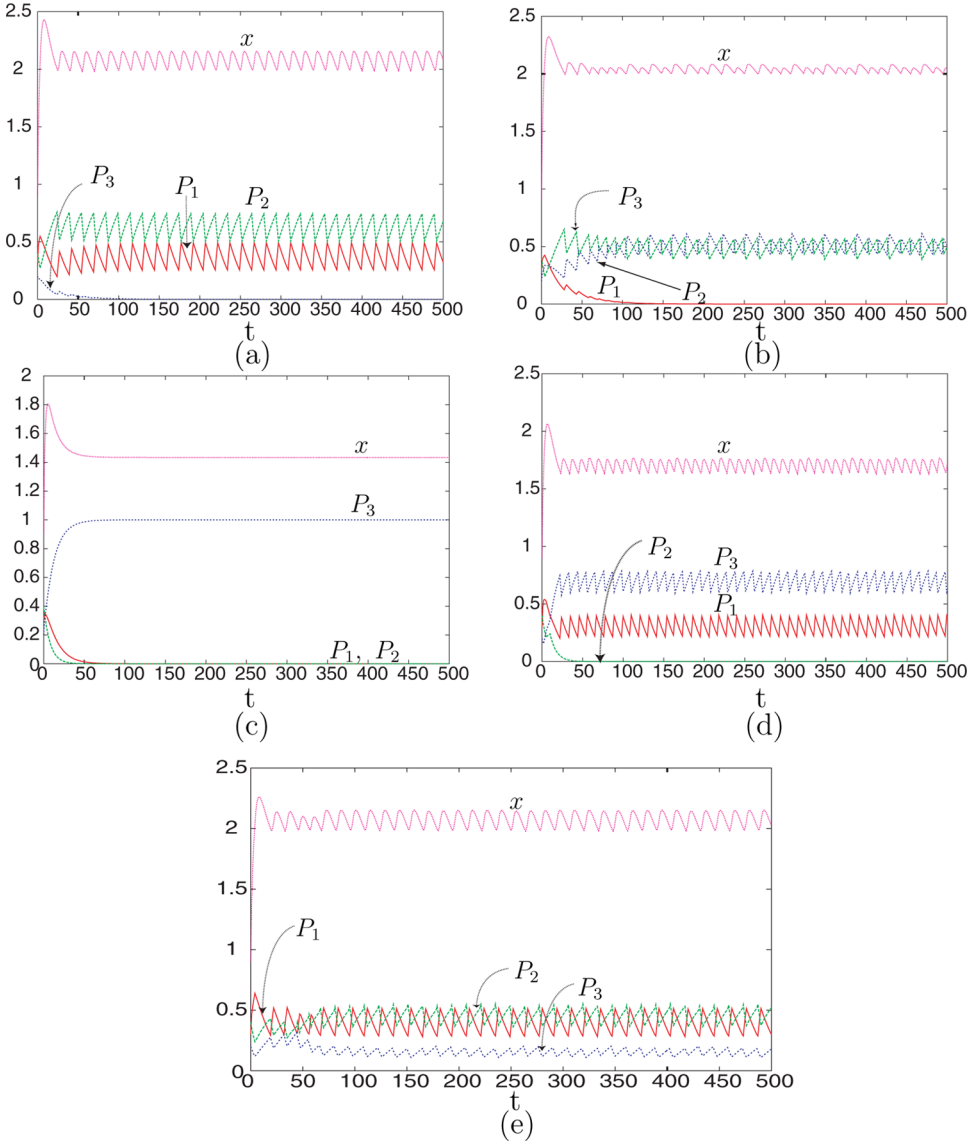


Figure 15. The temporal sequence of P_1 , P_2 , P_3 , and x for system (1) with Type III plants 2 and 3 ($n = 3$). The initial condition is $(P_1(0), P_2(0), P_3(0), x(0)) = (0.3, 0.4, 0.2, 0.9)$. (a)–(e) correspond to the AREA I–AREA V, respectively. The parameters are the same as figure 14 except for (a) $(m_3, l_3) = (1.0, 0.2)$, (b) $(m_3, l_3) = (2.0, 0.2)$, (c) $(m_3, l_3) = (4.0, 0.2)$, (d) $(m_3, l_3) = (4.0, 1.0)$, (e) $(m_3, l_3) = (3.47, 1)$. The time interval is $t \in [0, 500]$.

figures 2, 5 and 10). However, three or more species can not coexist at an interior equilibrium in general (see Lemma 3 and figures 4, 8 and 14). Two important results are the following.

(i) For the two-species model with Type I functions β_i , the parameter region of mutually invisable is identical with the region of coexistence. The numerical simulations in figure 5 suggest that this property also holds with Type II functions β_i . We find a large difference between the region of equilibrium coexistence for models with Type I and II functions β_i . As an example, for fixed $\delta_2 = 0.12$ in figure 2(b) we see that it is only for $m_2 \approx 1.1$ that the coexistence occurs for Type I functions β_i , while, on the other hand, for Type II functions β_i

we find in figure 5(b) that various values of m_2 ensure coexistence (for large l_2). In general the coexistence region for Type II function β_i is wider than that for Type I.

(ii) A remarkable difference between the models Type III functions β_i and those with Type I or II is the possibility for two or three species coexistence by means of the periodic oscillations. For models with Type I and Type II function β_i , numerical simulations suggest that there are no periodic solutions (see figures 2 and 5). Furthermore, three species cannot coexist in general (see figures 4 and 8). On the other hand, under certain circumstances a periodic coexistence solution can occur in the case of Type III functions β_i , as illustrated in figure 12(b) for the two-species case and figure 15(e) for the three-species case. The mechanism responsible for periodic coexistence seems to be the oscillation of the nutrient x between two regions $l_2 > \alpha_2(x)$ and $l_2 < \alpha_2(x)$. For example, in figure 12(b), where $a_2 = 4.7, m_2 = 2$ and $l_2 = 0.7$ and the value of x satisfying $\alpha_2(x) = l_2$ is $x = 2.53077$, we observe that x oscillates about $x = 2.53077$ in figure 12(b). A proof of observation remains an open mathematical problem.

In the lottery type models, it can happen under certain parameter conditions that seeds occupy vacant space even when there is an insufficient amount of seeds. However, this problem does not occur in this study since there are enough seeds to occupy any vacant space in the event of coexistence (see figures 13 and 16, where the difference between $\sum_{j=1}^n \beta_j(\alpha_j(x))$ and $1 - \sum_{j=1}^n (1 - \delta_j)P_j$ is always positive. We checked this only by numerical simulations and the problem remains to be **unsolved** mathematically).

It is well known that competitive exclusion holds for chemostat models, that is, only single species can survive under a single resource. Huisman and Weissing [13] showed that nine species can coexist under three kinds of resources in a state of sustained oscillations for the chemostat model. Our results show that two species can coexist at a stable equilibrium point under a single resource for a lottery model with limited nutrient availability. Further, three species can coexist in a periodic oscillation even under a single resource for the model with discontinuous nutrient utilization functions. Our conjecture is that four or more species can coexist under a single resource when the species adopt the discontinuous functions. Our results show that one needs to pay close attention to how plants utilize nutrients for seed production in order to understand the outcome of competition for a limited nutrient.

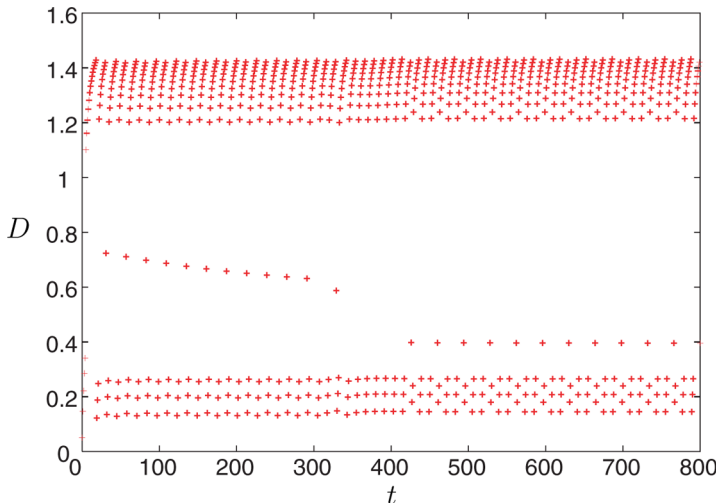


Figure 16. The temporal sequence of $D = \sum_{j=1}^3 \beta_j(\alpha_j(x))P_j - \{1 - \sum_{j=1}^3 (1 - \delta_j)P_j\}$ with initial condition $(P_1(0), P_2(0), P_3(0), x(0)) = (0.3, 0.4, 0.2, 0.9)$ for system (1) with Type III plants 2 and 3 ($n = 3$). The parameters are the same as figure 15(e). The time interval is $t \in [0, 800]$.

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Appendix A: The Jacobian matrix of system (1)

Consider system (1). Define F_i and F_x as follows:

$$\begin{aligned}
 F_i &= (1 - \delta_i) + \left\{ 1 - \sum_{j=1}^n (1 - \delta_j) P_j \right\} \frac{\beta_i(x)}{\sum_{j=1}^n \beta_j(x) P_j} \\
 &= \left\{ \beta_i(x) + \sum_{j=1}^n \{ (1 - \delta_i) \beta_j(x) - (1 - \delta_j) \beta_i(x) \} P_j \right\} \left(\sum_{j=1}^n \beta_j(x) P_j \right)^{-1} \\
 & \qquad \qquad \qquad i = 1, \dots, n,
 \end{aligned}$$

$$F_x = \left(x - \sum_{j=1}^n \alpha_j(x) P_j \right) q + s,$$

where $\beta_i(x) = \beta_i(\alpha_i(x))$ and we can rewrite (1) as $P_i(t+1) = F_i P_i$, $x(t+1) = F_x$. Now, the derivative of $F_i P_i$ with respect to P_k or x is given as follows:

$$\begin{aligned}
 \frac{\partial F_i P_i}{\partial P_k} &= F_i \Delta_{ik} + P_i \frac{\partial F_i}{\partial P_k} \\
 &= F_i \Delta_{ik} - R_i F_k
 \end{aligned}$$

where $R_i = \beta_i P_i / \sum_{j=1}^n \beta_j P_j$. In fact, we can check $P_i \partial F_i / \partial P_k = -R_i F_k$:

$$\begin{aligned} P_i \frac{\partial F_i}{\partial P_k} &= P_i \frac{\partial}{\partial P_k} \left\{ 1 - \sum_{j=1}^n (1 - \delta_j) P_j \right\} \frac{\beta_i(x)}{\sum_{j=1}^n \beta_j(x) P_j} \\ &= -\beta_i(x) P_i \frac{(1 - \delta_k) \sum_{j=1}^n \beta_j(x) P_j + (1 - \sum_{j=1}^n (1 - \delta_j) P_j) \beta_k(x)}{(\sum_{j=1}^n \beta_j(x) P_j)^2} \\ &= -\frac{\beta_i(x) P_i}{\sum_{j=1}^n \beta_j(x) P_j} \frac{\beta_k(x) + \sum_{j=1}^n ((1 - \delta_k) \beta_j(x) - (1 - \delta_j) \beta_k(x)) P_j}{\sum_{j=1}^n \beta_j(x) P_j} \\ &= -R_i F_k. \end{aligned}$$

Further,

$$\begin{aligned} \frac{\partial F_i P_i}{\partial x} &= \left\{ 1 - \sum_{j=1}^n (1 - \delta_j) P_j \right\} \frac{\partial}{\partial x} \frac{\beta_i(x) P_i}{\sum_{j=1}^n \beta_j(x) P_j} \\ &= \left\{ 1 - \sum_{j=1}^n (1 - \delta_j) P_j \right\} P_i \frac{\sum_{j=1}^n \left(\beta_j(x) \frac{d\beta_i(x)}{dx} - \frac{d\beta_j(x)}{dx} \beta_i(x) \right) P_j}{(\sum_{j=1}^n \beta_j(x) P_j)^2} \\ &= \frac{1 - \sum_{j=1}^n (1 - \delta_j) P_j}{\left\{ \sum_{j=1}^n \beta_j(x) P_j \right\}^2} \sum_{j=1}^n \left(\beta_j(x) \frac{d\beta_i(x)}{dx} - \beta_i(x) \frac{d\beta_j(x)}{dx} \right) P_i P_j, \\ \frac{\partial F_x}{\partial P_k} &= -\alpha_k(x) q, \\ \frac{\partial F_x}{\partial x} &= \left(1 - \sum_{j=1}^n \frac{d\alpha_j(x)}{dx} P_j \right) q. \end{aligned}$$

As a result, the Jacobian matrix is given as follows:

$$J = \begin{pmatrix} F_1(1 - R_1) & -R_1 F_2 & \cdots & -R_1 F_n & \frac{\partial F_1 P_1}{\partial x} \\ -R_2 F_1 & F_2(1 - R_2) & \cdots & -R_{n-1} F_n & \frac{\partial F_2 P_2}{\partial x} \\ \vdots & & \ddots & \vdots & \vdots \\ -R_n F_1 & \cdots & -R_n F_{n-1} & F_n(1 - R_n) & \frac{\partial F_n P_n}{\partial x} \\ -\alpha_1(x)q & -\alpha_2(x)q & \cdots & -\alpha_n(x)q & \left(1 - \sum_{j=1}^n \frac{d\alpha_j(x)}{dx} P_j \right) q \end{pmatrix}. \quad (5)$$

Appendix B: Proofs of Theorems 1 and 2

We have a characteristic equation of system (4) at the interior equilibrium as

$$0 = |J - zI|$$

$$= \begin{vmatrix} 1 - R_1 - z & -R_1 & \frac{\partial F_1 P_1}{\partial x} \\ -R_2 & 1 - R_2 - z & \frac{\partial F_2 P_2}{\partial x} \\ -\alpha_1(x)q & -\alpha_2(x)q & \left(1 - \sum_{j=1}^2 \frac{d\alpha_j(x)}{dx} P_j\right) q - z \end{vmatrix}_{P_1=P_{1+}^I, P_2=P_{2+}^I, x=x_+^I}. \quad (6)$$

From $\sum_{j=1}^2 (\partial F_j P_j / \partial x) = 0$, (6) can be rewritten as

$$(1 - R_1 - R_2 - z) \begin{vmatrix} 1 - z & \frac{\partial F_1 P_1}{\partial x} \\ \alpha_2(x)q - \alpha_1(x)q & \left(1 - \sum_{j=1}^2 \frac{\partial \alpha_j(x)}{\partial x} P_j\right) q - z \end{vmatrix}_{P_1=P_{1+}^I, P_2=P_{2+}^I, x=x_+^I} = 0.$$

Note that one eigenvalue is $z = 1 - R_1 - R_2 = 0$. From the Jury criteria, we know that the absolute values of all eigenvalues of 2×2 matrix K are less than one, if the following conditions hold:

$$\begin{aligned} 1 + \text{tr}(K) + \det(K) &> 0, \\ 1 - \text{tr}(K) + \det(K) &> 0, \\ \det(K) &< 1. \end{aligned}$$

Define K as follows:

$$K = \begin{pmatrix} 1 & \frac{\partial F_1 P_1}{\partial x} \\ (\alpha_2(x) - \alpha_1(x))q & \left(1 - \sum_{j=1}^2 \frac{d\alpha_j(x)}{dx} P_j\right) q \end{pmatrix}.$$

$\text{tr}(K)$, $\det(K)$ at the equilibrium point E_+^I are as follows:

$$\begin{aligned} \text{tr}(K)|_{P_1=P_{1+}^I, P_2=P_{2+}^I, x=x_+^I} &= 1 + \left(1 - \sum_{j=1}^2 \frac{d\alpha_j(x_+^I)}{dx} P_{j+}^I\right) q, \\ \det(K)|_{P_1=P_{1+}^I, P_2=P_{2+}^I, x=x_+^I} &= \left(1 - \sum_{j=1}^2 \frac{d\alpha_j(x_+^I)}{dx} P_{j+}^I - \frac{\partial F_1 P_1}{\partial x} (\alpha_2(x_+^I) - \alpha_1(x_+^I))\right) q. \end{aligned}$$

Then, $\text{tr}(K)$ is always positive. Note that $0 < d\alpha_j/dx < 1$ because of $m_j \leq a_j$. Hence $1 + \text{tr}(K) + \det K > 0$ if $1 - \text{tr}(K) + \det(K) > 0$. So, we need to consider the signs of $1 - \text{tr}(K) + \det(K)$, $\det(K) - 1$. First we consider $1 - \text{tr}(K) + \det(K)$.

$$\begin{aligned} 1 - \text{tr}(K) + \det(K) &= -\frac{\partial F_1 P_1}{\partial x} (\alpha_2(x'_+) - \alpha_1(x'_+))q \\ &= -\frac{1 - \sum_{j=1}^2 (1 - \delta_j) P_{j+}^I}{\left\{ \sum_{j=1}^2 \beta_j(x'_+) P_{j+}^I \right\}^2} \left(\beta_2(x'_+) \frac{d\beta_1(x'_+)}{dx} - \beta_1(x'_+) \frac{d\beta_2(x'_+)}{dx} \right) \\ &\quad \times P_{1+}^I P_{2+}^I (\alpha_2(x'_+) - \alpha_1(x'_+))q \\ &= -\frac{P_{1+}^I P_{2+}^I}{\sum_{j=1}^2 \beta_j(x'_+) P_{j+}^I} \left(\delta_2 \frac{d\beta_1(x'_+)}{dx} - \delta_1 \frac{d\beta_2(x'_+)}{dx} \right) \\ &\quad \times (\alpha_2(x'_+) - \alpha_1(x'_+))q, \end{aligned}$$

where we used $\{1 - \sum_{j=1}^2 (1 - \delta_j) P_{j+}^I\} / \sum_{j=1}^2 \beta_j(\alpha_j(x'_+)) = \delta_1 / \beta_1(\alpha_1(x'_+)) = \delta_2 / \beta_2(\alpha_2(x'_+))$.

From the definition of x'_+ , we have,

$$\begin{aligned} \delta_2 \frac{\partial \beta_1(x)}{\partial x} - \delta_1 \frac{\partial \beta_2(x)}{\partial x} \leq 0 &\iff \delta_2 \frac{c_1 m_1 a_1}{(a_1 + x'_+)^2} \leq \delta_1 \frac{c_2 m_2 a_2}{(a_2 + x'_+)^2} \\ &\iff \frac{a_1}{(a_1 + x'_+)^2} \leq \Gamma \frac{a_2}{(a_2 + x'_+)^2} \\ &\iff \Gamma^2 a_1 \leq \Gamma a_2 \\ &\iff \Gamma \leq \frac{a_2}{a_1}, \end{aligned} \tag{7}$$

where $\Gamma = c_2 \delta_1 m_2 / c_1 \delta_2 m_1$. Since an interior equilibrium point exists, we have $a_2/a_1 > \Gamma > 1$. From them, $1 - \text{tr}(K) + \det(K) > 0$ holds if and only if $\alpha_2(x'_+) - \alpha_1(x'_+) > 0$. Note that $\alpha_2(x'_+) - \alpha_1(x'_+) > 0$ if $\hat{x}'_2 < x'_+ < \hat{x}'_1$ from Lemma 4. Hence $1 - \text{tr}(K) + \det(K) > 0$ if $\hat{x}'_2 < x'_+ < \hat{x}'_1$. Now we will check if $\det(K) < 1$ under the condition $\alpha_2(x'_+) - \alpha_1(x'_+) > 0$.

$$\begin{aligned} \det(K) &= \left(1 - \sum_{j=1}^2 \frac{\partial \alpha_j(x'_+)}{\partial x} P_{j+}^I - \frac{dF_1 P_1}{dx} (\alpha_2(x'_+) - \alpha_1(x'_+)) \right) q \\ &= \left(1 - \sum_{j=1}^2 \frac{d\alpha_j(x'_+)}{dx} P_{j+}^I - \frac{P_{1+}^I P_{2+}^I}{\sum_{j=1}^2 \beta_j(x'_+) P_{j+}^I} \right. \\ &\quad \left. \times \left(\delta_2 \frac{d\beta_1(x'_+)}{dx} - \delta_1 \frac{d\beta_2(x'_+)}{dx} \right) (\alpha_2(x'_+) - \alpha_1(x'_+)) \right). \end{aligned}$$

From the definition of the interior equilibrium, we have $(\alpha_2(x_+^I) - \alpha_1(x_+^I))P_{1+}^I = \alpha_2(x_+^I) - (s - (1 - q)x_+^I)/q$ and

$$\begin{aligned}
 \det(K) &= \left[1 - \sum_{j=1}^2 \frac{d\alpha_j(x_+^I)}{dx} P_{j+}^I - \frac{P_{1+}^I P_{2+}^I}{\sum_{j=1}^2 \beta_j(x_+^I) P_{j+}^I} \left(\delta_2 \frac{d\beta_1(x_+^I)}{dx} - \delta_1 \frac{d\beta_2(x_+^I)}{dx} \right) \right. \\
 &\quad \left. \times (\alpha_2(x_+^I) - \alpha_1(x_+^I)) \right] q \\
 &= \left[1 - \sum_{j=1}^2 \frac{d\alpha_j(x_+^I)}{dx} P_{j+}^I - \frac{P_{1+}^I P_{2+}^I}{\sum_{j=1}^2 \beta_j(x_+^I) P_{j+}^I} \left(\delta_2 c_1 \frac{d\alpha_1(x_+^I)}{dx} - \delta_1 c_2 \frac{d\alpha_2(x_+^I)}{dx} \right) \right. \\
 &\quad \left. \times (\alpha_2(x_+^I) - \alpha_1(x_+^I)) \right] q \\
 &= \left[1 - \frac{d\alpha_1(x_+^I)}{dx} \left\{ P_{1+}^I + \delta_2 c_1 (\alpha_2(x_+^I) - \alpha_1(x_+^I)) \frac{P_{1+}^I P_{2+}^I}{\sum_{j=1}^2 \beta_j(x_+^I) P_{j+}^I} \right\} \right. \\
 &\quad \left. - \frac{d\alpha_2(x_+^I)}{dx} \left\{ P_{2+}^I - \delta_1 c_2 (\alpha_2(x_+^I) - \alpha_1(x_+^I)) \frac{P_{1+}^I P_{2+}^I}{\sum_{j=1}^2 \beta_j(x_+^I) P_{j+}^I} \right\} \right] q \\
 &< \left[1 - \frac{d\alpha_1(x_+^I)}{dx} P_{1+}^I - \frac{d\alpha_2(x_+^I)}{dx} P_{2+}^I \left\{ 1 - \delta_1 \frac{c_2 \alpha_2(x_+^I)}{\sum_{j=1}^2 \beta_j(x_+^I) P_{j+}^I} \right\} \right] q. \quad (8)
 \end{aligned}$$

From (3), $\beta_1(x_+^I) > \delta_2 \beta_1(x_+^I) = \delta_1 \beta_2(x_+^I)$ holds. Then,

$$\begin{aligned}
 \sum_{j=1}^2 \beta_j(x_+^I) P_{j+}^I - \delta_1 c_2 \alpha_2(x_+^I) &= \sum_{j=1}^2 \beta_j(x_+^I) P_{j+}^I - \delta_1 \beta_2(x_+^I) \\
 &= \sum_{j=1}^2 \beta_j(x_+^I) P_{j+}^I - \delta_1 \beta_2(x_+^I) (P_{1+}^I + P_{2+}^I) \\
 &= (\beta_1(x_+^I) - \delta_1 \beta_2(x_+^I)) P_{1+}^I + (1 - \delta_1) \beta_2(x_+^I) P_{2+}^I > 0. \quad (9)
 \end{aligned}$$

Therefore, (8) and (9) imply that $\det(K) < 1$. Consequently, we showed that if there exists an interior equilibrium of system (4) and $1 < \Gamma < a_2/a_1$ and $\alpha_2(x_+^I) > \alpha_1(x_+^I)$ hold, it is stable. This conclusion on an interior equilibrium can be applied for the system with Type III species under the assumption that $\alpha_2(x_+^{III}) > l_2$.

From table 1, both the boundary equilibria E_{I1} and E_{I2} are stable (bistable state) if and only if $(\Gamma - 1)\hat{x}_1^I < a_2 - \Gamma a_1$ and $(\Gamma - 1)\hat{x}_2^I > a_2 - \Gamma a_1$. From the definition of boundary and interior equilibria, we have a bistable state if and only if $\alpha_2(x_+^I) - \alpha_1(x_+^I) < 0$ holds. In fact, if we have a bistable state, then

$$\begin{aligned}
 (\Gamma - 1)\hat{x}_1^I &< a_2 - \Gamma a_1 \\
 \hat{x}_1^I &< x_+^I
 \end{aligned}$$

$$s - (1 - q)x_+^I < s - (1 - q)\hat{x}_1^I = \frac{m_1\hat{x}_1^I q}{a_1 + \hat{x}_1^I}$$

$$s - (1 - q)x_+^I < \frac{m_1\hat{x}_1^I q}{a_1 + \hat{x}_1^I} < \frac{m_1x_+^I q}{a_1 + x_+^I} = \alpha_1(x_+^I)q.$$

Similarly, we find the following:

$$s - (1 - q)x_+^I > \frac{m_2x_+^I q}{a_2 + x_+^I} = \alpha_2(x_+^I)q.$$

This shows that $\alpha_2(x_+^I) - \alpha_1(x_+^I) < 0$ and $1 - \text{tr}(K) + \det(K) < 0$ if we have a bistable case. Hence, an interior equilibrium is unstable for bistable case.

Appendix C: The stability of interior fixed point of (1) with Type II

We need to check if $1 - \text{tr}(K) + \det(K) > 0$ and $\det(K) < 1$, where K is given by

$$K = \begin{pmatrix} 1 & \frac{\partial F_1 P_1}{\partial x} \\ (\alpha_2(x) - \alpha_1(x))q & \left(1 - \sum_{j=1}^2 \frac{d\alpha_j(x)}{dx} P_j\right)q \end{pmatrix}.$$

$$1 - \text{tr}(K) + \det(K) = -\frac{dF_1 P_1}{dx} (\alpha_2(x_+^{II}) - \alpha_1(x_+^{II}))q$$

$$= -\frac{P_{1+}^{II} P_{2+}^{II}}{\sum_{j=1}^2 \beta_j(x_+^{II}) P_{j+}^{II}} \left(\delta_2 \frac{d\beta_1(x_+^{II})}{dx} - \delta_1 \frac{d\beta_2(x_+^{II})}{dx} \right)$$

$$\times (\alpha_2(x_+^{II}) - \alpha_1(x_+^{II}))q.$$

From the definition of the interior equilibrium, we have

$$\delta_2 \beta_1(x_+^{II}) = \delta_1 \beta_2(x_+^{II})$$

$$\delta_2 c_1 \frac{m_1 x_+^{II}}{a_1 + x_+^{II}} = \delta_1 c_2 \left(\frac{m_2 x_+^{II}}{a_2 + x_+^{II}} - l_2 \right)$$

$$\frac{x_+^{II}}{a_1 + x_+^{II}} = \frac{\Gamma x_+^{II}}{a_2 + x_+^{II}} + C,$$

where $C = -\Gamma l_2 / m_2$.

$$\delta_2 \frac{d\beta_1(x_+^{II})}{dx} - \delta_1 \frac{d\beta_2(x_+^{II})}{dx} \leq 0 \iff \delta_2 \frac{c_1 m_1 a_1}{(a_1 + x_+^{II})^2} \leq \delta_1 \frac{c_2 m_2 a_2}{(a_2 + x_+^{II})^2}$$

$$\iff \frac{a_1}{(a_1 + x_+^{II})^2} \leq \Gamma \frac{a_2}{(a_2 + x_+^{II})^2}$$

$$\begin{aligned}
&\Leftrightarrow \frac{a_1}{a_1 + x_+^{II}} \left(\frac{\Gamma}{a_2 + x_+^{II}} + \frac{C}{x_+^{II}} \right) \\
&\leq \frac{a_2}{a_2 + x_+^{II}} \left(\frac{1}{a_1 + x_+^{II}} - \frac{C}{x_+^{II}} \right) \\
&\Leftrightarrow a_1(\Gamma x_+^{II} + C(a_2 + x_+^{II})) \leq a_2(x_+^{II} - C(a_1 + x_+^{II})) \\
&\Leftrightarrow a_1\Gamma - a_2 \leq -((a_1 + a_2)x_+^{II} + 2a_1a_2) \frac{C}{x_+^{II}}. \quad (10)
\end{aligned}$$

This gives the first two conditions in table 2 for the stability of E_+^{II} . Similar to Appendix B, $\det(K)$ satisfies

$$\det(K) < \left[1 - \frac{d\alpha_1(x_+^{II})}{dx} P_{1+}^{II} - \frac{d\alpha_2(x_+^{II})}{dx} P_{2+}^{II} \left\{ 1 - \delta_1 \frac{c_2\alpha_2(x_+^{II})}{\sum_{j=1}^2 \beta_j(x_+^{II}) P_{j+}^{II}} \right\} \right] q.$$

Then,

$$\begin{aligned}
\sum_{j=1}^2 \beta_j(x_+^{II}) P_{j+}^{II} - \delta_1 c_2 \alpha_2(x_+^{II}) &= \{c_1 \alpha_1(x_+^{II}) - \delta_1 c_2 \alpha_2(x_+^{II})\} P_{1+}^{II} \\
&\quad + c_2 \{\alpha_2(x_+^{II}) - l_2 - \delta_1 \alpha_2(x_+^{II})\} P_{2+}^{II}. \quad (11)
\end{aligned}$$

From equation (11), $\det(K) < 1$ if $c_1 \alpha_1(x_+^{II}) / (\delta_1 c_2 \alpha_2(x_+^{II})) > 1$ and $\delta_1 \alpha_2(x_+^{II}) / (\alpha_2(x_+^{II}) - l_2) < 1$, which gives the last condition in table 2.