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The Periodical Population Dynamics of Lottery Models Including the Effect of Undeveloped Seeds

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Summary. The mechanism that promotes coexistence of species has not been completely clarified yet. We propose that the amount of nutrient can be one of the factors that promote coexistence of species. Plant species have to reproduce seeds to produce descendants. Even if plant species do reproduce seeds, it is not ensured that every seed will bud. The amount of seeds that can bud successfully depends on the amount of nutrient: if the nutrient is scarce, then every seed cannot bud, but if the nutrient is rich, then every seed can bud. We also assume that the amount of seeds reproduced by one plant individual depends on the amount of nutrient. We show that, in this situation, the population dynamics of plants exhibits a complex behavior, which promotes coexistence of species.

Key words: Space, nutrient, reproduction function, effective availability, undeveloped seed.

11.1 Introduction

Based on the lottery model proposed by Chesson and Warner [1,2], we consider the effect of undeveloped seeds on the population dynamics. Most plant species are influenced by an abiotic or biotic environment in the reproduction phase (Lambers [8]). The amount of nutrient may be insufficient for plants to grow their sprouts or seedlings. We consider the situation where plants reproduce both undeveloped and developed seeds depending on the amount of nutrient.

The standard lottery model (Chesson and Warner [1],Chesson [2]) is given by the following nonautonomous difference equation:

$$\begin{aligned} P_i(t+1) &= (1-\delta_i(t))P_i(t) \\ &\quad + S(P_1(t), \dots, P_n(t)) \frac{\beta_i(t)P_i(t)}{\sum_{j=1}^{n} \beta_j(t)P_j(t)}, \quad i = 1, \dots, n, \end{aligned} \tag{11.1}$$

where $S(P_1(t), \dots, P_n(t)) = 1 - \sum_{j=1}^{n}(1-\delta_j(t))P_j(t)$. The vital coefficients $\beta_i(t)$ and $\delta_i(t)$ depend on time t, so the equation (11.1) is a nonautonomous system. The initial condition satisfies $P_i(0) \geq 0$, $i = 1, \ldots, n$, and $\sum_{j=1}^{n} P_j(0) = 1$. The variable $P_i(t)$ denotes the occupation rate of space by plant species i at year t. There are n plant species in a single habitat. Every year, each plant species i reproduces the developed seeds, the amount of which is given by $\beta_i(t)P_i(t)$. Additionally, every year adult plants are removed at the rate $\delta_i(t)$, and this removal creates the vacant space $S(P_1(t), \ldots, P_n(t)) = 1 - \sum_{j=1}^{n}(1 - \delta_j(t))P_j(t)$, which is immediately occupied by the individuals randomly chosen from the pool of the developed seeds. In model (11.1), it is implicitly assumed that nutrients are always sufficiently available for all plant species. The studies of Chesson and Warner [1] 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. Therefore, we see that the temporal heterogeneity promotes coexistence in the lottery model.

Following these seminal papers, the effects of temporal fluctuations in the recruitment process have been analyzed intensively (e.g., see Hatfield and Scheibling [6], Chesson and Huntly [3]). The lottery model also provides a basis for understanding the coexistence of multiple species in terrestrial systems (Laurie et al. [9]). Additionally, Dewi and Chesson [5] studied a lottery model with a stage structure and Comins and Noble [4] studied a lottery model with different patches. The recent works of Muko and Iwasa [10,11] considered the other mechanism which promotes coexistence. They incorporated the spatial heterogeneity into the standard lottery model (11.1). Their model includes multiple habitats, each of which has different mortality and natality rates of the species. Their study shows that the heterogeneity of mortality rates promotes coexistence of species, but natality rates does not (Muko and Iwasa [10]). By these two studies, we see that the spatial heterogeneity promotes coexistence in a lottery model.

Besides a lottery model, Neuhauser and Pacala [12] studied a Lotka–Volterra equation with explicit spatial factors. By using a chemostat model, Huisman and Weissing [7] showed that nine species can coexist under three kinds of resources.

This paper is organized as follows. In Section 11.2, we derive a new lottery model, which incorporates the effect of undeveloped seeds, and show some basic properties of the model. In Section 11.3, we show the results of simulations for two or three species cases. The final section includes our discussion.

11.2 Model

Our model is the following autonomous difference equation:

$$\begin{cases} P_i(t+1) = (1-\delta_i)P_i(t) \\ \qquad\qquad + S(P_1(t), \ldots, P_n(t)) \dfrac{\beta_i(x(t))P_i(t)}{\sum_{j=1}^{n} \beta_j(x(t))P_j(t)} \qquad i = 1, \ldots, n, \\ x(t+1) = (x(t) - \sum_{j=1}^{n} \alpha_j(x(t))P_j(t))q + s, \end{cases} \tag{11.2}$$

where $S(P_1, \dots, P_n) = 1 - \sum_{j=1}^{n}(1-\delta_j)P_j$. The parameters δ_i $(0 \le \delta_i \le 1)$ and the variables $P_i(t)$ have the same meaning as those in model (11.1). Let us first consider the second equation in (11.2). The function $\alpha_i(x)$ is the amount of nutrient consumed through the space occupied by plant species i:

$$\alpha_i(x) = \frac{m_i x}{a_i + x}, \tag{11.3}$$

where x is the amount of a limiting nutrient contained in a unit area of the habitat, m_i is the maximum number of seeds reproduced from the space occupied by an individual of plant species i, and a_i is the Michaelis–Menten (or half-saturation) constant. Since plant species can uptake only the nutrient in soil, $x(t) - \sum_{j=1}^{n} \alpha_j(x(t)) > 0$ must hold for $t > 0$. This is ensured if $m_i/a_i \le 1$. The parameter $s (s > 0)$ denotes a constant inflow and q $(0 < q < 1)$ denotes washout rate. The total amount of the nutrient consumed through the space occupied by the plants is given as follows:

$$\sum_{j=1}^{n} \alpha_j(x)P_j.$$

The function $\beta_i(x)$ is the number of the developed seeds reproduced from the space occupied by plant species i. In this chapter, we assume

$$\beta_i(x) = \begin{cases} c_i \rho_i \alpha_i(x) & (l_i \le x) \\ 0 & (0 < x < l_i), \end{cases}$$

where $c_i > 0$ denotes the conversion rate from nutrient to the number of seeds of species i. $\rho_i > 0$ denotes the rate of nutrient used to produce seeds of plant species i. $l_i \ge 0$ is a positive constant. We assume $l_n = 0$. This assumption shows that species n does not reproduce any undeveloped seeds. Under the condition $0 < x < l_i$ any seeds of species $i \ne n$ cannot bud. This means that if the nutrient is scarce (i.e., $0 < x < l_i$), then any seeds are not able to bud. Therefore, if the nutrient in the soil is scarce, species $i \ne n$ reproduces only undeveloped seeds. All parameters $(\delta_i, m_i, a_i, c_i, \rho_i, l_i, q, s)$ in (11.2) are constant. Therefore, (11.2) is an autonomous system.

11.2.1 The Basic Properties of Model (11.2)

We define $\Omega := \{(P_1, \dots, P_n, x) \in \mathbf{R}^{n+1} \mid P_1 \ge 0, \dots, P_n \ge 0, \sum_{j=1}^{n} P_j = 1, x > 0\}$. Then we can show that Ω is forward invariant.

Proposition 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* $t \ge 0$.

Proof Let $(P_1(t), \dots, P_n(t), x(t)) \in \Omega$. Then it follows from (11.2) that

$$\sum_{j=1}^{n} P_j(t+1) = 1.$$

Since $\beta_i(x)$ and $S(P_1, P_2, \ldots, P_n)$ are nonnegative, $P_i(t+1) \geq 0$ holds for all $i = 1, 2, \ldots, n$. Finally, we prove $x(t+1) \geq 0$. In fact, $\max_{x \geq 0}(m_i/(a_i + x)) = m_i/a_i$, and we have the following inequalities:

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

This completes the proof. □

From the second equation of (11.2), $x(t+1) \leq x(t)q + s$ is satisfied for all $t \geq 0$. This implies that $x(t) \leq 2s/(1-q)$ for sufficiently large $t > 0$. Hence by combining with Proposition 1, we have the following proposition.

Proposition 2 *Every solution of system (11.2) with the initial condition* $(P_1(0), \ldots, P_n(0), x(0)) \in \Omega$ *is bounded.*

Proof From Proposition 1, if $(P_1(0), \ldots, P_n(0), x(0)) \in \Omega$, then $(P_1(t), \ldots, P_n(t), x(t)) \in \Omega$ for all $t \geq 0$. So, we consider the boundedness of x. If $(P_1(t), \ldots, P_n(t), x(t)) \in \Omega$, then $(x(t) - \sum_{j=1}^{n} \alpha_j(x(t))P_j(t))q + s < qx(t) + s$ 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. This completes the proof. □

These propositions imply that the occupation rate P_i always satisfies $0 \leq P_i \leq 1$ and the amount of nutrient is always positive and is bounded above.

11.3 Simulations

In this section, we show the simulation results for the cases with two and three species.

11.3.1 The Case with Two Species ($n = 2$)

Fig. 11.1 is the result of the numerical simulations of system (11.2) with two species ($n = 2$). In Fig. 11.1, there are two types of area: in AREA I and AREA III, one species survives; in AREA II and AREA IV, two species coexist.

In AREA I (resp. AREA III), species 2 (resp. species 1) survives and species 1 (resp. species 2) is excluded (see Fig. 11.2 (a) and (c)). In AREA I and III, one of the boundary fixed points $E_2(P_1, P_2, x) = (0, 1, x_2)$ and $E_1(P_1, P_2, x) = (1, 0, x_1)$ is stable, respectively.

In AREA II, species can coexist (see Fig. 11.2 (b)) and there exists one positive fixed point to which all solutions of system (11.2) tend. In this situation, two boundary fixed points are unstable.

In AREA IV, species can coexist with sustained oscillations (see Fig. 11.2 (d)). In this area of parameters, x oscillates between the intervals $0 < x < l_1$ and $l_1 \leq x$. The solution tends to the boundary fixed point E_2 when x is located in the interval $0 < x < l_1$. The solution tends to E_1 when x is located in the interval $x \geq l_1$.

11.3.2 The Case with Three Species ($n = 3$)

In Fig. 11.3, we can find three types of area: in AREA I, II and IV, two species survive with sustained oscillations; in AREA III, one species survives; in AREA V, three species coexist with sustained oscillations.

In AREA I, species 2 and 3 can survive with sustained oscillations (see Fig. 11.4 (a)). In this region, species 1 cannot invade the $P_2 - P_3$ subsystem, since species 1 cannot reproduce a sufficient amount of developed seeds. Note that m_1 is small or l_1 is large in AREA I.

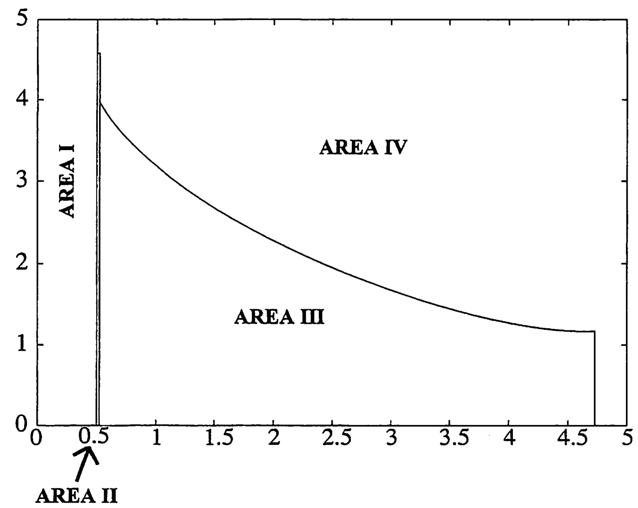

Fig. 11.1. The (m_1, l_1) parameter plane. In AREA I, only species 2 survives. In AREA II, two species coexist without oscillation. In AREA III, only species 1 survives. In AREA IV, species 1 and 2 coexist with a sustained oscillation. The parameters are $m_1 \in [0, 5]$, $l_1 \in [0, 4.7]$, $\delta_1 = \delta_2 = 0.12$, $m_2 = 0.3$, $a_1 = 4.7$, $a_2 = 1$, $l_2 = 0$, $q = 0.8$, $s = 1$, $\rho_1 = \rho_2 = 0.8$, $c_1 = c_2 = 2.5$. The initial condition is $(P_1(0), P_2(0), x(0)) = (0.3, 0.6, 0.9)$.

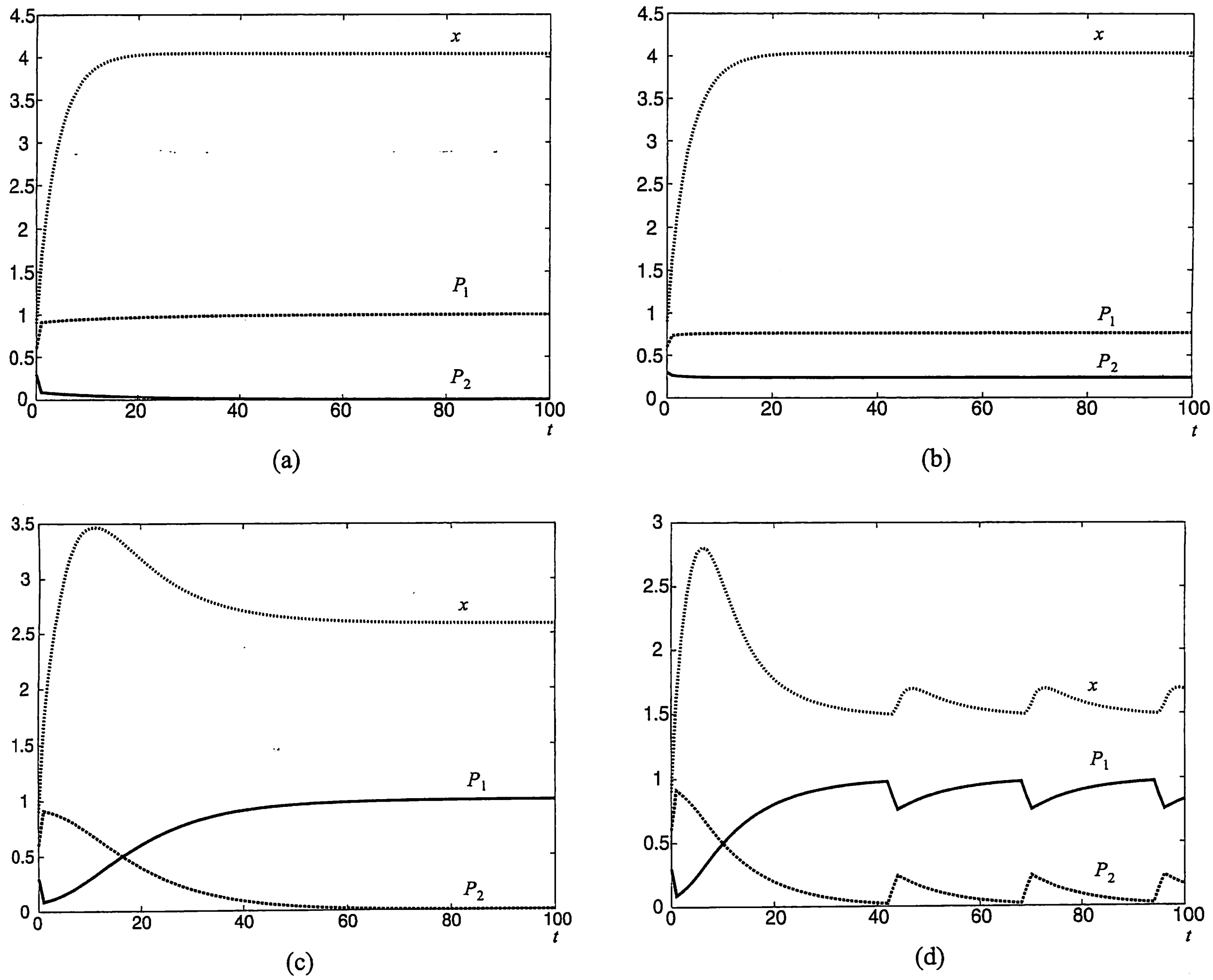

Fig. 11.2. The temporal sequence of P_1, P_2 and x with the initial condition $(P_1(0), P_2(0), x(0)) = (0.3, 0.6, 0.9)$. The parameters are $\delta_1 = \delta_2 = 0.12, m_2 = 0.3, a_1 = 4.7, a_2 = 1, l_1 = 1.5, l_2 = 0, q = 0.8, s = 1, \rho_1 = \rho_2 = 0.8, c_1 = c_2 = 2.5$, (a) $m_1 = 0.3$ (AREA I in Fig. 11.1), (b) $m_1 = 0.52$ (AREA II in Fig. 11.1), (c) $m_1 = 1.7$ (AREA III in Fig. 11.1), (d) $m_1 = 3.7$ (AREA IV in Fig. 11.1).

In AREA II, species 1 and 2 can survive (see Fig. 11.4 (b)). In this region, species 1 invades the $P_2 - P_3$ subsystem and eliminates species 3.

In AREA III, only species 1 survives (see Fig. 11.4 (c)). In this region, species 1 can reproduce a sufficient number of developed seeds. Note that m_1 is large and l_1 is small in AREA III and species 1 is the strongest there.

In AREA IV, species 1 and 3 can survive with sustained oscillations (see Fig. 11.4 (d)). In this region, species 1 can invade the $P_2 - P_3$ subsystem. After the invasion of species 1, species 2 is eliminated and species 3 survives. Note that $l_2 > l_3$ and $m_3 < m_2$ in AREA IV.

Finally, in AREA V, three species can survive with sustained oscillations (see Fig. 11.4 (e)). Although we need future investigations, we think that the temporal fluctuation of x plays a crucial role for the coexistence.

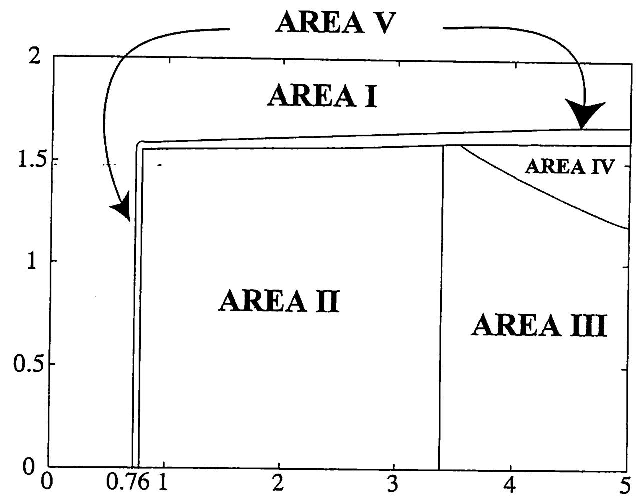

Fig. 11.3. The (m_1, l_1) parameter plane. In AREA I, species 2 and 3 coexist with sustained oscillations. In AREA II, species 1 and 2 coexist with sustained oscillations. In AREA III, only species 1 survives. In AREA IV, species 1 and 3 coexist with sustained oscillations. In AREA V, three species coexist with sustained oscillations. The parameters are $m_1 \in [0, 5], l_1 \in [0, 2]$, $m_2 = 3.2, m_3 = 0.3, a_1 = 5, a_2 = 4.7, a_3 = 1, l_2 = 1.6, l_3 = 0, \delta_1 = \delta_2 = \delta_3 = 0.12$, $\rho_1 = \rho_2 = \rho_3 = 0.8, c_1 = c_2 = c_3 = 2.5, q = 0.8, s = 1$. The initial condition is $(P_1(0), P_2(0), P_3(0), x(0)) = (0.2, 0.4, 0.3, 0.9)$.

11.4 Discussion

In this chapter, we have considered the effect of undeveloped seeds. In Section 11.2, we proposed model (11.2), which is based on the lottery model (11.1). We investigated model (11.2) to understand the effect of undeveloped seeds on population dynamics.

From the result of numerical simulations, we see that three species coexist in a wide range of the parameter space (see Fig. 11.3). For (11.2) with two species, in AREA II of Fig. 11.1, two species can coexist at an interior fixed point. On the other hand, in system (11.2) with three species, an interior fixed point does not exist. That is, even if three species coexist, there are no interior fixed points. For this case, it is shown that three species can coexist with a sustained oscillation (see AREA V of Fig. 11.3 and Fig. 11.4 (e)). It is known that the sustained oscillations do not exist in the lottery model (11.1) if all coefficients are constants. Furthermore, it is known that in the original lottery model, species coexist under the temporal fluctuation of vital coefficients. Our results show that the incorporation of undeveloped seeds leads to the temporal fluctuation of populations and ensures the coexistence of three species with a sustained oscillation.

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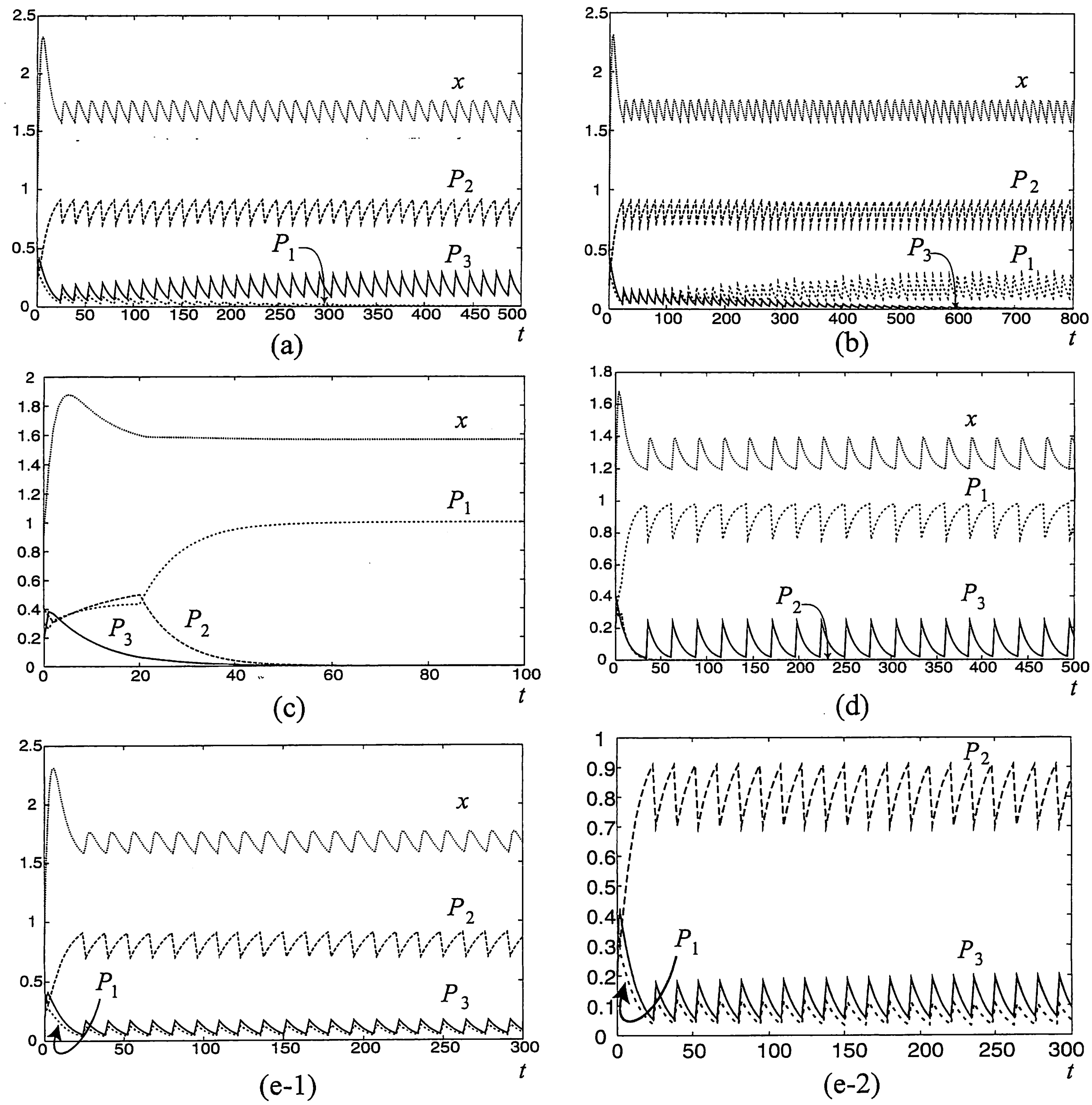

Fig. 11.4. The temporal sequence of P_1, P_2, P_3 and x with the initial condition $(P_1(0), P_2(0), P_3(0), x(0)) = (0.2, 0.4, 0.3, 0.9)$. The parameters are $\delta_1 = \delta_2 = \delta_3 = 0.12$, $m_2 = 3.2$, $m_3 = 0.3$, $a_1 = 5$, $a_2 = 4.7$, $a_3 = 1$, $l_1 = 1.2$, $l_2 = 1.6$, $l_3 = 0$, $q = 0.8$, $s = 1$, $\rho_1 = \rho_2 = \rho_3 = 0.8$, $c_1 = c_2 = c_3 = 2.5$, (a) $m_1 = 0.7$ (AREA I in Fig. 11.3), (b) $m_1 = 0.8$ (AREA II in Fig. 11.3), (c) $m_1 = 3.6$ (AREA III in Fig. 11.3), (d) $m_1 = 5$ (AREA IV in Fig. 11.3), (e-1) and (e-2) $m_1 = 0.76$ (AREA V in Fig. 11.3). (e-2) gives the expanded temporal sequence of P_1, P_2, P_3.

References

1. Chesson, P., Warner, R. R.: Environmental variability promotes coexistence in lottery competitive system. Am. Nat., **117**, 923–943 (1981).
2. Chesson, P.: The stabilizing effect of a random environment. J. Math. Biol., **15**, 1–36 (1982).
3. Chesson, P., Huntly, N.: The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am. Nat., **150**, 519–553 (1997).

4. Comins, H. N., Noble, I. R.: Dispersal, variability and transient niches: Species coexistence in a uniformly variable environment. Am. Nat., **126**, 706–723 (1985).
5. Dewi, S., Chesson, P.: The age-structured lottery model. Theor. Popul. Biol., **117**, 923–943 (1981).
6. Hatfield, J. S., Scheibling, R. E.: Diffusion analysis and stationary distribution of the two-species lottery competition model. Theor. Popul. Biol., **36**, 251–266 (1989).
7. Huisman, J., Weissing, F. J.: Biodiversity of plankton by species oscillations and chaos. Nature., **402**, 407–410 (1999).
8. Lambers, H., Chapin III, F. S., Pons, T. L.: *Plant Physiological Ecology*. Springer-Verlag, New York (1998).
9. Laurie, H., Mustart, P. J., Cowling, R. M.: A shared niche? The case of the species pair, *Protea obtusifolia Leucadendron meridianum*. Oikos., **79**, 127–136 (1997).
10. Muko, S., Iwasa, Y.: Species coexistence by permanent spatial heterogeneity in a lottery model. Theor. Popul. Biol., **57**, 273–284 (2000).
11. Muko, S., Iwasa, Y.: Incomplete mixing promotes species coexistence in a lottery model with permanent spatial heterogeneity. Theor. Popul. Biol., **64**, 359–368 (2003).
12. Neuhauser, C., Pacala, W.: An explicitly spatial version of the Lotka–Volterra model with interspecific competition. Ann. Appl. Probab., **9**, 1226–1259 (1999).