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Journal of Theoretical Biology

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Synchronized reproduction promotes species coexistence through reproductive facilitation

Yu-Yun Chen^{a,b,*}, Sze-Bi Hsu^{b,c}

^a Department of Natural Resources and Environmental Studies, National Donghwa University, Hualien 974, Taiwan

^b Mathematics Division, National Center for Theoretical Science, Hsinchu 300, Taiwan

^c Department of Mathematics, National Tsing Hua University, Hsinchu 300, Taiwan

ARTICLE INFO

Article history:

Received 29 May 2010

Received in revised form

10 January 2011

Accepted 10 January 2011

Available online 15 January 2011

Keywords:

Synchrony

Recruitment enhancement

Indirect mutualism

Species coexistence

ABSTRACT

Theories for species coexistence often emphasize niche differentiation and temporal segregation of recruitment to avoid competition. Recent work on mutualism suggested that plant species sharing pollinators provide mutual facilitation when exhibit synchronized reproduction. The facilitation on reproduction may enhance species persistence and coexistence. Theoretical ecologists paid little attention to such indirect mutualistic systems by far. We propose a new model for a two-species system using difference equations. The model focuses on adult plants and assumes no resource competition between these well-established individuals. Our formulas include demographic parameters, such as mortality and recruitment rates, and functions of reproductive facilitation. Both recruitment and facilitation effects reach saturation levels when flower production is at high levels. We conduct mathematical analyses to assess conditions of coexistence. We establish demographical conditions permitting species coexistence. Our analyses suggest a “rescue” effect from a “superior” species to a “weaker” species under strong recruitment enhancement effect when the later is not self-sustainable. The facilitation on rare species may help to overcome Allee effect.

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1. Introduction

Species coexistence and mechanisms maintaining species diversity have been the major focus in ecology. It was traditionally assumed that, species utilizing the same resource are subject to competitive exclusion (Connell et al., 2004; Fargione and Tilman, 2006). Major hypotheses explaining species coexistence involve avoidance of competition. For example competing species may coexist in a community through spatial segregation or resource partitioning (Harpole and Tilman, 2007; Huchingson, 1959). In addition, segregated recruitment events also reduce strength of competition. Temporally variable reproduction among species allows recruitment and establishment of the inferior competitors in the time of low inter-specific competition (Chesson, 2003). The mechanism is especially important in sessile organisms which face strong competition for space (Chesson, 2003; Warner and Chesson, 1985). Despite the popularity of mechanisms reducing inter-specific competition, these mechanisms may not be sufficient to explain the maintenance of biodiversity in all systems.

Insufficient supply of recruits is an important constraint for forest species and may impact biodiversity. Empirically, densities of natural populations upon recruitment may not be high enough

to cause significant density-dependent mortality (Augspurger and Kitajima, 1992). Competition among recruits thus may not be as influential as recruitment limitation for species persistence. Seed addition experiments in a neotropical forest demonstrated enhanced seedling recruitment and survival when reducing seed limitation (De Steven and Wright, 2002; Wright et al., 2005). Understanding mechanisms that lessen recruitment limitations and how they affect demographic dynamics of species are therefore crucial for the understanding of species coexistence.

Recruitment limitation could be reduced via positive interactions such as mutualism and other indirect facilitations. In plants, facilitation may occur directly, such as nutrient enrichment (Bronstein, 2009), or indirectly, such as provision of nesting sites for pollinators (Hansen et al., 2007). A less discussed form of indirect plant–plant mutualism is enhanced pollination via shared pollinators. Previous studies suggested a positive relationship between flowering magnitude and the success of pollination (Kelly and Sork, 2002). Large floral display (Moeller, 2004) and high levels of pollen and nectar resources attract nomadic pollinators as well as increase recruitment of residential pollinators (Appanah, 1993; Isagi et al., 1997; Sakai, 2002), thus enhances pollination success. Theoretical models demonstrated evolution of synchronized flowering at the population level via enhanced reproduction (Isagi et al., 1997; Satake and Iwasa, 2000). The models, however, did not provide flexibility to discuss demographical dynamics at the community level.

* Corresponding author at: Department of Natural Resources and Environmental Studies, National Donghwa University, Hualien 974, Taiwan. Tel.: +886 3 8633324.
E-mail address: ychen@mail.ndhu.edu.tw (Y.-Y. Chen).

In addition to enhancement of pollination efficiency, recruitment rate may also increase via increased seed and seedling survival rates. Janzen (1974) suggested that seeds facing predation may enhance survivorship by two means: extensive length of time with no reproduction, which causes decreased populations of seed predators, and massive production of seeds in a short time intermittently. In consequence, seeds produced in synchronous reproduction collectively increase the efficiency to satiate predators and facilitate seed survival of the population (community) as a whole. Cases of massive flower and seed production and predator satiation were evident at both the population and the community level (Curran and Leighton, 2000; Numata et al., 2003; Sakai et al., 1999).

To understand the role of the reproductive enhancement on species persistence and species coexistence, we construct models to explore demographical performance in two sympatric and spatially well-mixed species. These species are assumed to rely solely on sexual reproduction for future recruitment and share the same guild of pollinators. Reproductions of both species are periodic as often seen in natural systems (Sakai, 2001). The assumption of periodic reproduction led us to the construction of difference equations (see models below). In the intervening interval between reproductive events, all individuals acquire resources in order to recover its reserve level for the next reproductive event. During this non-reproduction time, a population may decrease in size due to mortality. If the intervening period is too long, decrease of populations during non-reproductive season may go beyond tolerable degrees and cause a collapse of populations. We intend to discuss conditions that allow and disapprove coexistence of the two species.

2. Models and stability analysis

In this study, all models focus on individuals that are capable of reproduction. We assume that such individuals have reached maturity and that resource competition has little influence on such individuals. Two species on focus (populations x and y) reproduce at periods p_1 and p_2 . Adult survival rates of the two species are b_1 and b_2 , respectively. The sympatric species may reproduce asynchronously when a lag in flowering time is involved. This leads to little inter-specific interaction and the two-species model may be considered as an one-dimensional model. When no time lag is involved for flowering, species may reproduce synchronously at the common multiples of the species' periods. We discuss the demographical dynamics of two sympatric species for asynchronous and occasional synchronous reproduction in Sections 2.1 and 2.2, respectively. The models do not include spatial context thus we do not describe immigration and emigration of individuals.

2.1. Asynchronous reproduction

We begin our model construction with a simple case when no reproductive synchrony of the two species occurs. The discrete map for the dynamics of one species is written as

$$\begin{cases} x_{n+1} = bx_n & n \neq 0 \pmod{p} \\ x_{n+1} = bx_n + h(x_n) & n = 0 \pmod{p} \end{cases} \quad (1)$$

where x_{n+1} and x_n are the abundances of population x at time $n+1$ and n , respectively and $0 < b < 1$, and n denotes the time step on focus. For the focal population, pollination efficiency and fruit production reach an upper limit at high flowering magnitude (large population size) due to resource availability and saturated pollination service. Thus we assume that the recruitment function $h(x_n)$ follows a Michaelis–Menten kinetics such that $h(x_n) = ux_n/(k+x_n)$, where the maximum recruitment rate (u) and the half-saturation constant k are positive values.

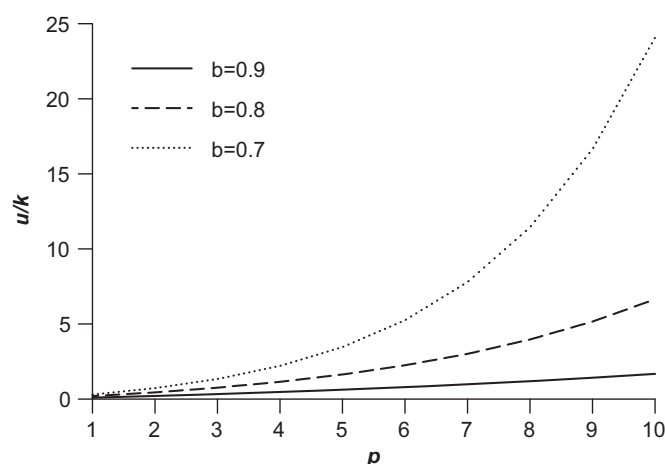


Fig. 1. Correlation between reproductive period and index of marginal increase of recruitment rate (u/k) when $\sigma=1$. We show three cases with adult survival rate $b=0.7, 0.8$, and 0.9 , respectively.

We conduct routine computation on (1) and obtain the periodic map (p -map, hereafter) $x_{n+p} = b^p x_n + h(b^{p-1} x_n)$ for the focal species. For convenience, we rewrite the p -map as $\bar{x} = f(x) = b^p x + h(b^{p-1} x)$. By taking the derivative of $f(x)$, we obtain $f'(x) = b^p + b^{p-1} h'(b^{p-1} x)$, where $h'(x) = uk/(k+x)^2 > 0$. Stability of fixed points of the system could be examined with the derivative of $f(x)$. For the fixed point of $x=0$, we obtain the net population growth rate σ defined as $f'(0) = b^p + b^{p-1} u/k$. When $\sigma < 1$, indicating a negative net population growth rate, the fixed point $x=0$ is asymptotically stable. On the other hand, $\sigma > 1$ indicates the fixed point at $x=0$ is unstable and there exists a stable and unique fixed point $x^* > 0$ (Appendix, Theorem 1). By reformulating $\sigma > 1$ we obtain $b^{p-1} u/k > 1 - b^p$, where $1 - b^p$ is the cumulative mortality rate and $b^{p-1} u/k$ is the recruitment rate at the time of reproduction. The focal population persists when the recruitment rate is higher than its cumulative mortality rate. The persisting population size is predicted to be $x^* = [ub^{p-1} - k(1 - b^p)] / [(1 - b^p)b^{p-1}]$ at the time of reproduction when $\sigma > 1$.

We explore the influence of reproductive and demographical properties on persistence. We first examine the relationship between u/k and p . Under the assumption of $\sigma=1$, we obtain a positive relationship between u/k and periodicity p (Fig. 1). The upper half of the curve of $\sigma=1$ is the parameter space which allows persistence of the species. As p increases, a higher value of recruitment rate u/k is required for persistence. An increased p also indicates a decreased population size for the focal species. In Fig. 1 we also examine the effect of adult survival rate b on the above correlation. A higher survival rate (b) reduces the slope of the curves, indicating a lower requirement of recruitment rate for species persistence when adult survival rate is high. The difference in the requirement of recruitment rate for persistence increases with higher p -values (Fig. 1).

2.2. Synchronous reproduction

In the case of synchronized reproduction, the two species reproduce at periods of p_1 and p_2 , respectively. Synchrony of two reproductive events takes place at a period of the least common multiples (p) of p_1 and p_2 , where $p = m_1 p_1 = m_2 p_2$ and m_1 and m_2 are positive integers. Parameters m_1 and m_2 are the frequencies of flowering events of species x and y , respectively, between any two synchronized reproductive events.

When two species reproduce simultaneously, the community exhibits a large floral display and presents a large quantity of resources for pollinators thus enhances pollination rates (Callaway, 1995). Massive flowering is then followed by enhanced mast fruiting.

Flower and seed numbers of each species may reach an upper limit due to resource limitation, hence the saturated recruitment function. Seed germination and subsequent recruitment often drop to a lower level due to predation, results in a low recruitment rate while reproducing asynchronously. Synchronized seeding, which may satiate seed/seedling predators, often leads to higher seed/seedling survival (Sun et al., 2007). We describe this enhancement on recruitment by using the Michaelis–Menten kinetics, which allows enhancement at each level of community participation yet concerns resource limitation on facilitation at high level of reproduction. The recruitment enhancement functions are written as $l_1 = 1 + \nu_1 y_n / (a_1 + y_n)$ and $l_2 = 1 + \nu_2 x_n / (a_2 + x_n)$, where ν_1 and ν_2 are maximum enhancement rates for species x and y , respectively. Parameters a_1 and a_2 are the half-saturation sizes of the populations.

The model for the case of synchronized reproduction is as the following:

$$f(n, x_n, y_n) = \begin{cases} F(x_n) & n \neq 0 \pmod{p_1} \\ F(x_n) + h_1(x_n) & n = 0 \pmod{p_1}, n \neq 0 \pmod{p_2} \\ F(x_n) + h_1(x_n)l_1(y_n) & n = 0 \pmod{p_1}, n = 0 \pmod{p_2} \end{cases} \quad (2)$$

$$g(n, x_n, y_n) = \begin{cases} G(y_n) & n \neq 0 \pmod{p_2} \\ G(y_n) + h_2(y_n) & n = 0 \pmod{p_2}, n \neq 0 \pmod{p_1} \\ G(y_n) + h_2(y_n)l_2(x_n) & n = 0 \pmod{p_1}, n = 0 \pmod{p_2} \end{cases} \quad (3)$$

where $F(x_n) = b_1 x_n$ and $G(y_n) = b_2 y_n$, $0 < b_1, b_2 < 1$. Recruitment functions are $h_1(x_n) = u_1 x_n / (k_1 + x_n)$ and $h_2(y_n) = u_2 y_n / (k_2 + y_n)$, where u_1 and u_2 are recruitment rates for species x and y , respectively, when each species reproduces alone.

With routine computations on (2) and (3), we obtain the following p -map:

$$\begin{cases} \bar{x} = F(x, y) = b_1^{p_1} f^{(m_1-1)}(x) + h_1(b_1^{p_1-1} f^{(m_1-1)}(x))l_1(b_2^{p_2-1} g^{(m_2-1)}(y)) \\ \bar{y} = G(x, y) = b_2^{p_2} g^{(m_2-1)}(y) + h_2(b_2^{p_2-1} g^{(m_2-1)}(y))l_2(b_1^{p_1-1} f^{(m_1-1)}(x)) \end{cases} \quad (A2)$$

where $f(x) = b_1^{p_1} x + h_1(b_1^{p_1-1} x)$, $f^{(m_1-1)}(x) = \underbrace{f(f(\dots(f(x))))}_{m_1-1 \text{ times}}$,

$g(y) = b_2^{p_2} y + h_2(b_2^{p_2-1} y)$, and $g^{(m_2-1)}(y) = \underbrace{g(g(\dots(g(y))))}_{m_2-1 \text{ times}}$. In appendix

(Lemma 2) we show that every positive orbit $O^+_{(x_0, y_0)} = \{(x_n, y_n)\}_{n=0}^\infty$, provided $x_0, y_0 > 0$, is bounded.

There exists three fixed points (Appendix) for the system (A2): $(0, 0)$, $(x^*, 0)$, and $(0, y^*)$. Stability of these fixed points indicates possibilities of species persistence and coexistence. We explore demographical and reproductive requirement for sustainability of the system with stability analysis. We first obtain the Jacobian of the discrete map (A2) at (x, y)

$$J(x, y) = \begin{bmatrix} \frac{\partial F}{\partial x} & \frac{\partial F}{\partial y} \\ \frac{\partial G}{\partial x} & \frac{\partial G}{\partial y} \end{bmatrix} \quad (4)$$

where

$$\frac{\partial F}{\partial x} = (b_1^{p_1} + b_1^{p_1-1} h_1'(b_1^{p_1-1} f^{(m_1-1)}(x))l_1(b_2^{p_2-1} g^{(m_2-1)}(y))) \left(\frac{d}{dx} f^{(m_1-1)}(x) \right)$$

$$\frac{\partial F}{\partial y} = h_1(b_1^{p_1-1} f^{(m_1-1)}(x))b_2^{p_2-1} l_1'(b_2^{p_2-1} g^{(m_2-1)}(y)) \left(\frac{d}{dy} g^{(m_2-1)}(y) \right)$$

$$\frac{\partial G}{\partial x} = h_2(b_2^{p_2-1} g^{(m_2-1)}(y))b_1^{p_1-1} l_2'(b_1^{p_1-1} f^{(m_1-1)}(x)) \left(\frac{d}{dx} f^{(m_1-1)}(x) \right)$$

$$\frac{\partial G}{\partial y} = (b_2^{p_2} + b_2^{p_2-1} h_2'(b_2^{p_2-1} g^{(m_2-1)}(y))l_2(b_1^{p_1-1} f^{(m_1-1)}(x))) \left(\frac{d}{dy} g^{(m_2-1)}(y) \right) \quad (5)$$

We then conduct stability analysis for the fixed points in the following sections.

2.2.1. Stability of $(0, 0)$

From (5) we obtain eigenvalues of $f(0,0)$: $\lambda_1 = (b_1^{p_1} + b_1^{p_1-1} u_1 / k_1)^{m_1}$ and $\lambda_2 = (b_2^{p_2} + b_2^{p_2-1} u_2 / k_2)^{m_2}$. Let $\sigma_1 = (b_1^{p_1} + b_1^{p_1-1} (u_1 / k_1))$ and $\sigma_2 = (b_2^{p_2} + b_2^{p_2-1} (u_2 / k_2))$. We obtain local asymptotical stability for the fixed point $(0,0)$ when $\sigma_1 < 1$ and $\sigma_2 < 1$ (Theorem 3, appendix). We restate $\sigma_1 < 1$ and $\sigma_2 < 1$ as $b_1^{p_1-1} u_1 / k_1 < 1 - b_1^{p_1}$ and $b_2^{p_2-1} u_2 / k_2 < 1 - b_2^{p_2}$. Terms on the left hand side of the two restated formulas are recruitment rates of the two populations at the time of reproduction while the terms on the right hand sides are the cumulative mortality rates. When both cumulative mortality rates exceed the recruitment rates, the two populations become extinct at the steady state (Theorem 3, appendix). In this case, recruitment facilitation has no effect on the extinction of both species (Region A, Fig. 2). On the other hand, when recruitment rates are higher than mortality rates, i.e. $\sigma_1 > 1$ and $\sigma_2 > 1$, both populations persist in the community and could reach a steady state with population sizes of x_c and y_c (Theorem 7, appendix; Region D, Fig. 2). We will discuss on the species coexistence in region D again in later sections.

The first eigenvalue λ_1 is enlarged by m_1 power and the second eigenvalue λ_2 by m_2 power in the case of synchronous reproduction compared to the eigenvalue in the one-dimension case. The parameters m_1 and m_2 are positive integers indicating frequencies of reproduction during the interval of two synchronous flowering events. The frequencies of reproduction do not affect the stability for the equilibrium $(0, 0)$. Yet the speed of convergence of trajectories towards the equilibrium is faster when m_1 and m_2 are large.

2.2.2. Stability of $(x^*, 0)$

When $\sigma_1 > 1$, there exists a unique fixed point $(x^*, 0)$. The equilibrium population size x^* is the unique positive root of $f(x) = x$

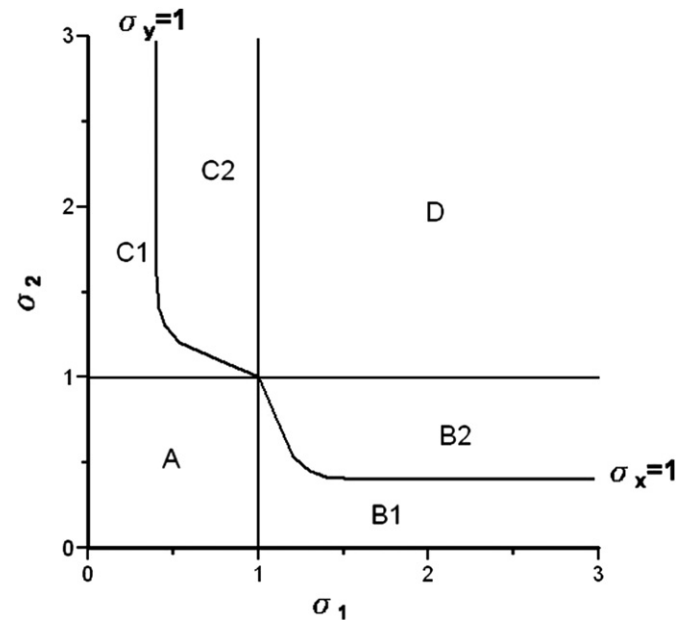


Fig. 2. Phase diagram. This case contains two reproductive periods p_1 and p_2 . The condition of $\sigma_1 < 1$ and $\sigma_2 < 1$ leads to extinction of both species (Region A). The condition of $\sigma_1 > 1$ and $\sigma_2 > 1$ leads to the coexistence of two species (Region D). Under the condition that $\sigma_1 > 1$ and $\sigma_2 < 1$, species x becomes the sole existence for the system if $\sigma_x < 1$ (Region B1). When $\sigma_1 > 1$ and $\sigma_2 < 1$, species y could invade the system if $\sigma_y > 1$ (Region B2). Under the condition that $\sigma_2 > 1$ and $\sigma_1 < 1$, species y becomes the only survivor when $\sigma_y < 1$. Species x could only invade the system when $\sigma_x > 1$ (under the condition that $\sigma_2 > 1$ and $\sigma_1 < 1$).

(Theorem 4, appendix) and $x^* = [u_1 b_1^{p_1-1} - k_1(1 - b_1^{p_1})] / [(1 - b_1^{p_1}) b_1^{p_1-1}] > 0$. From the stability analysis (Theorem 4(i), appendix) we obtain eigenvalues from the Jacobian of map (A2) at $(x^*, 0)$: $\lambda_1 = (f'(x^*))^{m_1} < 1$ and $\lambda_2 = (b_2^{p_2} + b_2^{p_2-1}(u_2/k_2)) \cdot l_2(b_1^{p_1-1} x^*) \cdot (b_2^{p_2} + b_2^{p_2-1}(u_2/k_2))^{m_2-1} := \sigma_x$. The later can be reformulated as

$$\sigma_x = \sigma_2^{m_2-1} \left(\sigma_2 + b_2^{p_2-1} \frac{u_2}{k_2} \frac{k_1(\sigma_1-1)}{a_2(1-b_1^{p_1})+k_1(\sigma_1-1)} v_2 \right) := H_2(v_2) \tag{6}$$

where $H_2(v_{2c})=1$ is satisfied, i.e. $\sigma_x=1$, we obtain the critical strength of recruitment enhancement v_{2c} .

Formula (6) describes the dynamical performance of population y in the existence of population x . A $\sigma_x > 1$ indicates existence of population y . By definition, the enhancement function l_2 is greater than one, thus $\sigma_2 > 1$ always leads to $\sigma_x > 1$ (Remark 1, appendix). This confirms our conjecture in the previous section that in the case of $\sigma_1 > 1$ and $\sigma_2 > 1$, species x and y co-occur in the community (Region D, Fig. 2).

Under the condition of $\sigma_1 > 1$ and $0 < \sigma_2 < 1$, two outcomes are possible. When considering a small recruitment enhancement (a small v_2), we observe $\sigma_x < 1$ and $(x^*, 0)$ is asymptotically stable. Thus population y could not persist in the system (Region B1, Fig. 2). On the other hand, a sufficiently large enhancement (a large v_2) leads to $\sigma_x > 1$ and the fixed point $(x^*, 0)$ becomes unstable. The high recruitment facilitation provided by species x enables species y to remain in the community (Region B2, Fig. 2). In this case, the two species coexist in the system even though species y does not persist alone.

The enhancement function l_2 is a function of the net population growth of species x , i.e. σ_1 and the recruitment enhancement rate provided by species x , i.e. v_2 . For a fixed σ_x we observe a negative correlation between σ_1 and v_2 . Hence, when population x grows slowly, a higher recruitment enhancement rate is needed in order to maintain population y (Fig. 3).

2.2.3. Stability of $(0, y^*)$

Using similar skill used in the previous section, we examine the stability of $(0, y^*)$ and obtain σ_y that describes the dynamic behavior of species x in the presence of species y : $\sigma_y = (b_1^{p_1} + b_1^{p_1-1})$

$(u_1/k_1) l_1(b_2^{p_2-1} y^*) (b_1^{p_1} + b_1^{p_1-1} (u_1/k_1))^{m_1-1}$ (Appendix). With similar underlying principles described in the previous section, we distinguished region C1 and C2 of Fig. 2. The region C1 is the parameter space where species x is not able to invade the system of species y . When $\sigma_y > 1$, species x can successfully invade the system. Again, invasion of species x is possible because a sufficiently strong reproductive facilitation on population x increases σ_y , even though x is not self-sustainable. Similar to the case of $(x^*, 0)$, it requires a higher recruitment enhancement rate (v_1) to maintain population x when net population growth of the facilitating species (y) is low (a small σ_2).

2.2.4. Species coexistence and reproductive frequency

Coexistence of two species is possible when both species are self-sustainable ($\sigma_1 > 1$ and $\sigma_2 > 1$). However, it is also possible for the two species to coexist even when one of the species has a negative

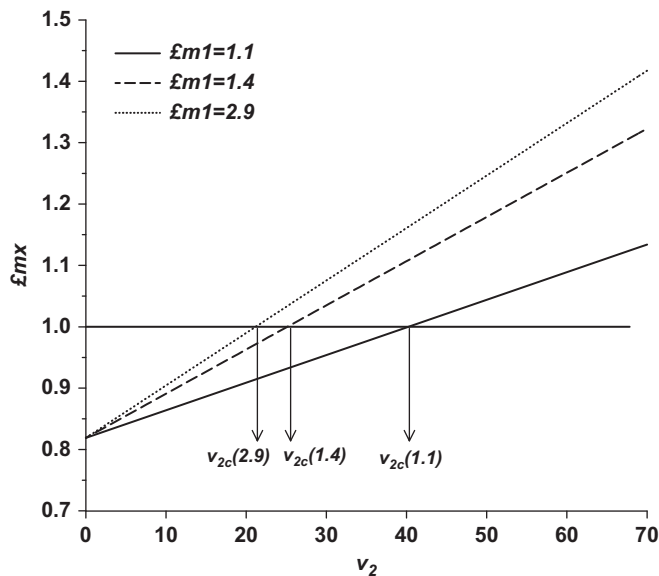


Fig. 3. Correlation between parameters σ_x and v_2 . The three inclining lines and the line of $\sigma_x=1$ intersect at v_{2c} , the lower bound of v_2 needed so that population y may persist in the community. We obtain these relations under of: $b_2=0.9, p_2=2, u_2/k_2=0.01, b_1=0.9, p_1=1$, and (1) $u_1/k_1=2$, (2) $u_1/k_1=0.5$, and (3) $u_1/k_1=0.2$ for lines of high, medium and low σ_1 values.

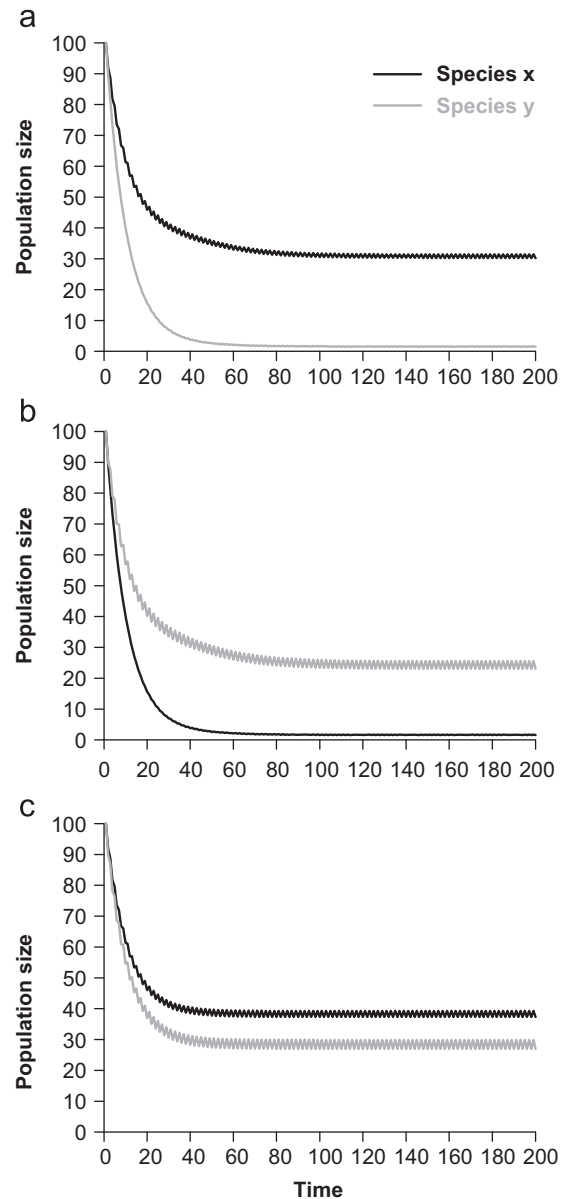


Fig. 4. Time series for populations x and y under conditions of (a) B2: $u_1=2, u_2=0.1, v_1=2, v_2=4.3$; (b) C2: $u_1=2, u_2=0.1, v_1=2, v_2=4.3$; and (c) D: $u_1=2, u_2=0.1, v_1=2, v_2=4.3$. In all cases, we assign the value of one to parameters k_1, a_1, k_2 , and a_2 . Species x and y have the same adult survival rates $b_1=b_2=0.9$ and their reproductive periods are $p_1=1, p_2=2$. Initial conditions for all three cases are $x_0=100$, and $y_0=100$. All three cases showed species coexistence.

net population growth ($\sigma_1 < 1$ or $\sigma_2 < 1$) and is unable to persist alone. We reformulate $\sigma_x > 1$ and $\sigma_y > 1$ as the following:

$$\sigma_2^{m_2-1} b_2^{p_2-1} (u_2/k_2) l_2 (b_1^{p_1-1} x^*) > 1 - \sigma_2^{m_2-1} b_2^{p_2} \tag{7}$$

$$\sigma_1^{m_1-1} b_1^{p_1-1} (u_1/k_1) l_1 (b_2^{p_2-1} y^*) > 1 - \sigma_1^{m_1-1} b_1^{p_1} \tag{8}$$

where parameters m_1 and m_2 are frequencies of flowering for species x and y during the interval between two synchronous events, respectively. Flowering frequencies m_1 and m_2 not only affects the speed of convergence but also the invasion of species y to the system of species x (Region B2, Fig. 2) and vice versa (Region C2, Fig. 2). In region B2, described by (7), a large m_2 (i.e. a small p_2), which implies a higher frequency of reproduction for species y , lowered the requirement of v_2 so that (7) holds. The same principle applies for the invasion by species y .

We conjecture that the uniqueness of the positive fixed point holds for the parameter regions B2, C2, and D. For all cases of coexistence (B2, C2, and D), there exists a unique positive fixed point which is asymptotically stable and both population sizes fluctuate periodically (Fig. 4). We demonstrated that the equilibrium points for regions B2, C2, and D in Fig. 2 are independent from the initial conditions (x_0, y_0) (Fig. 5).

3. Discussion

Species coexist in a community interact constantly. Previous literature recognizing relations among sympatric species greatly focused on direct interactions such as predation and competition. These interactions may lead to species exclusion if no mechanisms lessening the negative effect on one another intervene. Reports on non-trophic, indirect interactions, such as interference competition

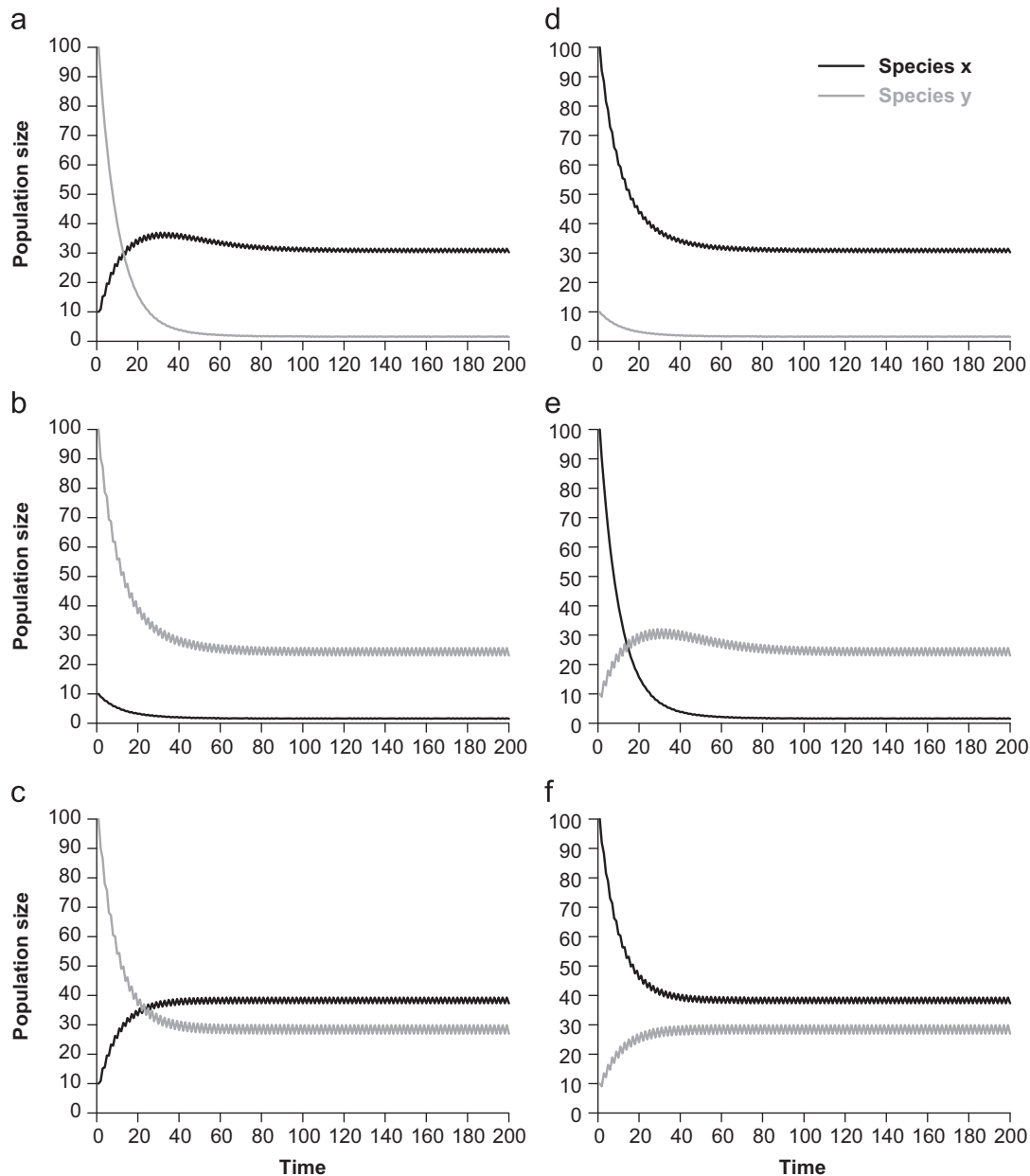


Fig. 5. Time series for populations x and y under conditions of (a) B2, (b) C2, and (c) D. All conditions follows Fig. 4 except the initial conditions: simulations (a)–(c) start from $x_0=10$, and $y_0=100$ and simulations (d)–(f) $x_0=100$, and $y_0=10$. All three cases showed species coexistence and (x_∞, y_∞) are the same despite the different initial values.

and facilitation suggested complexity and diversity of inter-specific interaction (Strauss, 1991). Recently, work on indirect facilitation and mutualism brought about more discussion on its importance for species coexistence (Callaway and Walker, 1997).

Plants exhibit several indirect mutualistic interactions such as shading (Callaway, 1998), nursing and provision of nesting sites (Bronstein, 2009). These positive interactions rely on differentiated requirement of resources for success. Earlier work suggested that species sharing the same pollinators compete for these agents and evolve character displacement to partition the utilization of pollinators (Ashton et al., 1988; Stone et al., 1998). However, Moeller (2004) observed no character displacement in flowering time of several *Clarkia* species. Moreover, tropical studies reported synchronized plant reproductive events in many occasions (Sakai et al., 1999; Curran and Leighton, 2000; Chen, 2007). These evidences may suggest mutualism rather than competition for species sharing the same resource. A recent study on plant pollination reported improved pollination success of the focal species from mixing with several other species (Moeller, 2004; Ghazoul, 2006). Experimental tests to investigate benefits of synchronized reproduction for multiple plant species are rare due to difficulties in data collection across large temporal and spatial scales (Andersen, 1989; Augspurger, 1981; Crawley and Long, 1995).

We describe here a hypothetical system of two species that reproduce periodically with difference equations. Periodic reproduction is widely observed in many forests (Sakai, 2001) yet rarely included in theoretical models (Holland and DeAngelis, 2010). This model differs from the Feldman et al. (2004) model in the use of discrete time approach and considers periodic productions of progenies. We focus more on the periodic reproductive behavior of the two species. The assumption of periodicity leads to intermittent facilitation. We assumed saturation function for recruitment with the consideration of resource limitation, both biotic and abiotic. For example, flower number may be limited by resource and fruit number by pollination service. Following fruiting, recruitment may be further lowered by seed/seedling predation. Yet the level of seed/seedling mortality is lowered due to predator satiation. We assumed a saturation function for reproductive facilitation to reflect such effect as the community presents more seeds. However, this saturation function still take into the consideration the upper limit set by resource limitation. Although Feldman et al. (2004) suggested that the sigmoid curve for pollinator response to resource for facilitation models, we demonstrate that a saturation curve allows the effect. Our models allow us to analytically assess the importance of reproductive and demographic parameters on species coexistence under periodic patterns.

From the analysis on the model of synchrony, we found that reproductive facilitation is in aid for species coexistence when at least one species could persist alone and when the effect of facilitation from the persisting species to the other is large enough. The relations of the two populations fall into three types: (1) neither species can persist (Region A of Fig. 2), (2) only the one species persists (Regions B1 and C1 of Fig. 2), and (3) two species coexist (Regions B2, C2, and D of Fig. 2). The first case of extinction of both species occurs when neither of the net population growth rates is sufficient to maintain the populations, due to high mortality or low recruitment. In forest communities, recruitment rates for species are usually low (De Steven and Wright, 2002). Thus adult survival and reproductive periodicity is important for population persistence. When periods of reproduction is extremely long or when adult survival rates are low, net growth rate may be greatly reduced and lead to extinction. This is particularly evident in disturbed area and often lead to loss of species.

In the case of species coexistence, two sources can be identified. (I) When both species exhibit high net population growth rates ($\sigma_1 > 1$ and $\sigma_2 > 1$), coexistence is evident. Because the

model assumes no competition, these two conditions alone are sufficient for coexistence. (II) Coexistence is possible via strong reproductive facilitation when $\sigma_1 < 1$ or $\sigma_2 < 1$. The “weaker” species with a net population growth (e.g. $\sigma_1 < 1$) could be “rescued” by the “superior” species, which has a high net population growth (e.g. $\sigma_2 > 1$). In the rescue regions (Region B2: $\sigma_1 > 1$ and $\sigma_2 < 1$ and region C2: $\sigma_1 < 1$ or $\sigma_2 > 1$), inequalities (7) and (8) demonstrate increased cumulative mortality rate by the factor $\sigma_2^{m_2-1}$. The inequality also implies decreased recruitment that could be boosted by facilitation function l_2 . In simulations, the “weaker” population increases due to reproductive facilitation from the other species before it goes to extinction due to mortality. The rescue effect is independent from initial values, which suggest a benefit for rare species. In many natural systems, rare species suffer from Allee effect with which the species encounter little mates and face extinction risk. However, mating problem of rare species may be solved by shared pollinators when these pollen transmitting agents are attracted or recruited by the other species (Moeller, 2004). Our result implies that rare species might benefit from synchronized masting events due reproductive facilitation.

Although our model did not include cases of non-periodic flowering, it implies coexistence of episodic masting species through reproductive facilitation (Appanah, 1985; Corlett, 1990; Numata et al., 2003; Sakai et al., 1999). Moreover, the positive effect on recruitment via synchrony may become forces driving the evolution of inter-specific synchronization (Donaldson, 1993; Janzen, 1974; Kelly and Sork, 2002). Synchrony of seed production increases seed availability (Chen, 2007; Metz et al., 2008; Sun et al., 2007) for species participating in the events. Thus species inhabiting the same community, though competing for resources, may become mutualistic to each other. Our model suggested that the unpredictable and long intervening interval between mast events requires high recruitment or low adult mortality to sustain the populations. In addition, with long non-reproductive intervals, higher reproductive enhancement rates are needed to facilitate species coexistence. Further investigations, both empirically and theoretically, are needed to explore the evolution of the episodic events.

Our model of synchronized reproduction assumes a system of adult plants and neglects ecological processes such as resource competition. However, we do not mean to imply the unimportance of these processes. Indeed, in the years of high progeny density, negative density dependence may be in action and counteract with reproductive facilitation. However, in systems with severe seed limitation, important recruitment events may still depend on enhancement of progeny production and survival.

Acknowledgments

We thank the Mathematics Division of National Center for Theoretical Sciences, National Science Council, Republic of China for providing postdoctoral fellowship to Yu-Yun Chen during the study. The research is partially supported by National Science Council, Republic of China. We are also in debt for all the logistic support by the National Tsing Hua University. We are grateful for the helpful comments from two anonymous reviewers.

Appendix A. Mathematical analysis of the asymptotic behavior of the maps (A1), (A2)

A.1. One-dimensional dynamics

Consider the following one-dimensional map:

$$\bar{x} = F(x) := b^p f^{(m-1)}(x) + h(b^{p-1} f^{(m-1)}(x)), \quad x > 0 \quad (\text{A1})$$

where m is a positive integer,

$$f(x) = b^p x + h(b^{p-1}x), \quad h(x) = \frac{ux}{k+x}, \quad 0 < b < 1, \quad u, k > 0$$

$$f^{(k)}(x) = \underbrace{f \circ f \circ \dots \circ f(x)}_{k\text{-times}}$$

Theorem 1. Let $\{x_n\}_{n=1}^\infty, x_0 > 0$ be the iterates generated by the map (A1) and $\sigma := b^p + b^{p-1}(u/k)$. Then

- (i) If $\sigma < 1$, then $\lim_{n \rightarrow \infty} x_n = 0$.
- (ii) If $\sigma > 1$, then $\lim_{n \rightarrow \infty} x_n = x^*$ where x^* is the unique positive fixed point of the map (A1).

Moreover, x^* satisfies $x^* = (ub^{p-1} - k(1 - b^p)) / ((1 - b^p)b^{p-1})$, $x^* = f(x^*)$, $0 < f'(x^*) < 1$.

Proof. It is easy to verify the following: $h'(x) = (uk / (k+x)^2) > 0$, $h''(x) = -2(uk / (k+x)^3) < 0$, $f'(x) = b^p + h'(b^{p-1}x)b^{p-1} > 0$, $f''(x) = h''(b^{p-1}x)(b^{p-1})^2 < 0$,

$$\begin{aligned} \frac{d}{dx}(f^{(m-1)}(x)) &= f'(f^{(m-2)}(x))f'(f^{(m-3)}(x)) \dots f'(x) > 0 \\ \frac{d^2}{dx^2}(f^{(m-1)}(x)) &= f''(f^{(m-2)}(x)) \left(\frac{d}{dx} f^{(m-2)}(x) \right) f'(f^{(m-3)}(x)) \dots f'(x) \\ &\quad + \dots + f'(f^{(m-2)}(x)) f''(f^{(m-3)}(x)) \dots f''(x) < 0 \end{aligned} \quad (A1.1)$$

$$f'(0) = b^p + b^{p-1} \frac{u}{k}, \quad f^{(k)}(0) = f(0) = 0$$

$$\begin{aligned} F'(0) &= \left(\frac{d}{dx} f^{(m-1)}(x) \right) \Big|_{x=0} (b^p + h'(0)b^{p-1}) \\ &= (f'(0))^{(m-1)} \left(b^p + \frac{u}{k} b^{p-1} \right) = \sigma^m \end{aligned}$$

Next we claim that there exists at most one positive fixed point of the map (A1). Suppose there are two positive fixed points \hat{x}_1, \hat{x}_2 with $0 < \hat{x}_1 < \hat{x}_2$. Then $F(0) = 0$, $\hat{x}_1 = F(\hat{x}_1)$ and $\hat{x}_2 = F(\hat{x}_2)$. By Rolle's Theorem, there exists \hat{x}_3, \hat{x}_4 , $0 < \hat{x}_3 < \hat{x}_1 < \hat{x}_4 < \hat{x}_2$ such that $F'(\hat{x}_3) = 1$ and $F'(\hat{x}_4) = 1$. Apply Rolle's Theorem again, there exists \hat{x}_5 , $\hat{x}_3 < \hat{x}_5 < \hat{x}_4$ such that $F''(\hat{x}_5) = 0$. However, from (A1.1) for any $x > 0$, $F'(x) = (b^p + h'(b^{p-1}f^{(m-1)}(x))b^{p-1}) / ((d/dx)f^{(m-1)}(x)) > 0$,

$$\begin{aligned} F''(x) &= h''(b^{p-1}f^{(m-1)}(x)) \left(b^{p-1} \frac{d}{dx} f^{(m-1)}(x) \right)^2 \\ &\quad + (b^p + h'(b^{p-1}f^{(m-1)}(x))b^{p-1}) \frac{d^2}{dx^2} (f^{(m-1)}(x)) < 0 \end{aligned}$$

This leads to a contradiction.

If $\sigma < 1$ then $F'(0) < 1$. From the uniqueness of positive fixed point, the monotonicity of $F(x)$ and $F(x) < x$ for x large, it follows that the curve $y = F(x)$ is below the line $y = x$. Thus $\lim_{n \rightarrow \infty} x_n = 0$. If $\sigma > 1$ then $F'(0) > 1$. Then there exists a unique positive fixed point x^* . The monotonicity of $F(x)$ implies that $\lim_{n \rightarrow \infty} x_n = x^*$. We note that $x^* = F(x^*) = f(f^{(m-1)}(x^*)) = f^{(m)}(x^*)$. From the uniqueness of positive fixed point, we have $x^* = f(x^*)$. It is easy to verify that $f'(x^*) = b^{p_1} + (k_1(1 - b^{p_1}) / k_1 + b^{p_1-1}x^*) < 1$. \square

A.2. Two-dimensional dynamics

Consider the following two-dimensional p -map

$$\begin{aligned} \bar{x} = F(x, y) &= b_1^{p_1} f^{(m_1-1)}(x) + h_1(b_1^{p_1-1} f^{(m_1-1)}(x)) l_1(b_2^{p_2-1} g^{(m_2-1)}(y)) \\ \bar{y} = G(x, y) &= b_1^{p_2} g^{(m_2-1)}(y) + h_2(b_2^{p_2-1} g^{(m_2-1)}(y)) l_2(b_1^{p_1-1} f^{(m_1-1)}(x)) \end{aligned} \quad (A2)$$

where $0 < b_1, b_2 < 1$, m_1, m_2, p_1 , and p_2 are positive integers, $m_1 p_1 = m_2 p_2 = p$,

$$\begin{aligned} f(x) &= b_1^{p_1} x + h_1(b_1^{p_1-1} x), \quad g(y) = b_2^{p_2} y + h_2(b_2^{p_2-1} y) \\ h_1(X) &= \frac{u_1 X}{k_1 + X}, \quad h_2(Y) = \frac{u_2 Y}{k_2 + Y}, \quad u_i, k_i > 0, \quad i = 1, 2 \\ l_1(Y) &= 1 + \frac{v_1 Y}{a_1 + Y}, \quad l_2(X) = 1 + \frac{v_2 X}{a_2 + X}, \quad v_i, a_i > 0, \quad i = 1, 2 \end{aligned} \quad (A2.1)$$

Lemma 2. Every positive orbit $O_{(x_0, y_0)}^+ = \{(x_n, y_n)\}_{n=0}^\infty$ of the map (A2) with $x_0, y_0 > 0$ is bounded.

Proof. From the map (A2) and (A2.1), we have

$$\begin{aligned} F(x, y) \leq \tilde{F}(x) &:= b_1^{p_1} f^{(m_1-1)}(x) + (1 + v_1) h_1(b_1^{p_1-1} f^{(m_1-1)}(x)) \\ G(x, y) \leq \tilde{G}(y) &:= b_2^{p_2} g^{(m_2-1)}(y) + (1 + v_2) h_2(b_2^{p_2-1} g^{(m_2-1)}(y)) \end{aligned} \quad (A2.2)$$

Let $\{\tilde{x}_n\}, \tilde{x}_0 = x_0, \{y_n\}, \tilde{y}_0 = y_0$ be the iterates generated by the maps $\tilde{x} = \tilde{F}(x)$, $\tilde{y} = \tilde{G}(y)$, respectively. Claim: $x_n \leq \tilde{x}_n$, $y_n \leq \tilde{y}_n$, $n = 1, 2, \dots$ From the monotonicity of $\tilde{F}(x)$ and (A2.2), we have

$$\begin{aligned} x_1 &= F(x_0, y_0) \leq \tilde{F}(x_0) = \tilde{x}_1 \\ x_2 &= F(x_1, y_1) \leq \tilde{F}(x_1) \leq \tilde{F}(\tilde{x}_1) = \tilde{x}_2 \\ &\quad \vdots \\ x_n &= F(x_{n-1}, y_{n-1}) \leq \tilde{F}(x_{n-1}) \leq \tilde{F}(\tilde{x}_{n-1}) = \tilde{x}_n \end{aligned}$$

Similarly we can prove that $y_n \leq \tilde{y}_n$, for $n = 1, 2, \dots, n$. By Theorem 1, either $\lim_{n \rightarrow \infty} \tilde{x}_n = 0$ or $\lim_{n \rightarrow \infty} \tilde{x}_n = \tilde{x}_n^* > 0$. Hence $\{x_n\}_{n=0}^\infty$ is bounded. Similarly, we have that $\{y_n\}_{n=0}^\infty$ is bounded. Thus we complete the proof of Lemma 2. \square

Theorem 3. Let $\sigma_1 := b_1^{p_1} + b_1^{p_1-1}(u_1/k_1)$, $\sigma_2 := b_2^{p_2} + b_2^{p_2-1}(u_2/k_2)$.

- (i) If $\sigma_1 < 1$ and $\sigma_2 < 1$, then the fixed point $(0, 0)$ is asymptotically stable.
- (ii) If $\tilde{\sigma}_1 = b_1^{p_1} + b_1^{p_1-1}(u_1(1 + v_1)/k_1) < 1$, then $\lim_{n \rightarrow \infty} x_n = 0$.
- (iii) If $\tilde{\sigma}_2 = b_2^{p_2} + b_2^{p_2-1}(u_2(1 + v_2)/k_2) < 1$, then $\lim_{n \rightarrow \infty} y_n = 0$.

Proof.

- (i) The local stability of $(0, 0)$ is established in Section 2.2.
- (ii) From the proof of Lemma 2 and Theorem 1, we have $x_n \leq \tilde{x}_n$ and $\lim_{n \rightarrow \infty} \tilde{x}_n = 0$. Hence $\tilde{\sigma}_1 < 1$ implies $\lim_{n \rightarrow \infty} x_n = 0$.
- (iii) Similarly, $\tilde{\sigma}_2 < 1$ implies $\lim_{n \rightarrow \infty} y_n = 0$.

Let

$$\begin{aligned} \sigma_x &:= \left(b_2^{p_2} + b_2^{p_2-1} \frac{u_2}{k_2} \right)^{m_2-1} \left(b_2^{p_2} + b_2^{p_2-1} \frac{u_2}{k_2} l_2(b_1^{p_1-1} x^*) \right) \\ \sigma_y &:= \left(b_1^{p_1} + b_1^{p_1-1} \frac{u_1}{k_1} \right)^{m_1-1} \left(b_1^{p_1} + b_1^{p_1-1} \frac{u_1}{k_1} l_1(b_2^{p_2-1} y^*) \right) \end{aligned} \quad (A2.3)$$

Theorem 4. Let $0 < \sigma_2 < 1, \sigma_1 > 1$.

- (i) If $\sigma_x < 1$, then the fixed point $(x^*, 0)$ of the map (A2) is asymptotically stable, where x^* is the unique fixed point of $\tilde{x} = b_1^{p_1} f^{(m_1-1)}(x) + h_1(b_1^{p_1-1} f^{(m_1-1)}(x))$.
- (ii) If $\sigma_x < 1$ and $\tilde{\sigma}_2 = b_2^{p_2} + b_2^{p_2-1}(u_2(1 + v_2)/k_2) < 1$, then $(x^*, 0)$ is globally asymptotically stable.
- (iii) If $\sigma_x > 1$, then there exists a positive fixed point (x_c, y_c) of the map (A2) satisfying $x_c > x^*$.

Proof. (i) From (5) and (8) we have $\partial G / \partial x(x^*, 0) = 0$. Hence from Theorem 1 (ii) and (5) the eigenvalues of $J(x^*, 0)$ are

$$\lambda_1 = \frac{\partial F}{\partial x}(x^*, 0) = (b_1^{p_1} + b_1^{p_1-1} h_{11}(b_1^{p_1-1} x^*)) (f'(x^*))^{m_1-1} = (f'(x^*))^{m_1} < 1$$

$$\lambda_2 = \frac{\partial G}{\partial y}(x^*, 0) = (b_2^{p_2} + b_2^{p_2-1} h_2'(0)) l_2(b_1^{p_1-1} x^*) (g'(0))^{m_2-1}$$

$$= l_2(b_1^{p_1-1} x^*) (g'(0))^{m_2} =: \sigma_x$$

Thus if $\sigma_x < 1$ then $(x^*, 0)$ is asymptotically stable.

- (i) The local stability of $(x^*, 0)$ is established in the Section 2.2.
- (ii) From Theorem 3 (iii), it follows that $\lim_{n \rightarrow \infty} y_n = 0$. Then the asymptotic stability of $(x^*, 0)$ implies that $\lim_{n \rightarrow \infty} (x_n, y_n) = (x^*, 0)$.
- (iii) For any fixed $y \geq 0$, from Theorem 1 and the hypothesis $\sigma_1 > 1$, there exists a unique positive fixed point $\varphi(y)$ of $\bar{x} = F(x, y)$. Obviously $\varphi(0) = x^*$ and $\varphi(y)$ is strictly increasing in y . Consider the map $\bar{y} = G(\varphi(y), y)$. It is easy to verify that $(d/dy)G(\varphi(y), y)|_{y=0} = \sigma_x$. Thus the condition $\sigma_x > 1$ implies the existence of a unique positive fixed point y_c of the map $\bar{y} = G(\varphi(y), y)$.

Thus a positive fixed point (x_c, y_c) exists with $x_c = \varphi(y_c) > \varphi(0) = x^*$. □

Remark 1. Since $\tilde{\sigma}_2 < 1$ implies $\sigma_x < 1$, it is impossible that $\tilde{\sigma}_2 < 1$ in case (iii) of Theorem 4.

Similarly, we have the following Theorem.

Theorem 5. Let $0 < \sigma_1 < 1, \sigma_2 > 1$, then

- (i) if $\sigma_y < 1$, then the fixed point $(0, y^*)$ of the map (A2) is asymptotically stable where y^* is the unique positive fixed point of $\bar{y} = b_2^{p_2} g^{(m_2-1)}(y) + h_2(b_2^{p_2-1} g^{(m_2-1)}(y))$.
- (ii) If $\sigma_y < 1$ and $\tilde{\sigma}_1 = b_1^{p_1} + b_1^{p_1-1}(u_1(1+v_1)/k_1) < 1$, then $(0, y^*)$ is globally asymptotically stable.
- (iii) If $\sigma_y > 1$, then there exists a positive fixed point (x_c, y_c) of the map (A2) satisfying $y_c > y^*$.

Remark 2. Since $\tilde{\sigma}_1 < 1$ implies $\sigma_y < 1$, it is impossible that $\tilde{\sigma}_1 < 1$ in case (iii) of Theorem 5.

Theorem 6. If $\sigma_1 > 1$ and $\sigma_2 > 1$, then there exists a positive fixed point (x_c, y_c) of the map (A2) with $x_c > x^*$ and $y_c > y^*$.

Proof. From (A2.3) we note that $\sigma_1 > 1$ implies $\sigma_y > 1$ and $\sigma_2 > 1$ implies $\sigma_x > 1$. For any fixed $x \geq 0$, from Theorem 1 the map $\bar{y} = G(x, y)$ has a unique positive fixed point $\varphi(x)$. Obviously $\varphi(0) = y^*$ and $\varphi(x)$ is strictly increasing in x . Consider the map $\bar{x} = F(x, \varphi(x))$. It is easy to verify that $(d/dx)F(x, \varphi(x))|_{x=0} = \sigma_x > 1$. Hence by Theorem 1, there exists a unique positive fixed point x_c of $F(x, \varphi(x))$ satisfying $x_c > x^*$. Thus there exists a positive fixed point (x_c, y_c) with $y_c = \varphi(x_c) > y^*$.

In the following we shall state the results about the global behavior of iterates of the map (A2), provided that the uniqueness of the positive fixed point (x_c, y_c) holds. □

Definition. Consider a discrete map $\bar{x} = f(x)$ where $f : R_+^n \rightarrow R_+^n$, $f = (f_1 \dots f_n) \in C^1$, $R_+^n = \{(x_1 \dots x_n), x_i \geq 0, i = 1, 2, \dots, n\}$. We say the discrete system $\bar{x} = f(x)$ is cooperative if $(\partial f_i / \partial x_j)(x) \geq 0$ for all $i \neq j$ and for all $x \in R_+^n$.

Theorem A. (Jiang, 1994). Let p be a fixed point of the cooperative system $\bar{x} = f(x)$. Assume that for each $x \in R_+^n$, the positive orbit $O^+(x)$ is bounded. If p is a unique fixed point then p is globally asymptotically stable in R_+^n .

Remark 3. In his paper, Jiang prove Theorem A for a cooperative system $x' = f(x)$. It is easy to verify that the Theorem A also holds for a cooperative map $\bar{x} = f(x)$. For the mathematical properties of

cooperative map the reader may consult the review paper by Hirsch and Smith (2005).

$$\text{Let } X \in R_+^n, X_0 = \text{Int}(R_+^n), \partial X_0 = \text{bdry}(R_+^n).$$

Definition. A discrete map $\bar{x} = f(x)$, $f : X \rightarrow X$ is said to be uniformly persistent with respect to X_0 , and ∂X_0 if there exists $\eta > 0$ such that $\lim_{n \rightarrow \infty} \text{Inf } d(f^n(x), \partial X_0) \geq \eta$ for all $x \in X_0$.

The following is a uniform persistence Theorem for discrete map $\bar{x} = f(x)$.

Theorem B. (Freedman and So, 1989). Let the following (1)–(7) hold:

- (1) $f: X \rightarrow X$ is a continuous function.
- (2) $f(\partial X_0) \subset \partial X_0$
- (3) $f(X_0) \subseteq X_0$
- (4) $O^+(x)$ is a bounded positive orbit for all $x \in X$
- (5) $f|_{\partial X_0}$ is dissipative
- (6) $f|_{\partial X_0}$ has an acyclic covering $\pi = \{M_1 \dots M_R\}$
- (7) There is no positive orbit $\{x_n\}_{n \in \mathbb{Z}_+}$ such that $\{x_n\}_{n \in \mathbb{Z}_+} \subset W^+(M_i)$ for some i . Then the map $\bar{x} = f(x)$ is uniformly persistent with respect to ∂X_0 .

Applying Theorems A and B to the map (A2) yields the following results:

Theorem 7. Let

- (i) $\sigma_1 > 1$ and $\sigma_2 > 1$,
- (ii) $\sigma_1 > 1, 0 < \sigma_2 < 1$, and $\sigma_x > 1$,
- (iii) $\sigma_2 > 1, 0 < \sigma_1 < 1$, and $\sigma_y > 1$.

If one the (i)–(iii) holds then the map (A2) is uniformly persistent. Furthermore if the positive fixed point (x_c, y_c) is unique then (x_c, y_c) is globally asymptotically stable in R_+^2 .

Proof. We only prove the theorem for case (i). The case (ii) and (iii) can be proved using similar arguments. Let $\sigma_x > 1$ and $\sigma_y > 1$. Then $(x^*, 0)$ and $(0, y^*)$ are repellers with respect to $\text{Int}(R_+^2)$. Thus by Theorem B, the map (A2) is uniformly persistent. From Theorem A, if the positive fixed point (x_c, y_c) is unique then (x_c, y_c) is globally asymptotically stable in $\text{Int}(R_+^2)$. □

Remark 4. We conjecture that under either of the assumptions (i), (ii), (iii), the positive fixed point (x_c, y_c) of the map (A2) is unique.

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