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Discrete May–Leonard Competition Models I

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The local dynamics of two discrete-time models applicable to three competing plant species are shown to have properties similar to the May–Leonard (M-L) differential equation model. The dynamics of the two discrete models are shown to be similar. However, they are not dynamically consistent with the continuous M-L model. Unlike the continuous M-L model, the Hopf bifurcations of the discrete M-L models are not degenerate. The continuous M-L model is the limiting case of the discrete models.

Keywords: Lotka–Volterra; Competition; Difference equations; May–Leonard systems; Hopf bifurcation

1991 Mathematics Subject Classification: Primary: 39A11

INTRODUCTION

This paper describes the similarities and differences between the continuous May–Leonard (M-L) system of differential equations for three competing species and two discrete-time M-L systems derived from a plant competition model. The M-L system is a well-known 3-dimensional Lotka–Volterra competition model, where all three species have the same intrinsic growth rates.

Lotka–Volterra (L-V) competition is modeled by a system of differential equations describing the competition between two or more species that share and compete for the same resources, habitat or territory (interference competition). This is different from exploitative competition, where individuals do not directly interfere with one another, but compete indirectly through their consumption of a common resource [4]. The n -dimensional competitive L-V model is given by the following:

$$\frac{dx_i}{dt} = x_i \left(r_i - \sum_{j=1}^n a_{ij} x_j \right), \quad n \geq 2, \quad i = 1, \dots, n,$$

where x_i is the number or density of species i at time t , r_i is the intrinsic growth rate of species i , a_{ij} 's are the interaction parameters. The parameters r_i and a_{ij} are strictly positive. The dynamics of the 2-dimensional L-V competition model is well understood.

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If two species compete, there are no periodic solutions and all bounded trajectories converge to an equilibrium point. Less is known for the L-V model when $n > 2$. There have been extensive studies on 3-dimensional L-V models [9,18,20–22]. Zeeman [20], for example, has shown that non-trivial isolated periodic orbits do occur in some 3-dimensional competitive L-V systems.

The May–Leonard (M-L) competition model is a special 3-dimensional L-V competition model where all three competing species have the same intrinsic growth rates, $r_1 = r_2 = r_3 = r$, and the three species compete in the rock–scissors–paper manner: species 1 dominates species 2, species 2 dominates species 3 and species 3 dominates species 1.

The general L-V competition system can be scaled into the following form [20]:

$$x'_i = r_i x_i \left(1 - x_i - \sum_{j \neq i} a_{ij} x_j \right). \quad (1)$$

Then in the 3-dimensional case when $r_1 = r_2 = r_3 = r$, if we rescale the time by letting $\tau = rt$, the 3-dimensional L-V model (1) becomes the asymmetric May–Leonard model:

$$\begin{aligned} x'_1 &= x_1(1 - x_1 - \alpha_1 x_2 - \beta_1 x_3), \\ x'_2 &= x_2(1 - \beta_2 x_1 - x_2 - \alpha_2 x_3), \\ x'_3 &= x_3(1 - \alpha_3 x_1 - \beta_3 x_2 - x_3). \end{aligned} \quad (2)$$

May and Leonard [12] studied system (2) when $\alpha_i = \alpha$ and $\beta_i = \beta$ for $i = 1, 2, 3$, $0 < \alpha < 1 < \beta$ and $2 < \alpha + \beta$. They showed numerically that the symmetric system exhibits a general class of solutions with non-periodic oscillations of bounded amplitude but ever-increasing cycle time; asymptotically, the system cycles from being composed almost entirely of population 1, to almost entirely 2, to almost entirely 3, back to almost entirely 1, etc. Their model has only two parameters, α and β . Although it is a simple model, the M-L model demonstrates this complex phenomenon that does not occur in 2-dimensional L-V models.

The system (2) is called the symmetric M-L system if $\alpha_i = \alpha$ and $\beta_i = \beta$ for $i = 1, 2, 3$. Otherwise, the system is called asymmetric. Chi *et al.* [3] showed that the asymmetric M-L model also possesses the same properties as the symmetric one. In the case

$$0 < \alpha_i < 1 < \beta_i \quad (3)$$

and $A_i = 1 - \alpha_i$ and $B_i = \beta_i - 1$, they showed that the three-species equilibrium P_0 is globally asymptotically stable (g.a.s) if $B_1 B_2 B_3 < A_1 A_2 A_3$, unstable if $B_1 B_2 B_3 > A_1 A_2 A_3$ and if $B_1 B_2 B_3 = A_1 A_2 A_3$, a degenerate Hopf bifurcation occurs and there exists a family of neutrally stable periodic solutions. In the symmetric M-L model, P_0 is g.a.s if $\alpha + \beta < 2$, unstable if $\alpha + \beta > 2$, and a Hopf bifurcation occurs when $\alpha + \beta = 2$ [3].

Atkinson [2] and Allen *et al.* [1] derived an n -species annual plant competition model, a system of difference equations. They showed that the competition model exhibited some properties similar to the M-L model (2) in the case of three species. The dimensionless form for the n -species plant competition model is:

$$x_i(t+1) = \frac{(1 - b_i)x_i(t)}{x_i(t) + \sum_{j=1, j \neq i}^n k_{ij}x_j(t)} + b_i x_i(t), \quad (4)$$

where the b_i 's and k_{ij} are the seedbank and competition coefficients, respectively, and $0 < b_i < 1, k_{ij} > 0$ for all $i, j = 1, 2, \dots, n$. To relate the parameters in the discrete model to the original M-L model (2), we let $b_1 = b_2 = b_3 = b$ and denote the three-species, discrete M-L competition model as follows:

$$\begin{aligned}x_1(t+1) &= \frac{(1-b)x_1}{x_1 + \alpha_1 x_2 + \beta_1 x_3} + b x_1, \\x_2(t+1) &= \frac{(1-b)x_2}{\beta_2 x_1 + x_2 + \alpha_2 x_3} + b x_2, \\x_3(t+1) &= \frac{(1-b)x_3}{\alpha_3 x_1 + \beta_3 x_2 + x_3} + b x_3,\end{aligned}\tag{5}$$

where $x_i = x_i(t)$ for $i = 1, 2, 3$.

The discrete-time model (5) cannot entirely represent the dynamics of the continuous M-L model (2) because the equilibria of model (5) do not include zero, where all three species are extinct. Therefore, in addition to the discrete model (5), we study another discrete competition model modified from Eq. (5) that has the same equilibria as Eq. (5) but has an additional zero equilibrium. The model takes the following form:

$$x_i(t+1) = \frac{(1-b_i)x_i(t) - \Delta x_i(t)}{x_i(t) + \sum_{j=1, j \neq i}^n k_{ij}x_j(t)} + b_i x_i(t),$$

where $\Delta x_i(t) = x_i(t+1) - x_i(t)$. It is easy to see that this model has the same equilibria as Eq. (5). It can be expressed more simply as

$$x_i(t+1) = \frac{2(1-b_i)x_i(t)}{1 + x_i(t) + \sum_{j=1, j \neq i}^n k_{ij}x_j(t)} + b_i x_i(t).\tag{6}$$

It is also easy to see that model (6) has a zero equilibrium. The corresponding three-species, M-L competition model for this system satisfies

$$\begin{aligned}x_1(t+1) &= \frac{2(1-b)x_1}{1 + x_1 + \alpha_1 x_2 + \beta_1 x_3} + b x_1, \\x_2(t+1) &= \frac{2(1-b)x_2}{1 + \beta_2 x_1 + x_2 + \alpha_2 x_3} + b x_2, \\x_3(t+1) &= \frac{2(1-b)x_3}{1 + \alpha_3 x_1 + \beta_3 x_2 + x_3} + b x_3,\end{aligned}\tag{7}$$

where $x_i = x_i(t)$ for $i = 1, 2, 3$.

Ellner [5] considered a stochastic competition model for two annual plants that is similar to system (7). A generalization of the deterministic version of Ellner's equation arises in a model formulated by Jones and Perry [15] which is similar to our model (7). The advantage of system (7) is that it is closely related to the continuous M-L system (2) such that both systems (7) and (2) have a zero equilibrium. The zero or extinction equilibrium, where $x_i = 0$ for all $i = 1, 2, \dots, n$, is a singular point for systems (4) and (5). We distinguish these two systems by referring to the systems (4) and (5) as having no extinction equilibrium and systems (6) and (7) as having an extinction equilibrium.

To help us understand the biological meaning of some of the parameters in Eqs. (2), (5) and (7), we define $B_i = \beta_i - 1$ to be the *dominant factor* and $A_i = 1 - \alpha_i$ to be the *subdominant factor* with respect to species i . We use these two factors to measure the degrees of dominance and subdominance. For example, the first equation of (2) is $x_1' = x_1(1 - x_1 - \alpha_1 x_2 - \beta_1 x_3)$. Then $B_1 = \beta_1 - 1 > 0$ is the dominant factor of x_3 with respect to x_1 , and $A_1 = 1 - \alpha_1 > 0$ is the subdominant factor of x_2 with respect to x_1 . Therefore, for the symmetric M-L system (2), when the dominant factor is less than the subdominant factor, $B < A$ ($\alpha + \beta < 2$), we will find that none of the three species are dominant and the three species will eventually approach a positive equilibrium. In contrast, if the dominant factor is greater than the subdominant factor, the three species take turns becoming the dominant species.

Models (4) and (5) and models (6) and (7) differ from some of the discrete competition models that have been considered in the literature (e.g. Refs. [6,8,10,11]). Unlike the plant competition model, the models described in Refs. [8,10,11] are derived directly from their continuous counterparts using different discretization schemes.

Hofbauer *et al.* [8] studied the persistence behavior of the discrete n -species competition model

$$x_i(t+1) = x_i(t) \exp \left[r_i - \sum_{j=1}^n a_{ij} x_j(t) \right], \quad i = 1, 2, \dots, n. \quad (8)$$

In the case of three species, symmetric M-L competition, the model above takes the form:

$$\begin{aligned} x_1(t+1) &= x_1 \exp [r(1 - x_1 - \alpha x_2 - \beta x_3)], \\ x_2(t+1) &= x_2 \exp [r(1 - \beta x_2 - x_2 - \alpha x_3)], \\ x_3(t+1) &= x_3 \exp [r(1 - \alpha x_1 - \beta x_2 - x_3)], \end{aligned} \quad (9)$$

where $0 < \alpha < 1 < \beta$ and $r > 0$. Hofbauer *et al.* [8] showed that the dynamics of Eq. (9) are similar to those of the symmetric continuous M-L model (2). Liu and Elaydi [11] derived and analyzed a discrete, two-species competition model and related it to the continuous, two-species competition model. Their model extended to n -species takes the form:

$$x_i(t+1) = \frac{[1 + r_i \phi_i(h)] \cdot x_i(t)}{1 + \phi_i(h) \sum_{j=1}^n a_{ij} x_j(t)}, \quad i = 1, \dots, n. \quad (10)$$

In this article, we will study the two discrete time M-L competition models (5) and (7) that are derived from the annual plant competition model. The two discrete models (5) and (7) have behavior similar to the continuous M-L model (2) and do not exhibit the chaotic behavior inherent in many discrete analogues of continuous-time models. Models (8) and (10) differ from the discrete models (4) and (5) and models (6) and (7) that are studied in this investigation. Models (8) and (10) are analyzed in a separate paper [16]. A discretization scheme attributed to W. Kahan is applied to the continuous M-L model (2) and the comparison is carried out in another article [17].

We compare the dynamics of the continuous M-L model with those of models (4) and (5) and models (6) and (7). The discrete models (4) and (5) are analyzed in the second section and the dynamics of the discrete model (5) are related to model (2). In the third section, we study the discrete models (6) and (7) and show that the local dynamics are similar to

the discrete models (4) and (5). In the fourth section, we provide some numerical results and compare the discrete models with the continuous ones. We give some suggestions for future research directions in the fifth section.

DISCRETE MODEL WITH NO ZERO EQUILIBRIUM

General n -species Model

For system (4), an interior equilibrium $P_0 = (p_1, p_2, \dots, p_n)$ satisfies

$$p_i + \sum_{j \neq i}^n k_{ij} p_j = 1, \quad i = 1, 2, \dots, n. \quad (11)$$

The Jacobian matrix evaluated at P_0 is

$$J_{P_0} = I - \text{diag}[(1 - b_i)p_i] \begin{pmatrix} 1 & k_{12} & \cdot & k_{1n} \\ k_{21} & 1 & \cdot & k_{2n} \\ \cdot & \cdot & \ddots & \cdot \\ k_{n1} & k_{n2} & \cdot & 1 \end{pmatrix}, \quad (12)$$

where $\text{diag}[(1 - b_i)p_i]$ is a diagonal matrix with its diagonal elements to be $(1 - b_1)p_1, (1 - b_2)p_2, \dots, (1 - b_n)p_n$.

The following results hold for the discrete n -species model (4).

LEMMA 1 (Appeared in Ref. [1]) *If $x_i(0) > 0$, then*

$$0 \leq \liminf_{t \rightarrow \infty} x_i(t) \leq \limsup_{t \rightarrow \infty} x_i(t) \leq 1.$$

In addition, if $0 < x_i(0) \leq 1$, then $0 < x_i(t) \leq 1$ for $t > 0$.

LEMMA 2 *If $b_i = b$ for all $i = 1, 2, \dots, n$, and the interior equilibrium $P_0 = (p_1, p_2, \dots, p_n)$ exists, then b is an eigenvalue for J_{P_0} and $(p_1, p_2, \dots, p_n)^t$ is an eigenvector associated with b .*

Proof Since P_0 satisfies Eq. (11),

$$\begin{aligned} J_{P_0} \begin{pmatrix} p_1 \\ p_2 \\ \cdot \\ p_n \end{pmatrix} &= \begin{pmatrix} p_1 \\ p_2 \\ \cdot \\ p_n \end{pmatrix} - \text{diag}[(1 - b)p_i] \begin{pmatrix} 1 & k_{12} & \cdot & k_{1n} \\ k_{21} & 1 & \cdot & k_{2n} \\ \cdot & \cdot & \ddots & \cdot \\ k_{n1} & k_{n2} & \cdot & 1 \end{pmatrix} \begin{pmatrix} p_1 \\ p_2 \\ \cdot \\ p_n \end{pmatrix} \\ &= \begin{pmatrix} p_1 \\ p_2 \\ \cdot \\ p_n \end{pmatrix} - \text{diag}[(1 - b)p_i] \begin{pmatrix} 1 \\ 1 \\ \cdot \\ 1 \end{pmatrix} = b \begin{pmatrix} p_1 \\ p_2 \\ \cdot \\ p_n \end{pmatrix}. \end{aligned}$$

Hence, b is an eigenvalue of J_{P_0} with associated eigenvector $(p_1, p_2, \dots, p_n)^t$. \square

LEMMA 3 *If $b_i = b$ for all $i = 1, 2, \dots, n$, and the interior equilibrium $P_0 = (p_1, p_2, \dots, p_n)$ exists, then the set $\Gamma = \{(cp_1, cp_2, \dots, cp_n) | c > 0\}$ is an invariant set. In addition, if $X(0) \in \Gamma$, then $X(t) \rightarrow P_0$ as $t \rightarrow \infty$.*

Proof Let $X(0) \in \Gamma$. Then $X(0) = (\xi_0 p_1, \xi_0 p_2, \dots, \xi_0 p_n)$ for some $\xi_0 > 0$. Therefore, if $x_i(0) = \xi_0 p_i$, then

$$x_i(t+1) = \frac{(1-b)\xi_t p_i}{\xi_t} + b\xi_t p_i = (1-b+b\xi_t)p_i = \xi_{t+1} p_i,$$

where $\xi_{t+1} = 1-b+b\xi_t$ for $t = 0, 1, \dots$. This shows that Γ is an invariant set. One can verify that $\xi_t = 1-b^t + b^t \xi_0$. Since $0 < b < 1$, $\lim_{t \rightarrow \infty} \xi_t = 1$.

Therefore, $\lim_{t \rightarrow \infty} x_i(t) = \lim_{t \rightarrow \infty} \xi_t p_i = p_i$ for all $i = 1, 2, \dots, n$. This implies $\lim_{t \rightarrow \infty} X(t) = P_0$. \square

Discrete May–Leonard Model

Under the assumptions on the parameters given in Eq. (3), system (5) has three boundary equilibria: $e_1 = (1, 0, 0)$, $e_2 = (0, 1, 0)$ and $e_3 = (0, 0, 1)$. The existence of the interior equilibrium $P_0 = (p_1, p_2, p_3)$ was shown by Chi *et al.* [3]. The following lemma says that it is impossible for only two species to coexist.

LEMMA 4 *The system (5) has no boundary equilibria with two positive components. The interior equilibrium always exists.*

Proof One of the boundary equilibria with two components is

$$(x_1, x_2, x_3) = \left(\frac{\alpha_1 - 1}{\alpha_1 \beta_2 - 1}, \frac{\beta_2 - 1}{\alpha_1 \beta_2 - 1}, 0 \right).$$

Since $\alpha_1 - 1 < 0$ and $\beta_2 - 1 > 0$, x_1 and x_2 cannot both be positive. The same reasoning applies to the other two equilibria,

$$\left(0, \frac{\alpha_2 - 1}{\alpha_2 \beta_3 - 1}, \frac{\beta_3 - 1}{\alpha_2 \beta_3 - 1} \right) \quad \text{and} \quad \left(\frac{\alpha_3 - 1}{\alpha_3 \beta_1 - 1}, 0, \frac{\beta_1 - 1}{\alpha_3 \beta_1 - 1} \right). \quad \square$$

LEMMA 5 *Each of the boundary equilibria $e_1 = (1, 0, 0)$, $e_2 = (0, 1, 0)$ and $e_3 = (0, 0, 1)$ is a saddle node with a 2-dimensional stable manifold and a 1-dimensional unstable manifold.*

Proof The Jacobian matrix evaluated at e_1 is

$$J_{e_1} = \begin{pmatrix} (b+1)/2 & \alpha_1(b-1)/2 & \beta_1(b-1)/2 \\ 0 & \frac{b\beta_2 - b + 2}{\beta_2 + 1} & 0 \\ 0 & 0 & \frac{b\alpha_3 - b + 2}{\alpha_3 + 1} \end{pmatrix}.$$

One eigenvalue, $(b+1)/2$, is between 0 and 1 because $0 < b < 1$. In addition, because $\beta_2 + 1 > 2$ and $\alpha_3 + 1 < 2$, the other two eigenvalues λ_1 and λ_2 are positive and satisfy

$$\lambda_1 = \frac{b\beta_2 - b + 2}{\beta_2 + 1} = b + \frac{2(1-b)}{\beta_2 + 1} < b + \frac{2(1-b)}{2} = 1,$$

$$\lambda_2 = \frac{b\alpha_3 - b + 2}{\alpha_3 + 1} = b + \frac{2(1-b)}{\alpha_3 + 1} > b + \frac{2(1-b)}{2} = 1.$$

Therefore, two eigenvalues are between 0 and 1 and one eigenvalue is greater than 1. Hence, the equilibrium e_1 is a saddle node with 2-dimensional stable manifold and 1-dimensional unstable manifold. Similar arguments show that e_2 and e_3 are also saddle nodes. \square

For the discrete M-L model (5), the Jacobian matrix evaluated at P_0 is

$$J_{P_0} = I - \text{diag}[(1-b)p_i] \begin{pmatrix} 1 & \alpha_1 & \beta_1 \\ \beta_2 & 1 & \alpha_2 \\ \alpha_3 & \beta_3 & 1 \end{pmatrix}. \quad (13)$$

To determine the local stability of P_0 , we consider the symmetric system first. Let $\alpha_1 = \alpha$ and $\beta_i = \beta$. Then $A = 1 - \alpha > 0$ and $B = \beta - 1 > 0$. Let

$$f(A, B) = \frac{(B-A)(B-A+3)}{A^2 + AB + B^2}. \quad (14)$$

The function $f(A, B)$ is the product of a positive function, $(B-A+3)/(A^2 + AB + B^2)$, and the difference of dominant factor and subdominant factor, $B-A$. We have the following theorem.

THEOREM 1 Assume $\alpha_i = \alpha = 1 - A$ and $\beta_i = \beta = B + 1$ for $i = 1, 2, 3$. Then the interior equilibrium $P_0 = (1, 1, 1)/(\alpha + \beta + 1)$ of the symmetric M-L system (5) is l.a.s if $f(A, B) < b - 1$, and unstable if $f(A, B) > b - 1$. And as $b \rightarrow 1^-$, the stability criterion approaches that of the continuous M-L model (2), i.e. P_0 is l.a.s. if $\alpha + \beta < 2$ and unstable if $\alpha + \beta > 2$.

Note Theorem 1 says that if the dominant factor is much less than the subdominant factor, $f(A, B) < b - 1 < 0$, the three species will approach a stable positive equilibrium. However, for the continuous M-L model, the three species will approach a stable positive equilibrium if $f(A, B) < 0$. Therefore, for the discrete model to be close to the continuous model we need the seedbank coefficient b to be close to 1.

Proof of Theorem 1 If $\alpha_i = \alpha = 1 - A$ and $\beta_i = \beta = B + 1$ for $i = 1, 2, 3$ then $P_0 = (p, p, p)$ and $p = 1/(1 + \alpha + \beta)$. We know from Lemma 2 that b is an eigenvalue of J_{P_0} , it is not difficult to find the other two eigenvalues since the Jacobian matrix J_{P_0} is a circulant matrix [14]. The other two eigenvalues are

$$\lambda_{1,2} = \frac{1}{2} [2 - p(b-1)(\alpha + \beta - 2)] \pm \frac{\sqrt{3}}{2} p(b-1)(\alpha - \beta)i. \quad (15)$$

Since one of the eigenvalues $b < 1$, we only need to consider the magnitude of λ_1 and λ_2 to determine the local stability of P_0 . Then $|\lambda_{1,2}| < 1$ is

$$\frac{1}{4}[2 - p(b-1)(\alpha + \beta - 2)]^2 + \frac{3}{4}[p(b-1)(\alpha - \beta)]^2 < 1.$$

This leads to

$$\alpha + \beta - 2 < p(b-1)(\alpha^2 - \alpha - \alpha\beta - \beta + 1 + \beta^2).$$

After substituting $\alpha = 1 - A$ and $\beta = B + 1$ into the inequality, we obtain

$$B - A < p(b-1)(A^2 + AB + B^2). \quad (16)$$

Since $p = 1/(1 + \alpha + \beta) = 1/(B - A + 3) > 0$, we can divide both sides of Eq. (16) by $p(A^2 + AB + B^2)$ and get a new inequality

$$\frac{(B - A)(B - A + 3)}{A^2 + AB + B^2} < b - 1. \quad (17)$$

Hence, $f(A, B) < b - 1$. This proves that $|\lambda_{1,2}| < 1$ if and only if $f(A, B) < b - 1$. Therefore, if $f(A, B) < b - 1$, P_0 is l.a.s.

Since $B - A + 3 = \alpha + \beta + 1$ and $A^2 + AB + B^2$ are both greater than zero, as $b \rightarrow 1^-$, the inequality (17) becomes $B - A < 0$ or $\alpha + \beta < 2$ that is the stability criterion for the symmetric M-L model (2). \square

Note that at $b = 1$, all of the eigenvalues are one, the local stability of P_0 is indeterminate. In Fig. 1 is a graph of the stable region for the discrete M-L model (5) in $\alpha - \beta$ parameter

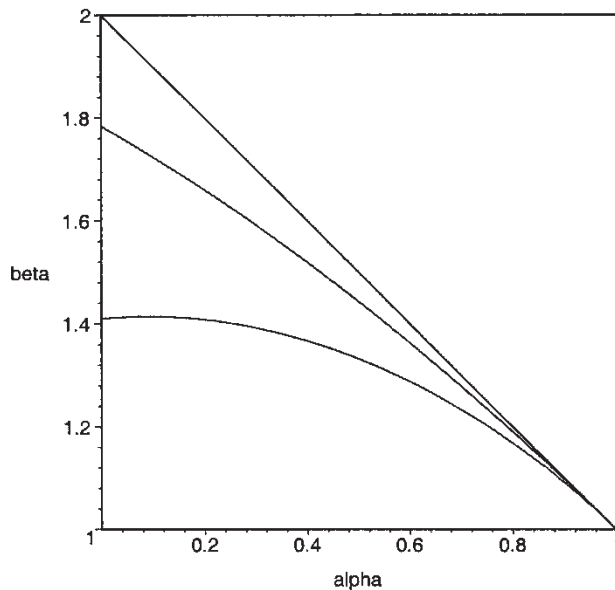


FIGURE 1 Region of stability in $\alpha - \beta$ parameter space for the discrete symmetric May-Leonard model (5): $b = 0.1$ (region below the bottom curve), $b = 0.75$ (region below the middle curve) and $\alpha + \beta < 2$ (region below the top line). The region $\alpha + \beta < 2$ is the stable region for the continuous May-Leonard model (2).

space for $b = 0.1$ and 0.75 . This stable region is smaller than the stable region of the continuous M-L model (2), where $\alpha + \beta < 2$.

In the above proof, we see that $|\lambda_{1,2}| = 1$ if and only if $f(A, B) = b - 1$. Therefore, if we let $\lambda(\mu) = (1/2)[2 - p(b - 1)(\alpha + \beta - 2)] + (\sqrt{3}/2)p(b - 1)(\alpha - \beta)i$ and $\mu = f(A, B) - (b - 1)$, then $|\lambda(\mu)| = 1$ if and only if $\mu = 0$.

We suspect a Hopf bifurcation may occur at $P_0 = (p, p, p)$ near $\mu = 0$. However, we have a 3-dimensional system which in general is more difficult to analyze than a 2-dimensional system. We need to use the method of center manifolds [19] to reduce the system to two dimensions at P_0 . First, we transform the equilibrium P_0 to the origin $(0, 0, 0)$. Let $Y = X - P_0$, then the discrete M-L model (5) becomes

$$Y' = J_{P_0} Y + \text{h.o.t.},$$

where h.o.t. means higher order terms. Since J_{P_0} has three distinct eigenvalues b , λ and $\bar{\lambda}$, there are eigenvectors $\mathbf{v}_1 = (p, p, p)^t$ and $\mathbf{v}_2 - i\mathbf{v}_3$ associated with b and λ , respectively. If we let the linear transformation $Y = (\mathbf{v}_1, \mathbf{v}_2, \mathbf{v}_3)(w_1, w_2, w_3)^t$, and $\lambda = \text{Re}(\lambda) + \text{Im}(\lambda)i$, then we have the transformed system

$$\begin{pmatrix} w_1' \\ w_2' \\ w_3' \end{pmatrix} = \begin{pmatrix} b & 0 & 0 \\ 0 & \text{Re}(\lambda) & -\text{Im}(\lambda) \\ 0 & \text{Im}(\lambda) & \text{Re}(\lambda) \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix} + \text{h.o.t.} \quad (18)$$

The new system (18) has the same dynamics near the origin as system (5) near P_0 . We can ignore the w_1 -space when considering the dynamics near the origin in $w_1 - w_2 - w_3$ space. Consider the 2-dimensional system in $w_2 - w_3$ space,

$$\begin{pmatrix} w_2' \\ w_3' \end{pmatrix} = \begin{pmatrix} \text{Re}(\lambda) & -\text{Im}(\lambda) \\ \text{Im}(\lambda) & \text{Re}(\lambda) \end{pmatrix} \begin{pmatrix} w_2 \\ w_3 \end{pmatrix} + \text{h.o.t.} \quad (19)$$

The dynamics near P_0 in the symmetric M-L model (5) is the same as the dynamics near the origin of the 2-dimensional system (19). Therefore, we can apply the Hopf bifurcation theorem for maps [7].

THEOREM 2 *A Hopf bifurcation occurs at P_0 in the symmetric M-L model (5) when $f(A, B) = b - 1$.*

Proof There are four conditions to verify [7]. Let $\mu = f(A, B) - (b - 1)$, and

$$\lambda(\mu) = \frac{1}{2}[2 - p(b - 1)(\alpha + \beta - 2)] + \frac{\sqrt{3}}{2}p(b - 1)(\alpha - \beta)i,$$

then $|\lambda(0)| = 1$ and $\lambda(\mu)$ and $\bar{\lambda}(\mu)$ are eigenvalues of J_{P_0} . Let F be defined by the 2-dimensional system (19), such that $F : \mathbb{R} \times \mathbb{R}^2 \rightarrow \mathbb{R}^2; (\mu, \mathbf{w}) \rightarrow F(\mu, \mathbf{w})$. Then (i) $F(\mu, 0) = 0$ for μ near 0.

Under the assumption $\beta > \alpha$, the imaginary part of $\lambda(\mu)$, $(\sqrt{3}/2)p(b - 1)(\alpha - \beta)$, is not zero. And we know that $\mu = 0$ if and only if $|\lambda(\mu)| = 1$. Therefore, (ii) $DF(\mu, 0)$ has two non-real eigenvalues $\lambda(\mu)$ and $\bar{\lambda}(\mu)$ for μ near 0, with $|\lambda(0)| = 1$.

When $\mu = 0$ we have

$$\mu = 0 \Rightarrow f(A, B) = b - 1 \Rightarrow f(A, B) < 0 \Rightarrow B < A. \quad (20)$$

After a tedious manipulation, we obtain

$$|\lambda(\mu)|^2 = \frac{A^2 + AB + B^2}{(B - A + 3)^2} \mu^2 + \frac{A - B}{B - A + 3} \mu + 1.$$

Then the derivative $|\lambda(\mu)|$ evaluated at $\mu = 0$ is

$$\frac{d}{d\mu} |\lambda(\mu)|_0 = \frac{A - B}{2(B - A + 3)},$$

which is greater than zero since $B - A + 3 = \alpha + \beta + 1 > 0$ and $A > B$. Therefore, we conclude (iii) $(d/d\mu)|\lambda(\mu)| > 0$ at $\mu = 0$.

At $\mu = 0$, after substituting $f(A, B) = b - 1$ into $\lambda(\mu)$ we obtain

$$\lambda(0) = \frac{(A + B)^2 + 2AB}{2(A^2 + AB + B^2)} + \frac{\sqrt{3}(A - B)(A + B)}{2(A^2 + AB + B^2)} i.$$

Since $A > B > 0$, the real part of $\lambda(0)$ is positive and the imaginary part of $\lambda(0)$ is never zero. The eigenvalues $\lambda(0)$ and $\bar{\lambda}(0)$ cannot equal ± 1 , $\pm i$ or $(-1 \pm \sqrt{3}i)/2$, which are the possible roots of $x^k = 1$ for $k = 1, 2, 3, 4$. Therefore, condition (iv) $\lambda^k(0) \neq 1$ for $k = 1, 2, 3, 4$ holds. By the Pioncaré–Andronov–Hopf bifurcation in Hale and Koçak [7, Theorem 15.31, page 474], conditions (i)–(iv) are sufficient conditions for a Hopf bifurcation to occur at $\mu = 0$ in system (19). Therefore, at P_0 in system (5) there is a Hopf bifurcation. \square

Asymmetric Discrete M-L Model

For the asymmetric M-L model (5), its interior equilibrium $P_0 = (p_1, p_2, p_3)$ satisfies

$$\begin{aligned} p_1 + \alpha_1 p_2 + \beta_1 p_3 &= 1, \\ \beta_2 p_1 + p_2 + \alpha_2 p_3 &= 1, \\ \alpha_3 p_1 + \beta_3 p_2 + p_3 &= 1. \end{aligned} \quad (21)$$

Let $A_i = 1 - \alpha_i$ and $B_i = \beta_i - 1$. Then $0 < A_i < 1$ and $B_i > 0$. Let Δ be the determinant of the coefficient matrix of the linear system (21). Then

$$\begin{aligned} \Delta &= B_1 B_2 B_3 + B_1 B_2 + B_2 B_3 + B_3 B_1 + A_1 B_2 + A_2 B_3 \\ &\quad + A_3 B_1 + A_1 A_2 + A_2 A_3 + A_3 A_1 (1 - A_2). \end{aligned} \quad (22)$$

Let

$$\Delta_1 = A_1 A_2 + A_2 B_3 + B_3 B_1, \quad \Delta_2 = A_2 A_3 + A_3 B_1 + B_1 B_2, \quad \Delta_3 = A_3 A_1 + A_1 B_2 + B_2 B_3.$$

Then $\Delta > 0$ and $\Delta_i > 0$ for $i = 1, 2, 3$ and we have $P_0 = (\Delta_1/\Delta, \Delta_2/\Delta, \Delta_3/\Delta)$ by solving the linear system (21) for P_0 using Cramer's Rule. Let

$$g(A_1, A_2, A_3, B_1, B_2, B_3) = \frac{\Delta(B_1B_2B_3 - A_1A_2A_3)}{\Delta_1\Delta_2\Delta_3}. \quad (23)$$

Then we have the following theorem for the local stability of P_0 for the asymmetric M-L system (5).

THEOREM 3 Assume $\alpha_i = 1 - A_i$ and $\beta_i = B_i + 1$ for $i = 1, 2, 3$. Then the equilibrium $P_0 = (p_1, p_2, p_3)$ of the asymmetric M-L system (5) is l.a.s if $g(A_1, A_2, A_3, B_1, B_2, B_3) < b - 1$, and unstable if $g(A_1, A_2, A_3, B_1, B_2, B_3) > b - 1$. As $b \rightarrow 1^-$, the stability criterion approaches that of the continuous M-L Model (2), i.e. P_0 is l.a.s. if $B_1B_2B_3 < A_1A_2A_3$ and unstable if $B_1B_2B_3 > A_1A_2A_3$.

Note The function $g(A_1, A_2, A_3, B_1, B_2, B_3)$ is the multiplication of a positive function, $\Delta/(\Delta_1\Delta_2\Delta_3)$, and the difference of the product of the dominant factors and the product of the subdominant factors, $B_1B_2B_3 - A_1A_2A_3$. Theorem 1 is a special case of Theorem 3. It is not difficult to check that $g(A, A, A, B, B, B) = f(A, B)$. Theorem 3 says that if the dominant factor is much less than subdominant factor, $g(A_1, A_2, A_3, B_1, B_2, B_3) < b - 1 < 0$, the three species will have a stable positive equilibrium. However, for the continuous M-L model, the three species have a positive equilibrium if $g(A_1, A_2, A_3, B_1, B_2, B_3) < 0$. Therefore, for the discrete model to be close to the continuous model we need the seedbank coefficient b to be close to 1.

Proof To determine the local stability of P_0 , we need to consider the eigenvalues of the Jacobian matrix J_{P_0} . For the discrete asymmetric system (5), the characteristic polynomial for the Jacobian matrix evaluated at $P_0 = (p_1, p_2, p_3)$ has the form $(x - b)(x^2 + a_1x + a_2) = 0$ because b is an eigenvalue. The coefficients a_1 and a_2 are

$$\begin{aligned} a_1 &= (1 - b)(p_1 + p_2 + p_3 - 1) - 2, \\ a_2 &= 1 + (b - 1)(p_1 + p_2 + p_3 - 1) + (b - 1)^2\Phi, \end{aligned} \quad (24)$$

where

$$\Phi = \frac{\Delta_1\Delta_2\Delta_3}{\Delta^2} > 0.$$

We can apply the Jury condition to $x^2 + a_1x + a_2 = 0$ (see Ref. [13]) to show the magnitude of $\lambda_{1,2}$ less than one. However, we also want to show the eigenvalues are complex. The discriminant of $x^2 + a_1x + a_2 = 0$ is

$$a_1^2 - 4a_2 = -(b - 1)^2[4\Phi - (p_1 + p_2 + p_3 - 1)^2]. \quad (25)$$

Since $p_i = \Delta_i/\Delta$ for $i = 1, 2, 3$, we have

$$p_1 + p_2 + p_3 - 1 = \frac{1}{\Delta}(A_1A_2A_3 - B_1B_2B_3). \quad (26)$$

The discriminant Eq. (25) becomes

$$-\frac{(b - 1)^2}{\Delta^2}[4\Delta_1\Delta_2\Delta_3 - (B_1B_2B_3 - A_1A_2A_3)^2],$$

which is less than zero because all of the parameters A_i 's and B_i 's are positive and both negative terms $-A_1^2 A_2^2 A_3^2$ and $-B_1^2 B_2^2 B_3^2$ can be cancelled out by expanding $4\Delta_1 \Delta_2 \Delta_3$. Therefore, the two eigenvalues satisfying $x^2 + a_1 x + a_2 = 0$ are complex numbers,

$$\lambda_{1,2} = -\frac{1}{2}a_1 \pm \frac{1}{2}\sqrt{4a_2 - a_1^2}i.$$

Hence, the Jury condition can be reduced to

$$|\lambda_{1,2}| < 1 \Leftrightarrow a_2 < 1.$$

This leads to

$$\frac{1 - p_1 - p_2 - p_3}{\Phi} < b - 1. \quad (27)$$

Substituting $\Phi = \Delta_1 \Delta_2 \Delta_3 / \Delta^2$ and the expression for $1 - p_1 - p_2 - p_3$ in Eq. (26), the inequality (27) becomes

$$\frac{\Delta(B_1 B_2 B_3 - A_1 A_2 A_3)}{\Delta_1 \Delta_2 \Delta_3} < b - 1. \quad (28)$$

Hence, $g(A_1, A_2, A_3, B_1, B_2, B_3) < b - 1$. Therefore,

$$|\lambda_{1,2}| < 1 \text{ if and only if } g(A_1, A_2, A_3, B_1, B_2, B_3) < b - 1.$$

We conclude that if $g(A_1, A_2, A_3, B_1, B_2, B_3) < b - 1$, P_0 is l.a.s.

Since Δ and Δ_i 's are all positive, if we let $b \rightarrow 1^-$, the inequality (28) becomes $B_1 B_2 B_3 - A_1 A_2 A_3 < 0$ which is the stability criterion for the asymmetric continuous M-L model (2). \square

We have shown that both eigenvalues λ_1 and λ_2 in Theorem 3 are complex numbers. The condition $|\lambda_{1,2}| = 1$ implies $g(A_1, A_2, A_3, B_1, B_2, B_3) = b - 1$. If we let $\lambda(\mu) = -(1/2)a_1 + (1/2)(4a_2 - a_1^2)^{1/2}i$ and $\mu = g - (b - 1)$, then $|\lambda(\mu)| = 0$ if and only if $\mu = 0$. Using similar arguments as we did for the symmetric case, when $\mu = 0$, the asymmetric system (5) has a 2-dimensional center manifold at P_0 . We can use the method of center manifolds to reduce the system to

$$\begin{pmatrix} w'_2 \\ w'_3 \end{pmatrix} = \begin{pmatrix} \operatorname{Re}(\lambda) & -\operatorname{Im}(\lambda) \\ \operatorname{Im}(\lambda) & \operatorname{Re}(\lambda) \end{pmatrix} \begin{pmatrix} w_2 \\ w_3 \end{pmatrix} + \text{h.o.t.} \quad (29)$$

On the center manifold we have the following theorem that is similar to Theorem 2.

THEOREM 4 *A Hopf bifurcation occurs at P_0 in the asymmetric M-L model (5) when $g(A_1, A_2, A_3, B_1, B_2, B_3) = b - 1$.*

Proof Let $\mu = g - (b - 1)$ and $\lambda(\mu) = -(1/2)a_1 + (1/2)(4a_2 - a_1^2)^{1/2}i$, where a_1 and a_2 are as in Eq. (24). Then $\lambda(\mu)$ and $\bar{\lambda}(\mu)$ are two of the eigenvalues of J_{P_0} . Let F be defined by the system (29), such that $F : \mathbb{R} \times \mathbb{R}^2 \rightarrow \mathbb{R}^2$; $(\mu, \mathbf{w}) \rightarrow F(\mu, \mathbf{w})$, then (i) $F(\mu, 0) = 0$ for μ near 0.

J_{P_0} always has complex conjugate eigenvalues since the discriminant of $x^2 + a_1 x + a_2 = 0$ is negative. Therefore, (ii) $DF(\mu, 0)$ has two non-real eigenvalues $\lambda(\mu)$ and $\bar{\lambda}(\mu)$ for μ near 0, with $|\lambda(0)| = 1$.

At $\mu = 0$ we have

$$\mu = 0 \Rightarrow g = b - 1 \Rightarrow g < 0 \Rightarrow B_1 B_2 B_3 < A_1 A_2 A_3. \quad (30)$$

After a lengthy calculation we obtain

$$|\lambda(\mu)|^2 = 1 + \frac{A_1 A_2 A_3 - B_1 B_2 B_3}{\Delta} \mu + \frac{\Delta_1 \Delta_2 \Delta_3}{\Delta^2} \mu^2.$$

Then the derivative of $\lambda(\mu)$ evaluated at $\mu = 0$ is

$$\frac{d}{d\mu} |\lambda(\mu)|_0 = \frac{A_1 A_2 A_3 - B_1 B_2 B_3}{2\Delta},$$

which is greater than zero since $\Delta > 0$ and $A_1 A_2 A_3 > B_1 B_2 B_3$. Therefore, we conclude

(iii) $(d/d\mu)|\lambda(\mu)| > 0$ at $\mu = 0$.

Substitute $g = b - 1$ into the expression $\lambda(\mu)$ so that $\mu = 0$. Then the real part of $\lambda(0)$ is

$$\frac{1}{2\Delta_1 \Delta_2 \Delta_3} (2\Delta_1 \Delta_2 \Delta_3 + 2A_1 A_2 A_3 B_1 B_2 B_3 - A_1^2 A_2^2 A_3^2 - B_1^2 B_2^2 B_3^2),$$

which is positive since the two negative terms $A_1^2 A_2^2 A_3^2$ and $B_1^2 B_2^2 B_3^2$ can be cancelled out by expanding $2\Delta_1 \Delta_2 \Delta_3$. So the real part of $\lambda(0)$ is positive. And we know that the imaginary part of $\lambda(0)$ is never zero. Therefore, the eigenvalues $\lambda(0)$ and $\bar{\lambda}(0)$ cannot equal ± 1 , $\pm i$, or $(-1 \pm \sqrt{3}i)/2$, which are the possible roots of $x^k = 1$, for $k = 1, 2, 3, 4$. Therefore, (iv) holds: $\lambda^k(0) \neq 1$ for $k = 1, 2, 3, 4$.

By the Pioncaré–Andronov–Hopf bifurcation in Hale and Koçak [7, theorem 15.31, page 474], conditions (i)–(iv) are sufficient conditions for a Hopf bifurcation to occur at the origin in $w_2 - w_3$ space when μ is near 0. Therefore, a Hopf bifurcation occurs at P_0 in system (5) near $g = b - 1$. \square

DISCRETE MODEL WITH A ZERO EQUILIBRIUM

General n -species Model

The system of difference equations (6) is similar to system (4), but system (6) has an additional equilibrium, the zero equilibrium. All of the results for systems (6) and (7) are similar to those for models (4) and (5).

LEMMA 6 For system (6), if $x_i(0) > 0$, then

$$0 \leq \liminf_{t \rightarrow \infty} x_i(t) \leq \limsup_{t \rightarrow \infty} x_i(t) \leq 2.$$

In addition, if $0 < x_i(0) \leq 2$, then $0 < x_i(t) \leq 2$ for $t > 0$.

Proof Note that from Eq. (6) we have $b_i x_i(t) \leq x_i(t+1) \leq 2(1 - b_i) + b_i x_i(t)$. The lemma follows immediately from iteration of the above inequalities:

$$b_i^t x_i(0) \leq x_i(t) \leq 2(1 - b_i^t) + b_i^t x_i(0). \quad \square$$

Note that if the interior of equilibrium P_0 of Eq. (6) exists, then P_0 also satisfies (11). The Jacobian matrix J_{P_0} is

$$J_{P_0} = I - \text{diag} \left[\frac{1}{2}(1 - b_i)p_i \right] \begin{pmatrix} 1 & k_{12} & \cdot & k_{1n} \\ k_{21} & 1 & \cdot & k_{2n} \\ \cdot & \cdot & \ddots & \cdot \\ k_{n1} & k_{n2} & \cdot & 1 \end{pmatrix}.$$

LEMMA 7 For system (6), if $b_i = b$ for all $i = 1, 2, \dots, n$, and the interior equilibrium $P_0 = (p_1, p_2, \dots, p_n)$ exists, then $(b + 1)/2$ is an eigenvalue for J_{P_0} and $(p_1, p_2, \dots, p_n)^t$ is an eigenvector associated with $(b + 1)/2$.

Proof The proof is similar to Lemma 2. \square

LEMMA 8 For system (6), if $b_i = b$ for all $i = 1, 2, \dots, n$, and the interior equilibrium $P_0 = (p_1, p_2, \dots, p_n)$ exists, then the set $\Gamma = \{(cp_1, cp_2, \dots, cp_n) | c > 0\}$ is an invariant set. In addition, if $X(0) \in \Gamma$, then $X(t) \rightarrow P_0$ as $t \rightarrow \infty$.

To prove Lemma 8 we need the following result from difference equations.

THEOREM 5 If $f(x)$ is a continuous function on $[0, a)$ and $f : [0, a) \rightarrow [0, a)$, $0 < a \leq \infty$ such that $x < f(x) < \bar{x}$ for $0 < x < \bar{x}$ and $\bar{x} < f(x) < x$ for $x > \bar{x}$, then the difference equation $x_{t+1} = f(x_t)$ has a globally asymptotically stable equilibrium at \bar{x} for any $x_0 \in (0, a)$.

Proof (of Lemma 8) The proof is similar to Lemma 3, but note that

$$\xi_{t+1} = f(\xi_t), \quad \text{where } f(x) = \frac{2(1-b)x}{1+x} + bx.$$

In this case $f(x)$ has a fixed point at 1 and $f(x)$ satisfies the hypotheses of Theorem 5. Hence, $\lim_{t \rightarrow \infty} \xi_t = 1$. \square

Discrete May–Leonard Model

For the discrete M-L model (7), at the extinction equilibrium $(0, 0, 0)$, the Jacobian matrix is:

$$J_0 = \begin{pmatrix} 2-b & 0 & 0 \\ 0 & 2-b & 0 \\ 0 & 0 & 2-b \end{pmatrix}.$$

Since $0 < b < 1$, all of its eigenvalues have magnitudes greater than one. The zero equilibrium is a repeller, the same behavior as the continuous M-L model (2).

The Jacobian matrix evaluated at the interior equilibrium $P_0 = (p_1, p_2, p_3)$ is different:

$$J_{P_0} = I - \text{diag} \left[\frac{1}{2}(1-b)p_i \right] \begin{pmatrix} 1 & \alpha_1 & \beta_1 \\ \beta_2 & 1 & \alpha_2 \\ \alpha_3 & \beta_3 & 1 \end{pmatrix}.$$

Define $f(A, B)$ and $g(A_1, A_2, A_3, B_1, B_2, B_3)$ as before. We have similar results for system (7).

All the proofs of the following Theorems 6–9 are similar to the corresponding theorems in section 2. To verify the results, replace $b - 1$ with $(b - 1)/2$ in the proofs.

THEOREM 6 Assume $\alpha_i = \alpha = 1 - A$ and $\beta_i = \beta = B + 1$ for $i = 1, 2, 3$. Then the equilibrium $P_0 = (p, p, p)$ of the symmetric M-L system (7) is l.a.s if $f(A, B) < (b - 1)/2$, and unstable if $f(A, B) > (b - 1)/2$. And as $b \rightarrow 1^-$, the stability criterion approaches that of the continuous model (2), i.e. P_0 is l.a.s. if $\alpha + \beta < 2$ and unstable if $\alpha + \beta > 2$.

THEOREM 7 A Hopf bifurcation occurs at P_0 in the symmetric M-L system (7) when $f(A, B) = (b - 1)/2$.

THEOREM 8 Assume $\alpha_i = 1 - A_i$ and $\beta_i = B_i + 1$ for $i = 1, 2, 3$. Then the equilibrium $P_0 = (p_1, p_2, p_3)$ of the symmetric M-L system (7) is l.a.s if $g(A_1, A_2, A_3, B_1, B_2, B_3) < (b - 1)/2$, and unstable if $g(A_1, A_2, A_3, B_1, B_2, B_3) > (b - 1)/2$. As $b \rightarrow 1^-$, the stability criterion approaches that of the continuous M-L Model (2), i.e. P_0 is l.a.s. if $B_1 B_2 B_3 < A_1 A_2 A_3$ and unstable if $B_1 B_2 B_3 > A_1 A_2 A_3$.

THEOREM 9 A Hopf bifurcation occurs at P_0 in the asymmetric M-L system (7) when $g(A_1, A_2, A_3, B_1, B_2, B_3) = (b - 1)/2$.

NUMERICAL EXAMPLES

We use the programming and graphing capability of Matlab to show some numerical examples and illustrate some of our findings.

Let $b = 0.75$ and $\alpha = 0.4$. We only illustrate the dynamics for the symmetric M-L models (5) or (7). For the asymmetric models, the dynamics are similar.

If $\beta = 1.4$, then $f(A, B) < b - 1$ and $\alpha + \beta < 2$. We show in Fig. 2(a) that P_0 is l.a.s. for the discrete model as well as for the continuous model in Fig. 2(b).

If β is increased to 1.5193844696, then $f(A, B) = b - 1$ and $\alpha + \beta < 2$. In Fig. 3(a), we see a Hopf bifurcation occurs and the solution approaches a stable periodic solution for the discrete M-L model (5). In Fig. 3(b), P_0 is still l.a.s. for the continuous M-L model (2).

If $\beta = 1.6$, then $f(A, B) > b - 1$ and $\alpha + \beta = 2$. We see in Fig. 4(a) that P_0 is unstable but we also observe a stable periodic solution. In Fig. 4(b), a Hopf bifurcation occurs in the continuous M-L model; there are a family of neutrally stable periodic solutions. Figure 4(b) shows two of these periodic solutions.

If $\beta = 1.8$, the equilibrium P_0 of both the continuous and the discrete M-L models is unstable (Fig. 5). The solution of the discrete model approaches a stable periodic solution (Fig. 5(a)), but the solution of the continuous model approaches the boundary cycle solution (Fig. 5(b)).

If β is large enough, for example, $\beta = 4.0$, then both the discrete and continuous M-L models show similar behavior. Their solutions approach the boundary cycle solution, which is heteroclinic cycle joining the boundary equilibria—(1, 0, 0), (0, 1, 0), (0, 0, 1). (Fig. 6).

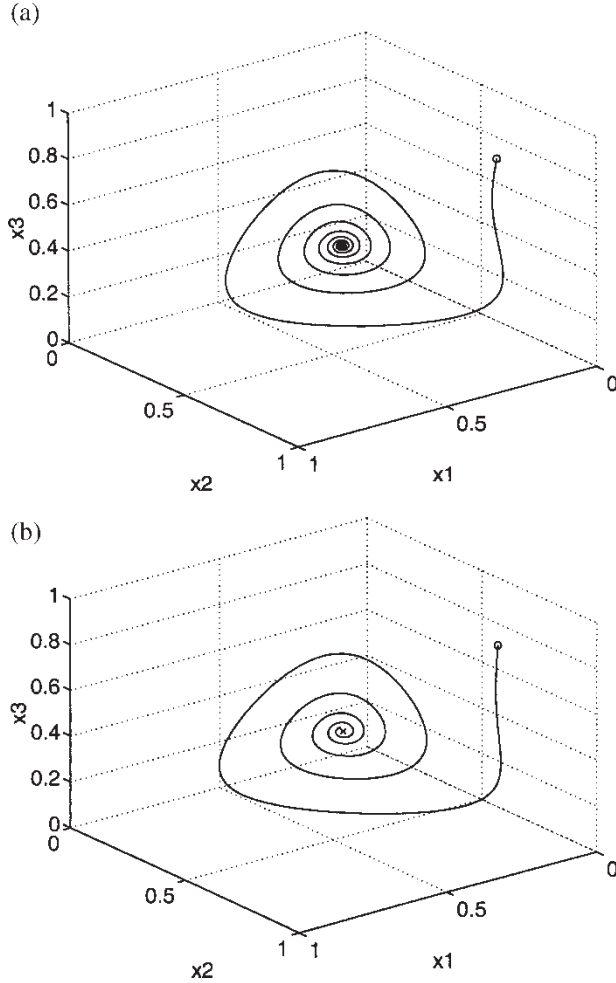


FIGURE 2 $\alpha = 0.4$, $\beta = 1.4$ (a) For the discrete system (5), $b = 0.75$, $f(A, B) = -0.7368 < b - 1$, P_0 (marked as X in the graph) is l.a.s. (b) For the continuous system (2), $\alpha + \beta < 2$, P_0 is l.a.s.

To confirm that a Hopf bifurcation occurs for the discrete M-L model (7), we choose $\beta = 1.55750973633500$ such that $f(A, B) = (b - 1)/2$. In Fig. 7, the solution approaches a stable periodic solution for the discrete M-L system with a zero equilibrium, model (7).

We compare the two discrete M-L models by choosing β to be 1.53, then $b - 1 < f(A, B) < (b - 1)/2$. Thus, P_0 is unstable for the discrete M-L system (5) with no zero equilibrium and is l.a.s. for system (7) with a zero equilibrium. See Fig. 8.

In our numerical experiments, we see that the Hopf bifurcation of the discrete M-L system with no zero equilibrium occurs if $\mu = f(A, B) - (b - 1) = 0$. But μ can range from 0 to 1.25 and we still see periodic solutions. In contrast to the bifurcation in the continuous model, the bifurcation is not degenerate. We also learn that the bifurcation is *supercritical*, i.e. solutions approach a stable periodic solution.

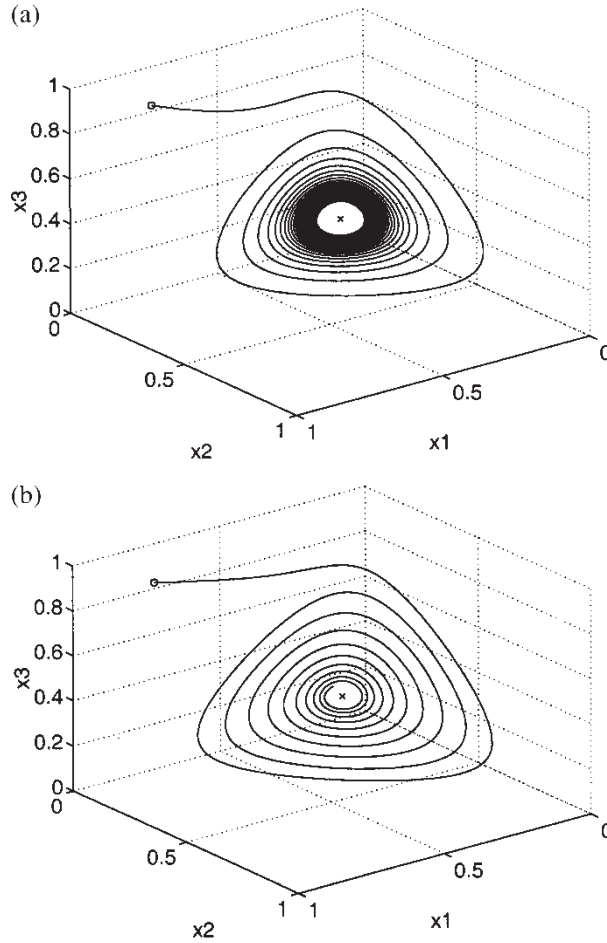


FIGURE 3 $\alpha = 0.4$, $\beta = 1.5193844697$ (a) For the discrete system (5), $b = 0.75$, $f(A, B) = -0.25 = b - 1$. We observe that solutions approach a stable periodic orbit. (b) For the continuous system (2), $\alpha + \beta < 2$, P_0 is l.a.s.

CONCLUSION AND FUTURE DIRECTIONS

Our purpose is to compare the dynamics of the discrete M-L models to the continuous M-L models. We have defined $B_i = \beta_i - 1 > 0$ as the dominant factor and $A_i = 1 - \alpha_i > 0$ as the subdominant factor. For the asymmetric discrete M-L model (5) if none of the three species are very dominant, $g(A_1, A_2, A_3, B_1, B_2, B_3) < b - 1 < 0$ then P_0 is locally asymptotically stable. For the continuous M-L model (2), however, P_0 is l.a.s. if $g(A_1, A_2, A_3, B_1, B_2, B_3) < 0$. Therefore, for the discrete model (5) to be close to the continuous model (2), the seedbank coefficient b needs to be close to 1, which is not a very reasonable assumption for the annual plants competition model (5).

The two discrete M-L systems (5) and (7) derived from a model for plant competition have similar dynamics. For the asymmetric M-L models, if $\mu = g - (b - 1) < 0$

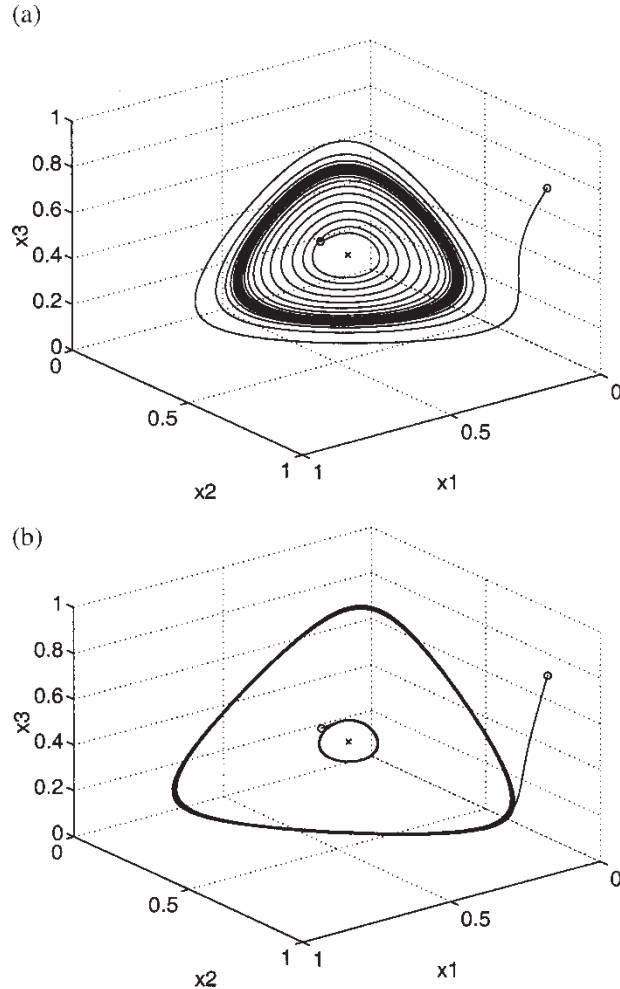


FIGURE 4 $\alpha = 0.4$, $\beta = 1.6$. (a) For the discrete system (5), $b = 0.75$, $f(A, B) = 0 > b - 1$, P_0 is unstable, we observe that the solutions approach a periodic solution. (b) For the continuous system (2), $\alpha + \beta = 2$, Hopf bifurcation occurs. We observe neutrally stable periodic solutions.

(or for system (7), $\mu = g - (b - 1)/2 < 0$), then P_0 is l.a.s., and if $\mu > 0$, then P_0 is unstable. The local dynamics of the discrete models (5) or (7) approach the local dynamics of continuous M-L model (2) as b approaches 1^- . Therefore, the continuous model is the limiting case of the discrete models.

We have shown that a Hopf bifurcation occurs in both the discrete systems (5) and (7). And through numerical experiments, the bifurcation appears to be supercritical. To show the supercritical bifurcation we need the normal form [19], but our systems (5) and (7) contain too many parameters and are too complicated to put in normal form. The Hopf bifurcation for the continuous M-L model is degenerate (in our notation, when $\mu = 0$; periodic solutions only exist when $\mu = 0$). In the discrete models, there exist periodic solutions if $\mu \geq 0$ and μ is not necessary small. In our numerical experiments, $b = 0.75$ and $\alpha = 0.4$, μ can be large as 1.25 and we still see

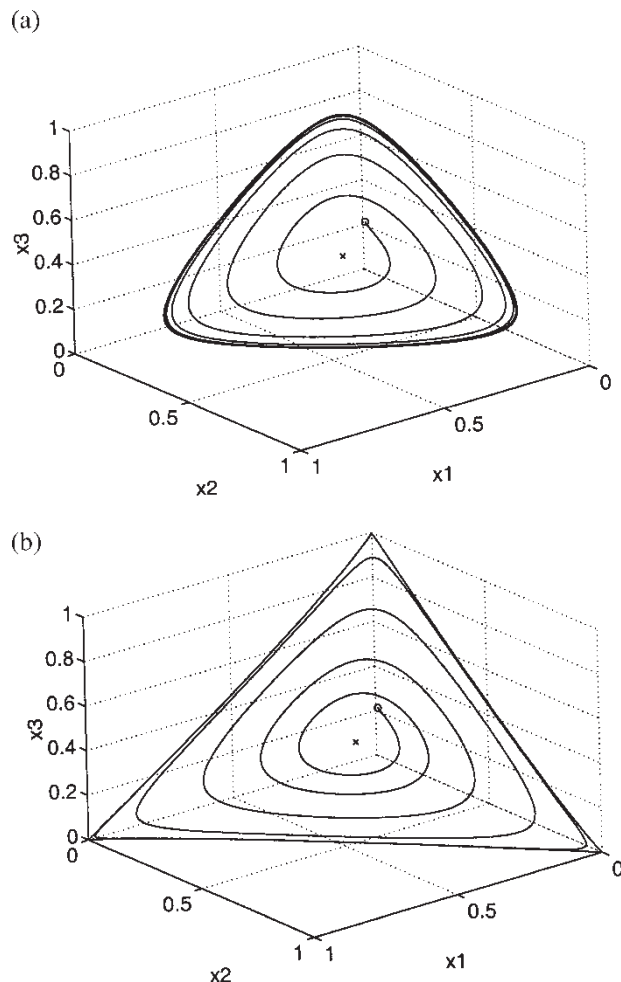


FIGURE 5 $\alpha = 0.4$, $\beta = 1.8$. (a) For the discrete system (5), $b = 0.75$, $f(A, B) = 0.4324 > b - 1$, P_0 is unstable. We also observe a stable periodic solution. (b) For the continuous system (2), $\alpha + \beta > 2$, P_0 is unstable.

the periodic solutions. The quantity $\mu = 1.25$ is significant since most of the parameters α_i and β_i are between 0 and 1.

Unlike the continuous M-L model, most of the results for our discrete models are local. The numerical simulations indicate that P_0 is globally stable for positive initial conditions. This is not easy to prove theoretically.

There are other versions of discrete competition models [8,11] that exhibit dynamics similar to the continuous M-L model. We study them in separate investigations [16,17]. Also in this paper, we showed the existence of Hopf bifurcations, but did not confirm whether they are super-critical or sub-critical bifurcations because of the difficulty in finding their normal forms. We will leave this as a future research project.

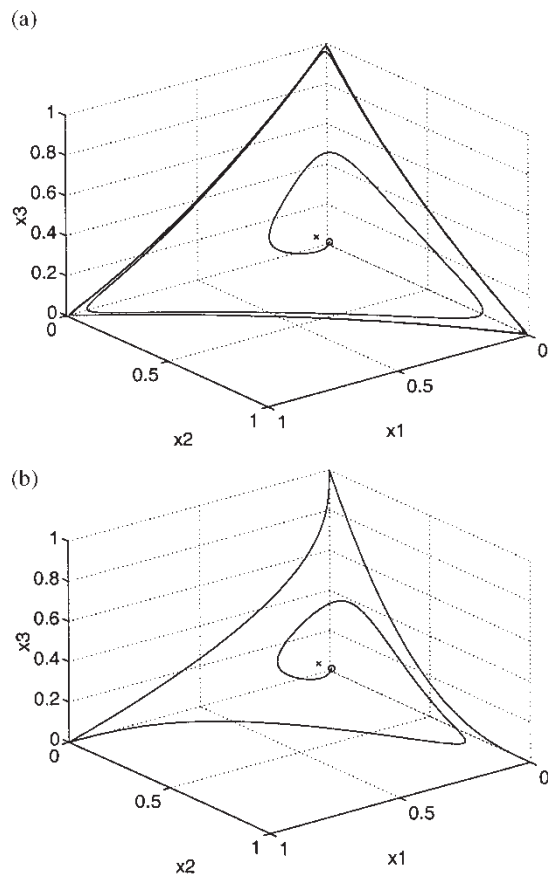


FIGURE 6 $\alpha = 0.4$, $\beta = 4.0$. (a) For the discrete system (5), $b = 0.75$, $f(A, B) = 1.1613 > b - 1$. The solution approaches e_2 , then e_1 , then e_3 . (b) For the continuous system (2), $\alpha + \beta > 2$. The solution approaches e_2 , then e_1 , then e_3 .

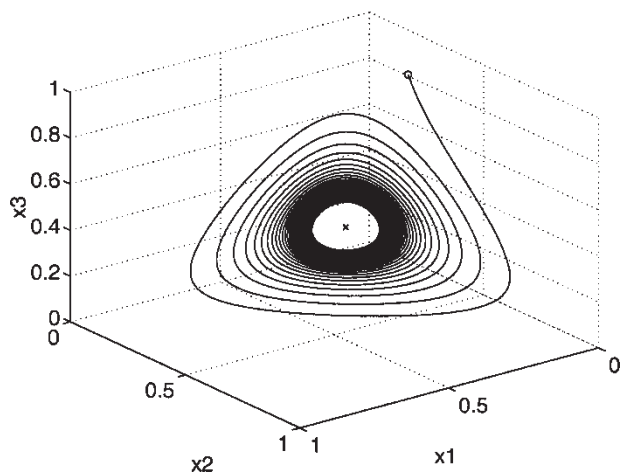


FIGURE 7 For the discrete system (7) with zero equilibrium, $b = 0.75$, $\alpha = 0.4$, $\beta = 1.55750973633500$, $f(A, B) = -0.125 = (b - 1)/2$. Hopf bifurcation occurs at P_0 .

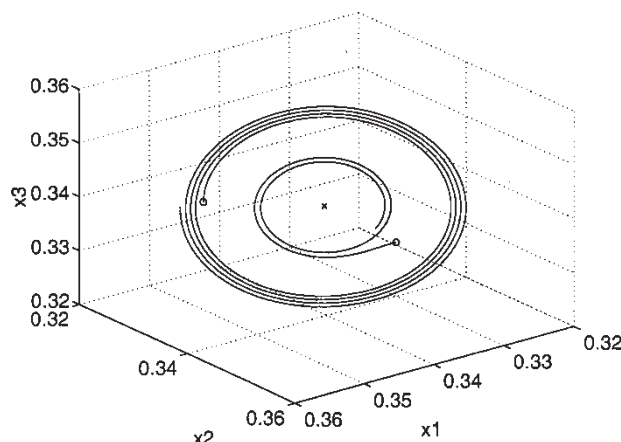


FIGURE 8 In the case $b = 0.75$, $\alpha = 0.4$, $\beta = 1.53$, $b - 1 < f(A, B) = -0.2139 < (b - 1)/2$, the solution of model (5) with no zero equilibrium spirals out (P_0 unstable), and the solution of model (7) with zero equilibrium spirals in (P_0 is stable).

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