Some Discrete Competition Models and the Principle of Competitive Exclusion

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Abstract

One of the fundamental tenets of ecology is the Competitive Exclusion Principle. According to this principle too much interspecific competition between two species results in the exclusion of one species. This Principle is supported by a wide variety of theoretical models, of which the Lotka/Volterra model based on differential equations is the most familiar. It is perhaps less well known that difference equations also played an important role in the historical development of the Competitive Exclusion Principle. The Leslie/Gower model was used in conjunction with influential competition experiments using species of *Tribolium* (flour beetles) carried out in the first half of the last century. This difference equation model exhibits the same dynamic scenarios as does the Lotka/Volterra model and also supports the Competitive Exclusion Principle. A recently developed competition for *Tribolium* species, however, exhibits a larger variety of dynamic scenarios and competitive outcomes, some of which seemingly stand in contradiction to the Principle. We discuss features of this model that differentiate it from the Leslie/Gower model. We give a simpler, lower dimensional "toy" model that illustrates some non-Lotka/Volterra dynamics.

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1 INTRODUCTION

Mathematical models of competition play a central role in theoretical ecology. Historically, the famous Lotka/Volterra competition model (and many other similar models) focused the study of interspecific competition on the notions of competitive exclusion, limiting similarity and ecological niche (notions that in fact had been around at least

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since Charles Darwin). The overwhelming majority of competition models supports the Principle of Competitive Exclusion, which asserts that “too much” interspecific competition results in the elimination of a species [10], [34], [50]. According to this principle, coexistence is not possible when one species in some way dominates a competitive interaction by direct confrontation and interference or by more efficiently utilizing one or more limited resources (e. g., see [2], [3], [4], [29], [30], [32], [40], [41], [48], [49], [57], [59], [62], [63], [65]). Put another way, to survive a species must find ways to avoid interspecific competition [1], [51]. Despite early criticism of this principle (e.g. see, [5], [6], [8]), it underlies (not always so explicitly) most thinking about the structure of ecosystems.

The prototypical competition model is, of course, the Lotka/Volterra system of two differential equations that describes the dynamics of two competing species. That model shows – as do virtually all existing theoretical models of interference competition – that coexistence is not possible (i.e., one species asymptotically goes extinct) when the intensity of interspecific competition is high, as measured by the magnitude of competition coefficients in the equations. From the 1930's to 1960's several biologists addressed this competitive exclusion principle by means of laboratory experiments involving pairs of species. Perhaps the most notable of these competition experiments were those of G. F. Gause [33], using yeast and protozoa, and T. Park [52], [53], [54] using insects with a more complicated life cycle (flour beetles of the genus *Tribolium*). The experimental results, which are today considered classic and still appear in most ecology textbooks, are interpreted as supporting the principle of competitive exclusion. One of Park's later experimental studies, however, yielded a “difficult to interpret” result that caught his attention and that of his renown collaborator P. H. Leslie [55], [46]. This result was seemingly at odds with the competitive exclusion principle in that neither species was eliminated during the course of the experiment (over 32 generations). Furthermore, the experimental results imply a dynamic scenario not permitted by Lotka/Volterra theory (nor, for that matter, by any competition model known to us), namely, a scenario with three attractors, two of which imply competitive exclusion and one of which implies competitive coexistence. Park and his collaborators addressed this anomalous “coexistence case” (as Park referred to it) with both experimental and model studies, but in the end they offered no theoretical or biological explanation [28], [46].

Park and Leslie did not use the Lotka/Volterra model in their competition studies. Instead they used a system of difference equations that predict the population abundance from one census to the next. Their model is based on the discrete logistic equation [45], [56]

$$x_{t+1} = b\frac{1}{1+x_t}x_t, \quad b > 0 \tag{1}$$

This difference equation defines a monotone map and therefore implies all solutions monotonically equilibrate. (The difference equation (1) is related to the logistic differential equations as follows. If a solution of the logistic differential equation is evaluated at equally spaced time intervals, the resulting sequence of population densities will satisfy a difference equation of this form.) If $b < 1$ then $x(t) \to 0$; if $b > 1$

then $x(t) \to b-1$. The Leslie/Gower competition model used by Park and Leslie in their studies [47] is given by the difference equations

$$\begin{aligned} x_{t+1} &= b_1 \frac{1}{1+x_t+c_1 y_t} x_t \\ y_{t+1} &= b_2 \frac{1}{1+c_2 x_t+y_t} y_t. \end{aligned} \tag{2}$$

This model couples two discrete logistic populations by means of the interspecific competition terms $c_1 y_t$ and $c_2 x_t$, which serve to decrease the recruitment of each species (at the next time step) due to the presence of the other species.

The system of difference equations (2) defines a monotone (semi) flow and has exactly the same set of possible dynamic scenarios as the Lotka/Volterra model [20], [60], [61]. If there exists no positive equilibrium then all orbits in the positive cone tend to an exclusion equilibrium lying on one of the positive coordinate axes. If there is a positive equilibrium, then it is either globally asymptotically stable in the positive cone (competitive coexistence) or it is a saddle. In the latter so-called "saddle" case all orbits in the positive cone not lying on the stable manifold tend to an exclusion equilibrium. (Thus, the Leslie/Gower model is the appropriate discrete analog of the Lotka/Volterra competition model.) The coexistence case occurs only if the competition coefficients c_1 and c_2 are sufficiently small (this is the competitive exclusion principle). Moreover, if both coefficients c_1 and c_2 are sufficiently large, then the saddle (competitive exclusion) case occurs.

The anomalous result in Park's experiment arose in a study of the saddle case when one culture did not result in competitive exclusion. Edmunds et al. [28] put forth an hypothesis that explains this result. Their hypothesis is based on an interference competition model different from (2). Their model can exhibit complex, dynamic scenarios that are considerably different from the four scenarios implied by the classic Lotka/Volterra theory.

The competition model studied in [28] is built on a dynamic model for stage structured species (also see [27]). The state variables in the model are the numbers of individuals in each of three distinct life cycle stages: a growth (larval) stage, a quiescent (pupal) stage, and a reproductive (adult) stage. The "LPA model"

$$\begin{aligned} L_{t+1} &= bA_t \exp(-c_{EL} L_t - c_{EA} A_t) \\ P_{t+1} &= (1-\mu_L) L_t \\ A_{t+1} &= P_t \exp(-c_{PA} A_t) + (1-\mu_A) A_t \end{aligned} \tag{3}$$

has exponential nonlinearities common to many population dynamics models. In the case of the *Tribolium* species used by Park in his experiments, these exponential nonliearities can be derived from an important mechanism that drives their dynamics, namely cannibalism [14], [19], [22]. The fact that movable stages of each species (larvae and adults) cannibalize both their own immovable stages (pupae and eggs) and those of the other species leads to an interference competitive interaction modeled by the equations

$$\begin{aligned}
L_{t+1} &= b_1 A_t \exp(-c_{EL} L_t - c_{EA} A_t) \exp(-c_{El} l_t - c_{Ea} a_t) \\
P_{t+1} &= (1 - \mu_L) L_t \\
A_{t+1} &= P_t \exp(-c_{PA} A_t) \exp(-c_{Pa} a_t) + (1 - \mu_A) A_t \\
l_{t+1} &= b_2 a_t \exp(-c_{el} l_t - c_{ea} a_t) \exp(-c_{eL} L_t - c_{eA} A_t) \\
p_{t+1} &= (1 - \mu_l) l_t \\
a_{t+1} &= p_t \exp(-c_{pa} a_t) \exp(-c_{pA} A_t) + (1 - \mu_a) a_t.
\end{aligned} \tag{4}$$

The LPA model (3) has a considerable track record of successes in describing the dynamics of *Tribolium* (and in particular the same species used by Park) [9], [11], [12], [13], [17], [18], [19], [22], [23], [24], [25], [26], [36], [37], [38], [39], [44]. Because of this record, we anticipate that one could successfully use the competition LPA model (4) to account for the results of Park's classic competition experiments and, perhaps, the anomalous result described above.

Edmunds [27] gives some fundamental analysis of (4). That analysis, together with computer explorations, shows that the competition model can exhibit the classic Lotka/Volterra dynamic scenarios for certain parameter ranges. However, the model can also exhibit many other dynamic scenarios unlike those of Lotka/Volterra. Edmunds et al. [28] use one such non-Lotka/Volterra scenario to offer a possible explanation of Park's anomalous result.

Using parameter values consistent with those estimated for *Tribolium casteneum* in many previous studies, Edmunds et al. found that coexistence was possible with *increases* in certain *inter*specific competition coefficients in the model (4), seemingly contrary to the competitive exclusion principle. (One intriguing finding of Park was that cannibalism rates for the anomalous "coexistence" culture had increased during the course of his experiment.) Specifically, as the interspecific competition coefficients c_{eL} and c_{El} increase, the equilibrium configuration in the model assumes that of the saddle case, as is typical in classic Lotka/Volterra theory. However, as these competition coefficients continue to increase, a critical point is reached where a sudden onset of stable coexistence 2-cycles occurs (by means of a saddle-node bifurcation). This dynamic scenario possesses three attractors: two exclusion equilibria and a coexistence 2-cycle. This configuration is robust against further increases in the competition coefficients, and the basins of attraction of the coexistence 2-cycles are significantly large. This bifurcation scenario has several interesting features that we would like to understand better (not only with regard to the *Tribolium* experiments, but with regard to the fact that (4) is a rather general model of competition between two species with a commonly occurring, three stage life cycle).

We would like to know what mechanisms, mathematical and biological, cause the following (non-Lotka/Volterra) phenomena to occur in a competition model:

(a) coexistence of two species is promoted by increasing the *inter*specific coefficients;

(b) multiple attractor scenarios in which competitive coexistence and exclusion attractors (not necessarily equilibria) appear together, with asymptotic outcomes dependent on initial conditions.

Property (a) stands out because it is seemingly at odds with a fundamental tenet underlying virtually all ecological studies involving competition and ecological niche. For example, a recent review of current theoretical and empirical thinking about competitive coexistence states that coexistence requires "that intraspecific competition is stronger than interspecific competition". In addition, coexistence necessitates "some form of niche difference or partitioning between species that increases the strength of intraspecific competition relative to that of interspecific competition" [1].

One approach to addressing phenomena (a) and (b) is to consider the differences between the Leslie/Gower competition model (discrete Lotka/Volterra model) and the competition LPA model and to investigate these differences individually (and in various combinations) in order to determine which promote (a) and/or (b). The three main differences between the two competition models are: the LPA model contains life cycle stages (time delays, to a mathematician); the LPA model has a "stronger" nonlinearity (an exponential or Ricker type nonlinearity); and in the LPA model there is explicit iteroparity (reproducing adults can live longer than one unit of time). We can ask: which of these properties when incorporated into the Leslie/Gower model will promote phenomena (a) and/or (b) and why?

We have only begun an investigation of these questions and we are far from having complete answers. However, in the next section we give an example that demonstrates how the addition of a life cycle stage (time delay) to the Leslie/Gower competition model can give rise to phenomena (a) and (b). In this example these phenomena are not as robust as they are in the competition LPA model. Nonetheless, the example demonstrates that the introduction of a single life cycle stage into one of the species in a competitive system is capable of producing both (a) and (b).

2 A STAGE STRUCTURED COMPETITION MODEL

The system of difference equations

$$\begin{aligned} J_{t+1} &= b_1 \frac{1}{1+A_t+c_1 y_t} A_t \\ A_{t+1} &= (1-\mu) J_t \\ y_{t+1} &= b_2 \frac{1}{1+c_2 J_t + y_t} y_t \end{aligned} \tag{5}$$

is a modification of the Leslie/Gower competition model (2) in which species x has been given two life cycle stages, a juvenile (non-reproducing) stage J and an adult (reproducing) stage A. According to the first equation, juvenile recruits at time $t+1$ are produced by the adult stage with an inherent, per capita recruitment rate b_1 that is discounted by a fraction dependent on the adult population numbers and the number of species y. The second equation simply states that a fraction μ of juveniles die and do not become adults in one unit of time. The final equation is the discrete logistic equation for species y in which there are competitive effects from the juvenile class J of the competing species. Clearly other types of life cycle histories and interspecific couplings could be used to modify the unstructured Leslie/Gower model, but here we will restrict attention to model (5). (See Section 3.)

In (5) species y is governed by the discrete logistic equation in the absence of the J, A species. Thus, when the species J, A is absent, species y will equilibrate (going extinct if $b_2 < 1$ and surviving if $b_2 > 1$). In the absence of the y species, the dynamics of the J, A species are described by the difference equations

$$\begin{aligned} J_{t+1} &= b_1 \frac{1}{1+A_t} A_t \\ A_{t+1} &= (1-\mu) J_t. \end{aligned} \tag{6}$$

This "delayed logistic" model has two equilibria

$$(J_e, A_e) = (0,0) \quad \text{and} \quad \left(\frac{n-1}{1-\mu}, n-1 \right) \tag{7}$$

where we have defined

$$n \triangleq b_1(1-\mu).$$

Biologically n is the inherent net reproductive number, i.e., n is the expected number of juveniles produced by one adult during the course of its lifetime [16], [14], [66]. As functions of n these two equilibrium branches cross at $n = 1$ where a transcritical bifurcation occurs. Clearly positive initial conditions $J_0 > 0$, $A_0 > 0$ yield positive solutions $J_t > 0$, $A_t > 0$. Similarly, non-negative initial conditions $J_0 \geq 0$, $A_0 \geq 0$ yield non-negative solutions $J_t \geq 0$, $A_t \geq 0$. Furthermore, the union of the non-negative coordinate axes in the J, A plane is forward invariant.

For non-negative initial conditions we have

$$\begin{aligned} 0 \leq J_{t+1} &\leq b_1 A_t \\ 0 \leq A_{t+1} &= (1-\mu) J_t \end{aligned} \tag{8}$$

and a straightforward induction argument shows that $n < 1$ implies $\lim_{t\to\infty} (J_t, A_t) = (0,0)$. (If each adult does not at least replace itself over its lifetime, the population will go extinct.)

On the other hand, if $n > 1$ then the trivial equilibrium $(J, A) = (0,0)$ is unstable and the positive equilibrium in (7) is globally asymptotically stable (GAS) in the positive cone. To see this, we calculate the Jacobian

$$\begin{pmatrix} 0 & \frac{b_1}{(A+1)^2} \\ 1-\mu & 0 \end{pmatrix}$$

and evaluate it at the two equilibria. For the trivial equilibrium the Jacobian has eigenvalues $\pm\sqrt{n}$. For the positive equilibrium the Jacobian has eigenvalues $\pm 1/\sqrt{n}$. These eigenvalues imply an exchange of local asymptotic stability (LAS) between the two equilibrium branches as n increases through the bifurcation value $n = 1$. To see that the positive equilibrium globally attracts positive initial conditions when $n > 1$, we note that the composite map

$$\begin{aligned} J_{t+2} &= n\frac{1}{1+(1-\mu)J_t}J_t \\ A_{t+2} &= n\frac{1}{1+A_t}A_t \end{aligned} \tag{9}$$

consists of two uncoupled, discrete logistic equations. It follows that

$$\lim_{t\to\infty} (J_{2t}, A_{2t}) = \left(\frac{n-1}{1-\mu}, n-1\right)$$

and from (6) that

$$\lim_{t\to\infty} (J_{2t+1}, A_{2t+1}) = \lim_{t\to\infty} \left(b_1\frac{1}{1+A_{2t}}A_{2t}, (1-\mu)J_{2t}\right) = \left(\frac{n-1}{1-\mu}, n-1\right).$$

The positive equilibrium is not, however, a global attractor for non-negative initial conditions. (The coordinate axes are invariant.) Using the composite equations we find that an initial condition $J_0 = 0$, $A_0 > 0$ (or $J_0 > 0$, $A_0 = 0$) produces a solution that tends to a 2-cycle

$$\left(\begin{array}{c} 0 \\ n-1 \end{array}\right) \to \left(\begin{array}{c} \frac{n-1}{1-\mu} \\ 0 \end{array}\right) \to \left(\begin{array}{c} 0 \\ n-1 \end{array}\right) \to \cdots \tag{10}$$

In this cycle the juvenile and adult classes are temporally separated and, for this reason, we refer to the cycle as a *synchronous* 2-cycle [15], [21]. This synchronous 2-cycle is GAS within the invariant coordinate axes. It is, however, unstable within the two dimensional J, A plane. Nonetheless, this 2-cycle will play an important role in the dynamics of the competition model (5).

Next we turn our attention to the two species competition system (5). We begin with an investigation of equilibria. The system (5) has the following equilibrium points (J, A, y):

$$E_0 : (0,0,0), \qquad E_1 : (0,0,b_2-1), \qquad E_2 : \left(\frac{n-1}{1-\mu}, n-1, 0\right)$$

$$E_3 : \left(\frac{(b_2-1)\,c_1-(n-1)}{c_1c_2-(1-\mu)}, (1-\mu)\frac{(b_2-1)\,c_1-(n-1)}{c_1c_2-(1-\mu)}, \frac{(n-1)\,c_2-(b_2-1)\,(1-\mu)}{c_1c_2-(1-\mu)}\right).$$

The inequalities (8) and $0 \leq y_{t+1} \leq b_2 y_t$ hold for solutions of the competition model (5) with non-negative initial conditions. It follows that the J, A species goes extinct if $n < 1$ and the y species goes extinct if $b_2 < 1$. Therefore, we assume

$$n > 1, \quad b_2 > 1.$$

This assumption implies both equilibria E_1 and E_2 are non-negative. It also implies that the extinction equilibrium E_0 is unstable, since eigenvalues of the Jacobian evaluated at the equilibrium are b_2, $\pm\sqrt{n}$. Therefore, the isolated invariant point E_0 is a repellor and no orbit can approach it as $t \to +\infty$; that is to say, E_0 is equal to its own stable set (it is clear from equations (5) that no orbit can reach E_0 in finitely many steps). It follows that the competition model is uniformly persistence with respect to E_0 [43].

The Jacobian

$$M(J,A,y) = \begin{pmatrix} 0 & b_1 \frac{yc_1+1}{(A+yc_1+1)^2} & -\frac{c_1 b_1 A}{(A+yc_1+1)^2} \\ 1-\mu & 0 & 0 \\ -\frac{c_2 b_2 y}{(y+Jc_1+1)^2} & 0 & b_2 \frac{Jc_2+1}{(y+Jc_2+1)^2} \end{pmatrix}$$

evaluated at the competitive exclusion equilibria E_1 and E_2 has eigenvalues

$$\frac{1}{b_2}, \quad \pm\sqrt{\frac{n}{(b_2-1)\,c_1+1}}$$

and

$$\pm\sqrt{\frac{1}{n}}, \quad \frac{(1-\mu)\,b_2}{(n-1)\,c_2+1-\mu}$$

respectively. The stability properties summarized in Table 1 follow from these calculations. The local stability analysis using the Jacobian evaluated at E_3 was performed, using the Jury conditions and the help of a computer algebra program, by Professor Lih-Ing Roeger[1].

The local stability properties of the equilibria in Table 1 are exactly the same as those in classical Lotka/Volterra theory. Equilibrium coexistence is possible if and only if the interspecific coefficients c_1 and c_2 are sufficiently small. However, unlike the Lotka/Volterra equilibrium scenarios, the stability properties in Table 1 are local and are not necessarily global. To see this, we turn our attention to 2-cycle solutions of the competition model (5).

In this paper we will not present a complete study of the existence and stability of 2-cycle solutions of the competition model. Instead we will focus on a particular branch of synchronous 2-cycles. The inherent synchronous 2-cycle (10) gives the *exclusion* synchronous 2-cycle

$$\begin{pmatrix} 0 \\ n-1 \\ 0 \end{pmatrix} \to \begin{pmatrix} \frac{n-1}{1-\mu} \\ 0 \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ n-1 \\ 0 \end{pmatrix} \to \cdots \tag{11}$$

for the competition model (5) (in which species y is absent). The (local asymptotic) stability of this 2-cycle can be determined from the eigenvalues of the Jacobian of the composite map, which is the product

$$M(0,n-1,0)M\left(\frac{n-1}{1-\mu},0,0\right) = \begin{pmatrix} \frac{1}{n} & 0 & -\frac{n-1}{n}\frac{b_2 c_1}{c_2(n-1)+1-\mu} \\ 0 & n & 0 \\ 0 & 0 & \frac{(1-\mu)b_2^2}{c_2(n-1)+1-\mu} \end{pmatrix} \tag{12}$$

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whose eigenvalues appear along the diagonal. This 2-cycle is unstable since $n > 1$.

If we consider stability of the cycle (11) within the invariant, non-negative coordinate planes $J = 0$ or $A = 0$ of the J, A, y phase space, then the 2-cycle (11) is LAS provided the eigenvalue in the lower right corner is less than 1. We say equilibria or cycles that lie in these invariant coordinate planes are *synchronously LAS* (or *sLAS*) if they are LAS within the invariant $J = 0$ or $A = 0$ coordinate planes (i.e., with respect to solutions whose J, A components are synchronous). If they are unstable in these invariant planes, then we say they are *synchronously unstable* (or *s-unstable*).

Thus, the exclusion 2-cycle (11) is sLAS if competition is sufficiently intense in the sense that

$$c_2 > c^* \triangleq (1-\mu)\,\frac{b_2^2 - 1}{n-1},$$

and it is s-unstable if competition is weak: $c_2 < c^*$. (Note $c^* > c_2^*$ in Table 1.) This loss of synchronous stability occurs because an eigenvalue of the Jacobian (12) passes through $+1$, which suggests a transcritical bifurcation with another branch of 2-cycles. To find this bifurcating branch of synchronous 2-cycles, we examine the fixed points of the composite map

$$\begin{pmatrix} 0 \\ A \\ y \end{pmatrix} \to \begin{pmatrix} \frac{n}{1-\mu}\frac{1}{1+A+c_{12}y}A \\ 0 \\ b_2\frac{1}{1+y}y \end{pmatrix} \to \begin{pmatrix} 0 \\ n\frac{1}{1+A+c_1 y}A \\ b_2^2\frac{1}{1+(1+b_2)y+c_2\frac{n}{1-\mu}\frac{1+y}{1+A+c_1 y}A}y \end{pmatrix},$$

which yields the equations

$$\begin{gathered} A = n - 1 - c_1 y \\ c_1 c_2 y^2 - \left(\left(1+b_2\right)\left(1-\mu\right) + c_2\left(n - c_1 - 1\right)\right) y + \left(b_2^2 - 1\right)\left(1-\mu\right) - c_2\left(n-1\right) = 0 \end{gathered} \tag{13}$$

for A and y. A positive solution $y > 0$ of the uncoupled second equation in (13) yields a non-negative, coexistence synchronous 2-cycle provided $0 < y < (n-1)/c_1$ (so that $A > 0$).

We are interested in the case when there is strong competition between the species, i.e., when c_1 and c_2 are both large. We can facilitate a study of this case by introducing a single parameter that measures the intensity of interspecific competition as follows. We fix the ratio

$$r \triangleq \frac{c_1}{c_2}$$

between the competition coefficients and define

$$c \triangleq c_2.$$

In terms of r and c the 2-cycle equations (13) become

$$A = n - 1 - rcy$$

$$rc^2y^2 - \left(\left(1+b_2\right)\left(1-\mu\right) + c\left(n - rc - 1\right)\right) y + \left(b_2^2 - 1\right)\left(1-\mu\right) - c\left(n-1\right) = 0. \tag{14}$$

The second (quadratic) equation has a solution $y = y(c)$ that satisfies $y(c^*) = 0$ and, consequently, bifurcates from the exclusion synchronous 2-cycle (11) at $c = c^*$. The direction of bifurcation is determined by the sign of $y'(c^*)$, which can be calculated by an implicit differentiation of (14):

$$\begin{gathered} y'(c^*) < 0 \quad \text{if } r < r^* \\ y'(c^*) > 0 \quad \text{if } r > r^* \\ r^* \triangleq \frac{1}{1-\mu}\left(\frac{n-1}{b_2-1}\right)^2 \frac{b_2}{b_2+1}. \end{gathered}$$

By the exchange of stability principle, the bifurcating coexistence synchronous 2-cycles are sLAS near the bifurcation point if $r < r^*$ and s-unstable if $r > r^*$. See Figure 1. (This can also be proved using a Liapunov-Schmidt analysis near the bifurcation point.) The coexistence 2-cycles are not LAS, however, with respect to nonsynchronous solutions near the bifurcation point (i.e., in the three dimensional J, A, y space).

FIGURE 1

FIGURE 2

When $r < r^*$ the branch of coexistence synchronous 2-cycles globally extends in one of two ways as shown in Figure 2. One possibility (Figure 2b) is that the bifurcating coexistence 2-cycle branch "turns around" and a saddle-node bifurcation of synchronous 2-cycles occurs. Numerical explorations indicate that s-LAS is lost along the branch when this occurs (i.e., the upper branch is s-unstable). The saddle-node bifurcation of 2-cycles occurs in a parameter region in which the equilibrium configuration is that of the competitive exclusion saddle case of Lotka/Volterra theory. The result is an interval of parameter values for which there are three attractors, two of which are exclusion equilibria and one of which is a coexistence 2-cycle. A numerical example is shown in Figure 3. This is the same scenario observed in the competition LPA model by Edmunds et al. [28].

It is interesting to note that it is possible for the synchronous coexistence 2-cycles to be LAS in the three dimensional J, A, y phase space. This occurs in the case shown in Figure 2b and 2c near each of the two saddle-node bifurcations. (Also see Figure 3b.)

FIGURE 3

3 CONCLUSIONS

In theoretical models of interference competition between two biological species, large values of interspecific competition coefficients (relative to intraspecific competition coefficients) typically imply that one species will go extinct. This is the basis of the principle of competitive exclusion, which states that in order for two species to coexist they must find a way to decrease their competitive interactions (i.e., find their own "niche"). A large number of mechanisms utilized by species to avoid competition has been identified (for a list of 120 such mechanisms see [51]), most of which involve spatial, temporal, or resource separation). None of these mechanisms are applicable to the coexistence case observed in Park's experiment with *Tribolium* or to the explanation based on the competition LPA model given in [28]. In the latter explanation, coexistence was promoted by an increase in interspecific competition coefficients and the onset of non-equilibrium coexistence attractors (properties (a) and (b)). In this paper we used the "toy" model example (5) to illustrate these phenomena.

The models we examined do not, however, exhibit the phenomena (a) and (b) in as robust a way as does the competition LPA model. A multiple attractor scenario of mixed coexistence and exclusion attractors can arise from the model (5) on an interval of sufficiently large values of the interspecific competition coefficients. However, unlike for the LPA model, this parameter interval is of finite length, and the coexistence 2-cycles are only synchronous stability (except on a small subinterval where they are LAS). Moreover, simulations show that the basins of attraction of the coexistence cycles of (5) are restricted to an open region close to the invariant coordinate planes. The coexistence cycles in the LPA model, on the other hand, have basins of attraction that are significantly large in phase space.

Nonetheless, example (5) does at least illustrate that the introduction of a life cycle stage into (even only one species in) a model that predicts the principle of competitive exclusion (i.e., that asymptotically has only the Lotka/Volterra scenarios) can exhibit the properties (a) and (b).

Properties (a) and (b) can appear more robustly in models that include other nonlinear interactions among the life cycle stages J and A and the competing species y :

$$\begin{aligned}
J_{t+1} &= b_1 \frac{1}{1 + c_{11}J_t + c_{12}A_t + c_{13}y_t} A_t \\
A_{t+1} &= (1-\mu) \frac{1}{1 + c_{21}J_t + c_{22}A_t + c_{23}y_t} J_t \\
y_{t+1} &= b_2 \frac{1}{1 + c_{31}J_t + c_{32}A_t + c_{33}y_t} y_t.
\end{aligned} \tag{15}$$

We presented the special case (5) in Section 2 because of its analytic tractability.

For example, a modification of (5) that includes a juvenile density effect in adult reproduction, namely the equations

$$\begin{aligned}
J_{t+1} &= b_1 \frac{1}{1 + c_{11}J_t + A_t + rcy_t} A_t \\
A_{t+1} &= (1-\mu) J_t \\
y_{t+1} &= b_2 \frac{1}{1 + cJ_t + y_t} y_t
\end{aligned}$$

with $c_{11} > 0$, exhibits the same bifurcation diagrams as appear in Figure 2. However, the interval for the interspecific competition coefficient c on which the coexistence synchronous 2-cycles are three dimensionally LAS is lengthened and the basins of attraction of the 2-cycles are considerably increased in size.

These examples demonstrate how life history characteristics can play an important role in the dynamics of interacting populations and, in particular, how they can promote competitive coexistence and hence ecological diversity (see [64], [7] and the references cited therein). An interesting open question is whether the phenomena (a) and (b) that arise in the competition LPA model, and in simpler competition models of the form (15), are in contradiction to the principle of competitive exclusion or whether they might, in some way, be reconciled with that principle.

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TABLES AND FIGURES

Equilibrium	Unstable	Locally asymptotically stable
E_1	$c_1 < c_1^*$	$c_1^* < c_1$
E_2	$c_2 < c_2^*$	$c_2^* < c_2$
E_3	$c_1^* < c_1,\ c_2^* < c_2$	$c_1 < c_1^*,\ c_2 < c_2^*$

TABLE 1. The local stability properties of the three nontrivial equilibria of competition model (5) are expressed in terms of the interspecific competition coefficients c_1 and c_2. The critical values of c_1 and c_2 in this table are $c_1^* \triangleq (n-1)\,/\,(b_2-1)\,,\ c_2^* \triangleq (1-\mu)\,(b_2-1)\,/\,(n-1)$.

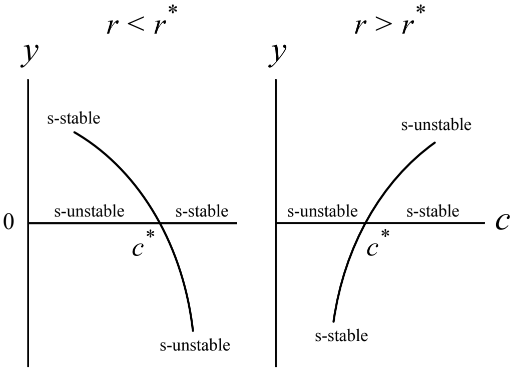

FIGURE 1. A branch $y = y(c)$ of solutions of equation (14) transcritically bifurcates with the trivial solution $y = 0$ at $c = c^*$. The positive solution branch yields coexistence synchronous 2-cycles of the competition model (5). In the "subcritical" bifurcation case $r < r^*$, the coexistence 2-cycles are synchronously LAS. They are unstable, however, with respect to non-synchronous solutions.jpb

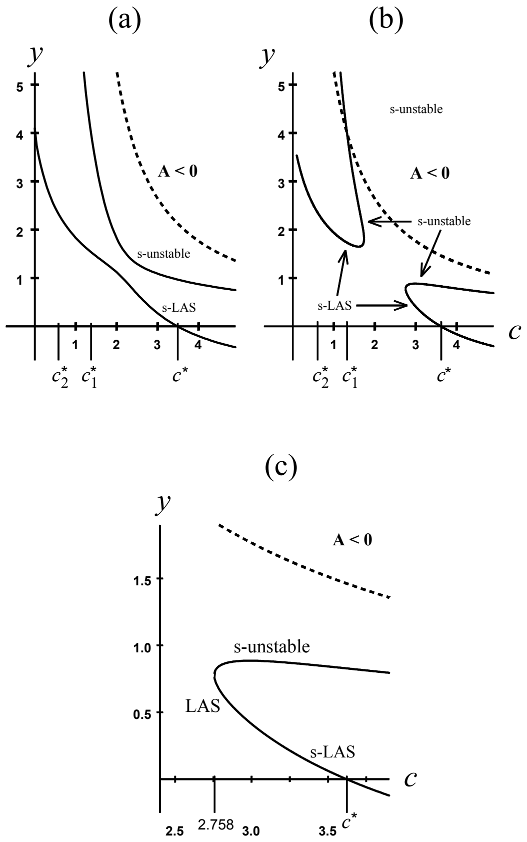

FIGURE 2. In (a) and (b) appear two examples of the subcritical bifurcation case ($r < r^*$) that illustrate the possible global geometry of the coexistence synchronous 2-cycle branch that bifurcates from $y = 0$ at $c = c^*$. Also shown is another branch of coexistence synchronous 2-cycles. Parameter values are $\mu = 0.2$, $b_2 = 5$, and $r = 1$. The broken line indicates the curve $A = n - 1 - rcy = 0$ below which $A > 0$. For $c > c_1^*$ the equilibrium configuration is the saddle competitive exclusion case of Lotka/Volterra theory (the exclusion equilibria E_1 and E_2 are LAS and the coexistence equilibrium E_3 is unstable).

In (a) $n = 6.5$ ($b_1 = 8.125$), $c_2^* = 0.5818$, $c_1^* = 1.375$, and $c^* = 3.491$. The bifurcating branch extends to the vertical axis where $c = 0$. Numerical simulations indicate that the 2-cycles from the other branch are s-unstable.

In (b) $n = 6.3$ ($b_1 = 7.875$), $c_2^* = 0.6038$, $c_1^* = 1.325$, and $c^* = 3.623$. The bifurcating branch "turns around" to form a saddle-node bifurcation of 2-cycles at $c = 2.758$. Numerical simulations indicate that the 2-cycles from the upper branch are s-unstable. A similar, but reverse saddle-node bifurcation also occurs at $c = 1.741$.

(c) Numerical simulations show that the synchronous 2-cycles are fully LAS in J, A, y phase space near the both saddle-node bifurcation points in (b). The parameter intervals of LAS are small, however: $2.758 < c < 2.835$ for the saddle-node bifurcation at $c = 2.758$ (shown) and $1.693 < c < 1.741$ for the saddle-node bifurcation at $c = 1.741$ (not shown).

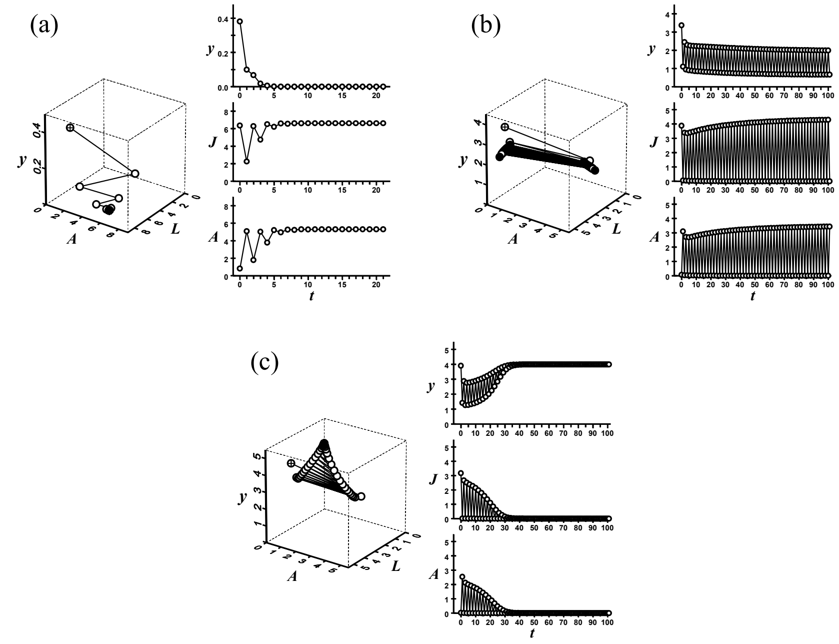

FIGURE 3. Three initial conditions produce solutions of the competition model (5) with three different attractors. (a) The solution with initial conditions $(J_0, A_0, y_0) = (6.362, 0.8290, 0.3819)$ tends to the exclusion equilibrium $E_2 = (6.625, 5.3, 0)$. (b) The solution with initial conditions $(J_0, A_0, y_0) = (3.881, 0.07095, 3.371)$ tends to a coexistence synchronous 2-cycle. **(c)** The solution with initial conditions $(J_0, A_0, y_0) = (3.173, 0.02234, 3.912)$ tends to the exclusion equilibrium $E_1 = (0, 0, 4)$. Parameter values are $\mu = 0.2$, $b_2 = 5$, $n = 6.3$. $(b_1 = 7.875)$, $r = 1$, $c = 2.8$ $(c_1 = c_2 = 2.8)$.