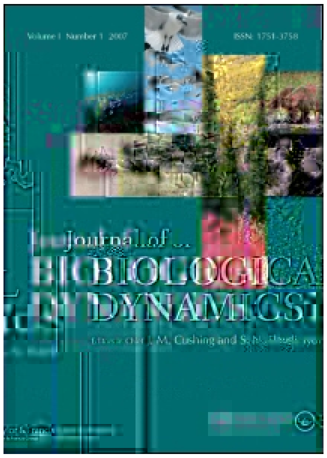

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Multiple mixed-type attractors in a competition model

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Multiple mixed-type attractors in a competition model

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We show that a discrete-time, two-species competition model with Ricker (exponential) nonlinearities can exhibit multiple mixed-type attractors. By this is meant dynamic scenarios in which there are simultaneously present both coexistence attractors (in which both species are present) and exclusion attractors (in which one species is absent). Recent studies have investigated the inclusion of life-cycle stages in competition models as a casual mechanism for the existence of these kinds of multiple attractors. In this paper we investigate the role of nonlinearities in competition models without life-cycle stages.

: Competitive exclusion principle; Coexistence cycles; Multiple attractors

A (*2000*): Primary 92D40, 92D25; Secondary 39A11

1. Introduction

In [1] the authors utilize a competition model to explain an unusual coexistence result observed and studied by T. Park and his collaborators in a series of classic experiments involving two species of insects (from the genus) [2–4]. The explanation offered in [1] is based on a single species model (called the LPA model) designed explicitly to account for the dynamics of the species involved. The LPA model has an impressive track record, spanning several decades, of describing and predicting the dynamics of populations, under a variety of circumstances in controlled laboratory experiments—dynamics that range from equilibrium and periodic cycles to quasi-periodic and chaotic attractors [5, 6]. This history of success adds credence to the two-species competition model used in [1] (called the *A*) and significant weight to the explanation given for the observed case of coexistence. The explanation entails, however, some unusual aspects with regard to classic competition theory, including non-equilibrium dynamics, coexistence under increased intensity of inter-specific competition, and the occurrence of multiple mixed-type attractors. By - we mean a scenario that includes at least one coexistence attractor and at least one exclusion attractor. A is one in which both species are present. An is one in which at least one species is absent and at least one species is

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present. Park observed the coexistence case in an experimental treatment that also included cases of competitive exclusion, that is to say, he observed a case of what we have termed to be multiple mixed-type attractors.

Competition theory is primarily an equilibrium theory that is exemplified, for example, by the classic Lotka–Volterra model and its limited number of asymptotic outcomes: a globally attracting coexistence equilibrium; a globally attracting exclusion equilibrium; or two attracting exclusion equilibria. (In this context, means within the positive cone of state space.) These three equilibration alternatives are illustrated by the

[7] (the discrete analog of the famous Lotka–Volterra differential equation model)

$$\begin{aligned} {}_{t+1} &= {}_{1\ t}\frac{1}{1+{}_{11\ t}+{}_{12\ t}} + {}_{1\ t} \\ {}_{t+1} &= {}_{2\ t}\frac{1}{1+{}_{21\ t}+{}_{22\ t}} + {}_{2\ t} \end{aligned} \tag{1}$$

where $t = 0, 1, 2, \ldots$ and the > 0 are the inherent birth rates, $(0 \leq \ < 1)$ the survival rates, and > 0 the density-dependent effects on newborn recruitment [8–10]. Leslie . used this model to study the experiments, but it is incapable of explaining the observed case of multiple mixed-type attractors. On the other hand, the competition LPA model used in [1] exhibits a greater variety of competition scenarios, including ones with multiple mixed-type attractors (also see [11, 12]).

The competition LPA model, although applied specifically to species of in [7], is none the less a el that, unlike the Leslie–Gowe (or a Lotka–Volterra type model in Leneral), accounts for life-cycle stages in the competing species. Therefore, the LPA model serves to illustrate that in Leneral-[177.9((when)-177.9(more)-177.9(biological-[177.9(details)-1

We provide formal proofs of this possibility (mathematical details appear in the Appendix) for the case of 2-cycle and equilibrium scenarios. An investigation for scenarios involving higher period cycles (or quasi-periodic or chaotic attractors) remains to be carried out, although we give in section 4 a numerical example involving higher period cycles and quasi-periodic attractors.

2. Equilibria

We can assume without loss in generality (by scaling the units of and) that $= 1$ in the Ricker competition model (2). Therefore, we will consider, after relabeling $_{12}$ as $_1$ and $_{21}$ as $_2$, the competition model

$$\begin{aligned} _{t+1} &= {}_1 {}_t \exp(- {}_t - {}_1 {}_t) + {}_1 {}_t \\ _{t+1} &= {}_2 {}_t \exp(- {}_2 {}_t - {}_t) + {}_2 {}_t. \end{aligned} \tag{3}$$

The $_1$ □ $(\ln {}_1, 0)$, $_2$ □ $(0, \ln {}_2) \in {}^2$ of the Ricker competition model (3) are biologically feasible (i.e. lie on the positive axes) if and only if the inherent net reproductive numbers □ $/(1-)$ satisfy > 1. Besides the trivial equilibrium $_0$ □ $(0, 0)$ and these two exclusion equilibria, there exists only one other equilibrium:

$$_3 \,\square\, \left(\frac{\ln {}_1 - {}_1 \ln {}_2}{1 - {}_1 {}_2}, \frac{\ln {}_2 - {}_2 \ln {}_1}{1 - {}_1 {}_2} \right). \tag{4}$$

The equilibrium $_3$ is a if it lies in the positive cone $^2_+$ □ $\{(,) : > 0, > 0\}$. Let □ $\{({}_1, {}_2) \in {}^2 : 0 \le {}_1, {}_2 < 1\}$ denote the unit square in ^{2}.

LEMMA 2.1 *A* $({}_1, {}_2) \in$. $({}_t, {}_t)$ (3) $({}_0, {}_0)$ $\bar{}^2_+$ $^2_+$. $_1 < 1$ $\lim_{t\to+\infty} {}_t = 0$. $_2 < 1$ $\lim_{t\to+\infty} {}_t = 0$.

If $_1 < 1$ then all solutions of the linear equation $'_{t+1} = {}_1 '_t + {}_1 '_t$ satisfy $\lim_{t\to+\infty} '_t = 0$. From the inequality $0 \le {}_{t+1} \le {}_1 {}_t + {}_1 {}_t$ and $'_0 = {}_0$, an induction shows $0 \le {}_t \le '_t$ for all $t = 0, 1, 2, \ldots$. A similar argument proves the assertion when $_2 < 1$. □

We assume throughout the rest of the paper that both inherent net reproductive numbers satisfy > 1. In this case, all solutions of (3) are bounded and at least one species does not go extinct, as the following dissipativity and persistence theorem shows. The proof appears in the Appendix.

of an exclusion equilibrium ($=$ 1 or 2) of the competition equations (3) is that the inherent net reproductive numbers satisfy

$$1 < \quad < \quad \square \exp(2/(1- \quad)). \tag{5}$$

The linearization principle provides sufficient conditions for stability according to the magnitude of the eigenvalues of the Jacobian (,) associated with (3) evaluated at an equilibrium point $=$ (,):

$$(\; , \;) = \begin{pmatrix} 1-(1- \;_1) & - \;_1(1- \;_1) \\ - \;_2(1- \;_2) & 1-(1- \;_2) \end{pmatrix}. \tag{6}$$

The Jacobians of the equilibria , $=$ 1 or 2, are triangular matrices whose eigenvalues appear along the diagonal. The equilibrium , $=$ 1 or 2, is hyperbolic if both eigenvalues

$$(1- \quad)(1-\ln \quad) + \quad , \qquad ^{-} + \quad , \qquad \neq$$

have absolute value unequal to 1 and, by the linearization principle [15], is (locally asymptotically) stable if both have absolute value less than 1. Thus, a necessary condition that be hyperbolic and stable is that

$$> \ln \quad / \ln \quad , \qquad \neq \; . \tag{7}$$

Sufficient for to be hyperbolic and stable is that, in addition, the inequalities (5) hold.

T

in more complicated models that include juvenile life-cycle stages [1, 8, 11, 13, 14]). To carry out this investigation by means of a single parameter problem, we introduce the notation $\square\ {}_2/\ {}_1,\ \square\ {}_1$ and re-write the competition model (3) as

$$
\begin{aligned}
{}_{t+1} &= {}_1(1 - {}_1)\ {}_t \exp(-\ {}_t - \ {}_t) + {}_1\ {}_t \\
{}_{t+1} &= {}_2(1 - {}_2)\ {}_t \exp(-\ {}_t - \ {}_t) + {}_2\ {}_t \\
&> 1,\ 0 \leq \quad < 1,\ \text{and}\ \ , \ > 0.
\end{aligned} \tag{8}
$$

Our goal is, for fixed birth rates , survivorships and competition ratio , to investigate the existence and stability of non-equilibrium coexistence attractors as functions of the inter-
8x

then used to estimate the bifurcation value * of the bifurcating 2-cycles generated by the solution branch $(\ , \ , \ ) = (\ , \ (\ ), \ (\ ))$. In that analysis, attention is restricted to $_1$ lying on the interval

$$\{ _1 : 1 - \ _1 < _1 < _1 \}, \quad _1 \ (1 - \ _1) \exp(2/(1 - \ _1)).$$

For $_1 \in$ the Ricker equation $_{t+1} = \ _1(1 - \ _1) \ _t \exp(- \ _t - \ _t) + \ _1 \ _t$ has a stable equilibrium.

THEOREM 3.2 *A* $(_1, _2) \in$ $_1 \in$. $_2 \ _2$,
2- *2-* (13) $=$

(1) (

assumption means that the survivorship $_1$ of species is larger than the survivorship $_2$ of species . Therefore, Theorem 3.4 requires that there be an asymmetry between the two species in the sense that one species has a high reproductive rate and low survivorship in contrast to the other species, which has a low reproductive rate and a high survivorship. Figure 2 illustrates the existence of multiple mixed-type attractors under these conditions.

Theorem 3.4 implies the local bifurcation of stable coexistence 2-cycle only for sufficiently large, namely, near the critical point *. An interesting question concerns the global extent of this bifurcating branch of 2-cycles. What is the 'spectrum' of values for which these coexistence 2-cycles occur? Numerous numerical explorations have shown that the bifurcation

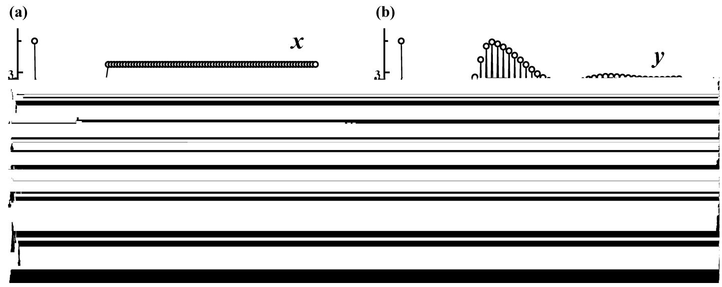

Figure 2. Each plot shows a solution of the Ricker competition model (8) with $_1 = 8$, $_2 = 10$, $_1 = 0.65$, $_2 = 0$, $= 1.1$ and $= 1.9$. In plot (a) the initial conditions $(_0, _0) = (0.2, 3.5)$ lead to competitive exclusion. In (b) the initial conditions $(_0, _0) = (0.19, 3.5)$ lead to a competitive coexistence 2-cycle. See figure 3(a).

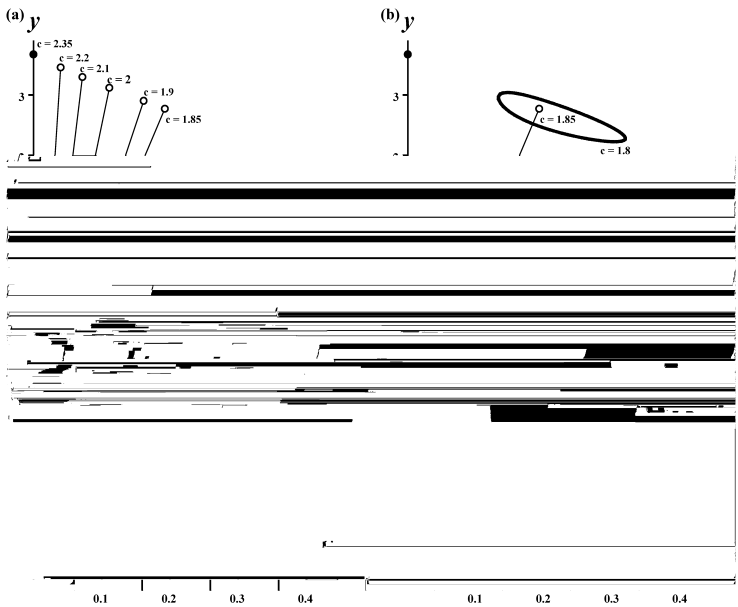

Figure 3. A sequence of phase plane plots shows the bifurcation of stable coexistence 2-cycles from the exclusion 2-cycles on the -axis in the Ricker competition model (8) as the competition coefficient decreases through the critical value $^* \approx 2.35$. Model parameters are $_1 = 8$, $_2 = 10$, $_1 = 0.65$, $_2 = 0$, and $= 1.1$. Plot (a) shows a sequence of stable 2-cycles (open circles with connecting lines) that eventually destabilize and give rise to stable, double invariant loops as shown in plot (b). In plot (c) the double invariant loops eventually collide, under further decreases in , and undergo a global, heteroclinic bifurcation involving the (saddle) coexistence equilibrium, the exclusion (saddle) equilibrium, the exclusion (saddle) 2-cycle located and their stable and unstable manifolds. For the parameter values in these plots, the exclusion equilibrium $_1 : (,) \approx (22.86, 0)$ is also stable and hence these plots contain multiple mixed-type attractors.

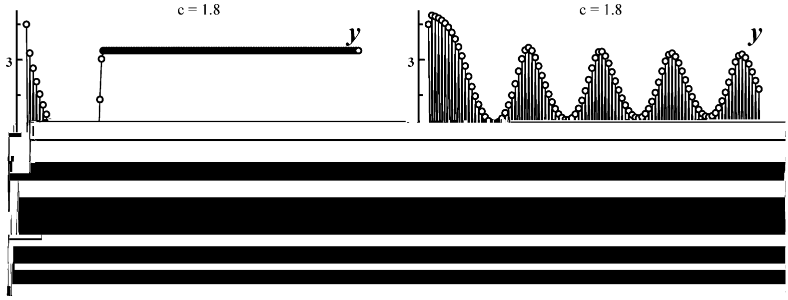

Figure 4. Each graph shows a solution of the Ricker competition model (8) with $_1 = 8$, $_2 = 10$, $_1 = 0.65$, $_2 = 0$, $= 1.1$ and $= 1.8$. In plot (a) the initial conditions $(_0, _0) = (0.12, 3.5)$ lead to competitive exclusion. In plot (b) the initial conditions $(_0, _0) = (0.01, 3.5)$ lead to a competitive coexistence quasi-periodic oscillation (see figure 3(b, c)).

sequence displayed in figure 3 is typical. As decreases, and the coexistence 2-cycles bifurcate from the exclusion 2-cycle on the -axis at $= ^*$, there exists a second critical value of at which the coexistence 2-cycles lose stability because of an invariant loop (Sacker/Neimark or discrete Hopf) bifurcation. The resulting coexistence (double) invariant loops persist until reaches a third critical value at which the loops disappear in a global heteroclinic bifurcation. See figures 3 and 4.

In this paper we have shown that the Ricker competition model (8) cannot display a multiple mixed-type attractor scenario with only equilibria. On the other hand, Theorem 3.4 shows that multiple mixed-type attractor scenarios are possible with non-equilibrium attractors, specifically, with stable competitive exclusion equilibria and stable coexistence 2-cycles. Multiple mixed-type attractors scenarios are also possible for model (8) that involve other combinations of higher period cycles, quasi-periodic (as in figure 4) and even chaotic attractors. Figure 5 shows one example. The analysis of such multiple attractor cases remains an open problem.

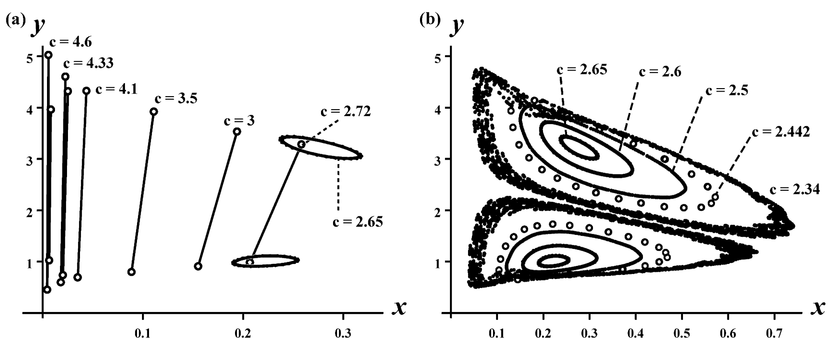

Figure 5. A sequence of phase plane plots shows the bifurcation of stable coexistence 4-cycles from the exclusion 4-cycles on the -axis in the Ricker competition model (8) as decreases from the critical value $^* \approx 4.77$. Model parameters are $_1 = 8$, $_2 = 14$, b56(2)Tj /4lrc]TJ1a337.0578 0 TD (8,)Tj /F4 1 Tf 1.0581 0 TD (b)T673 810

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$> \; ^{-1} \; ^{-1}/(1 - \;)$, any solution $\; t$ satisfies $\; t <$ for all large t. By (A1) it follows that there exists a $t^* = t^*(\;_0) \geq 1$ such that

3.2 Define $= - {}^*_0$ and $= - {}^*$ and re-write the composite, fixed point equations (15) as

$$(\,,\, ,) = 0, \qquad (\,,\, ,) = 0 \tag{A5}$$

$$\ _2 = \ _2 + \ _1\varepsilon + \ _2\varepsilon^2 + \ (\varepsilon^3)$$

Since $_0 > 0$ for $(\ _1, \ _2) \in$, the sign of in (A9) depends on that of $_1$, which in turn is the sign of the factor (ln $_1$). The term ( ) is a quadratic polynomial in