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Coexistence of competing juvenile–adult structured populations

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The Leslie-Gower model is a discrete time analog of the competition Lotka–Volterra model and is known to possess the same dynamic scenarios of that famous model. The Leslie–Gower model played a historically significant role in the history of competition theory in its application to classic laboratory experiments of two competing species of flour beetles (carried out by Park in the 1940s–1960s). While these experiments generally supported what became the Competitive Exclusion Principle, Park observed an anomalous coexistence case. Recent literature has discussed Park's 'coexistence case' by means of non-Lotka–Volterra, non-equilibrium dynamics that occur in a high dimensional model with life cycle stages. We study this dynamic possibility in the lowest possible dimension, that is to say, by means of a model involving only two species each with two life cycle stages. We do this by extending the Leslie–Gower model so as to describe the competitive interaction of two species with juvenile and adult classes. We give a complete account of the global dynamics of the resulting model and show that it allows for non-equilibrium competitive coexistence as competition coefficients are *increased*. We also show that this phenomenon occurs in a general class of models for competing populations structured by juvenile and adult life cycle stages.

1. Introduction

The classic principle of competitive exclusion requires, for the coexistence of two species, that competitive interference be low. In competition models this requirement generally means that those coefficients which measure the intensity of the inter-specific competition be sufficiently small (usually in relation to the coefficients measuring intraspecific competition). Put another way, large values of inter-specific competition coefficients imply one of the species necessarily goes extinct. This form of the principle finds its most forceful and straightforward expression in the famous Lotka–Volterra system of differential equations.

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In the early development of competition theory, controlled laboratory experiments played a significant role in establishing the competitive exclusion principle. Among these were the famous experiments performed by G. F. Gause [1] and by T. Park [2–5]. Both worked within the framework of the dynamic scenarios of Lotka–Volterra theory. The experimental results of Gause and Park are widely cited to this day as experimental validation of the competitive exclusion principle. However, one of Park's experiments yielded a 'difficult to interpret' result [5]. Whereas one of the two species typically went extinct in Park's experiments, consistent with the competitive exclusion principle, in this exceptional case neither species went extinct during the course of the experiment, which lasted over 32 generations. Park referred to this anomalous case as a 'coexistence case'. Moreover, Park's results implied a dynamic scenario not permitted by Lotka–Volterra theory (or any other competition theory known to us). This scenario consists of three attractors, two competitive exclusion attractors and one competitive coexistence attractor. Park and his collaborators addressed this 'coexistence case' with both experimental and model studies, but in the end they could offer no theoretical or biological explanation [5, 6].

Gause centered the theoretical component of his work on the Lotka–Volterra system of differential equations. That well-known competition model is based on the famous logistic equation. Park and his collaborators (who included P. H. Leslie) utilized, on the other hand, a discrete time competition model that is based on the discrete version of the logistic equation[†] [7–10], namely

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

Solutions x_t of this difference equation (which defines a monotone map) with $x_0 > 0$ equilibrate as $t \to +\infty$, converging to 0 if $b < 1$ or to the equilibrium $x = (b - 1)/c$ if $b > 1$. In the Leslie–Gower competition model [11]

$$x_{t+1} = b_1 \frac{1}{1 + c_{11} x_t + c_{12} y_t} x_t$$

$$y_{t+1} = b_2 \frac{1}{1 + c_{21} x_t + c_{22} y_t} y_t \quad b_i > 0, \quad c_{ii} > 0, \quad c_{ij} \geq 0 \ (i \neq j) \tag{2}$$

the dynamics of each species x and y, in the absence of the other, are governed by the discrete logistic (1). It turns out that solutions of the Leslie–Gower model obey the same four phase portrait alternatives of the Lotka–Volterra competition model [12, 13]. (See Appendix A1.) As a result, this model cannot explain the triple attractor case (with mixed types that include both coexistence and exclusion attractors) suggested by the coexistence case in Park's experiment.

Edmunds *et al.* [14] addressed the anomalous coexistence case of Park using a different competition model. Instead of basing their competition model on single-species logistic dynamics, these authors based their competition model on a well validated single-species model, developed and tested over several decades, that was designed specifically for the biological organisms used by Park (namely, beetle species of the genus *Tribolium*). This single-species model accounts for different life cycle stages in the life history of individuals (specifically, larval, pupal, and adult stages) and therefore is a three-dimensional model. It is no surprise, then, that this LPA model, unlike logistic type models, can have non-equilibrium attractors. Indeed, the model has been used to predict and account for observed chaotic dynamics in flour beetle experiments [15].

[†]Solutions of the logistic equation, when sampled at equally spaced census times, generate time sequences that satisfy this difference equation [7].

The LPA model is one of the most successful models available in population dynamics and ecology in terms of its rigorous connection to data and its quantitatively accurate, a priori predictions of detailed dynamic phenomena that have been validated repeatedly by controlled and replicated experiments [16]. The LPA model can be considered as a generic model for species that have a three-stage life cycle (growing/feeding juveniles followed by a pupal/quiescent stage and reproductive adulthood). Given these facts, it is interesting to consider competition models based on this single species model and to compare their asymptotic dynamics to those of classic Lotka–Volterra-type models. In what sense would such models support the principle of competitive exclusion? Can these models allow for new types of dynamic scenarios and competitive outcomes, perhaps some that challenge the exclusion principle? Can they offer a hypothesis that explains Park's anomalous coexistence case?

Edmunds *et al.* showed that the answers to the last two questions are 'yes'. First of all, they showed that the competition LPA model, with parameter values equal or near to those estimated for laboratory cultures of *Tribolium*, can exhibit the classical Lotka–Volterra equilibrium scenarios. Specifically, if certain inter-specific competition coefficients are small, the model predicts equilibrium coexistence and, as these coefficients increase past critical values, competitive exclusion occurs with the surviving species equilibrating to its inherent equilibrium state (carrying capacity). Moreover, just as with the Lotka–Volterra and the Leslie–Gower models, if both inter-specific competition coefficients are sufficiently large, the 'saddle' case results, in which the winning competitor depends on initial conditions. This saddle case is the dynamic scenario in which Park placed his competition experiments [5]. However, Edmunds *et al.* discovered something surprising in the competition LPA model. Namely, as the inter-specific competition coefficients increase even further, there can result a stable coexistence cycle (of period 2), which in the presence of the two exclusion equilibria constitutes a triple attractor case. This cycle arises from a 2-cycle saddle-node (or blue sky) bifurcation. The basin of attraction of the coexistence cycle is significantly large and is robust against further increases in the competition coefficients. Thus, in seeming contradiction to the competitive exclusion principle, the possibility of competitive coexistence is enhanced by *increased* competitive intensity. As Edmunds *et al.* point out, it is intriguing that Park reported an increase in competitive intensity (in this case, increased egg and pupae consumption in *Tribolium*) in the anomalous coexistence case discussed above.

The competition LPA model is a six-dimensional discrete dynamic system with a large number of parameters. Although some basic properties of the model have been established analytically [17], the non-equilibrium, non-Lotka–Volterra dynamics such as those reported by Edmunds *et al.* are difficult to analyze except by numerical simulations. This suggests that a study of simpler, low-dimensional 'toy' models that focuses on key model ingredients in the competition LPA model could be useful in establishing what kinds of biological mechanisms can account for such dynamics. Since the LPA competition model is a discrete time model, it is appropriate to use the Leslie–Gower model (1–2) as a point of reference, What are the differences between these two models and which of them are key to the appearance of non-equilibrium, non-Lotka–Volterra dynamics? Which of them result, for large values of inter-specific coefficients, in multiple attractors of mixed (coexistence and exclusion) types?

The two fundamental differences between the Leslie–Gower and the LPA competition models are that the LPA model has (1) life cycle stages and (2) 'stronger' (overcompensatory) nonlinearities. Life cycle stages are a kind of time lag in the dynamics of populations, and it is well known that time lags can cause dynamic oscillations. The stronger nonlinearities in the LPA model are of exponential (Ricker) type, instead of the rational polynomial type appearing in the discrete logistic (1). These type of nonlinearities are also well known to provide the possibility of equilibrium de-stabilization and oscillations (even bifurcation cascades to chaos).

A recent study [18] considers a two-stage (juvenile–adult), semelparous adaptation of the discrete logistic in interaction with an unstructured competitor (i.e. a competitor without life cycle stages). The authors show that a 2-cycle, saddle-node bifurcation can occur in this model, under certain circumstances, that results in multiple attractors of mixed types. Unlike in the competition LPA model example, however, the multiple attractor scenario is not particularly robust in that model. Our goal in this paper is to give a complete and global analysis of the asymptotic dynamics of a stage-structured Leslie–Gower competition model that, unlike that studied in [9], includes a juvenile-adult life cycle in both species. We will see in section 2 that this model leads, for large inter-specific competition coefficients, to a robust occurrence of a multiple attractor case which includes a coexistence 2-cycle in the presence of two competitive exclusion equilibria. This 2-cycle will not, on the other hand, arise from a saddle-node bifurcation. In section 3 we prove the occurrence of this triple attractor case in a general juvenile–adult competition model, in order to add further robustness to its occurrence.

2. A stage structured Leslie–Gower model

We begin with some notation. Let $R_+^m \triangleq \{(x_1, \ldots, x_m) \in R^m \colon x_i > 0\}$ denote the positive cone of m-dimensional Euclidean space. We denote the closure and the boundary of R_+^m by $\bar{R}_+^m$ and ∂R_+^m respectively.

In this section we consider a competition model that is built on a juvenile–adult version of the discrete logistic equation (1), namely, the equations

$$J_{t+1} = b \frac{1}{1 + dA_t} A_t$$

$$A_{t+1} = s \frac{1}{1 + cJ_t} J_t.$$

In this model there is a reproductive stage A whose juvenile production is self density regulated, and the coefficient $d > 0$ measures the intensity of the intrastage adult competition. The juvenile (or growing stage) also experiences intrastage competition that reduces its survivorship to the adult stage below the inherent survivorship rate s, $0 < s \le 1$. The coefficient $c > 0$ measures the intensity of the intrastage juvenile competition. By a choice of population units we can assume, without any loss in mathematical generality, that $c = 1$:

$$J_{t+1} = b \frac{1}{1 + dA_t} A_t$$

$$A_{t+1} = s \frac{1}{1 + J_t} J_t. \tag{3}$$

The coefficient $b > 0$ is the inherent per capita production of juveniles by adults. The unit of time equals the maturation period of juveniles and the population is assumed 'semelparous' in the sense that adult life span is less than one unit of time. Note that R_+^2, $\bar{R}_+^2$, ∂R_+^2 and $\bar{R}_+^2/\{(0, 0)\}$ are all forward invariant sets under the map defined by equations (3).

If the net reproductive number $n \triangleq bs$ (the expected number of juveniles produced by each newborn during its life span [19, 20]) is less than 1, then the eigenvalues of the Jacobian evaluated at the origin are $\pm n^{1/2}$ and the linearization principle implies that the origin $(J, A) = (0, 0)$ is *locally asymptotically stable* (LAS). Furthermore, all solutions of equations (3) initiating in the closed cone $\bar{R}_+^2$ tend asymptotically to the origin. This follows

from Theorem 1.8 in [21], but is not difficult to prove directly. The inequalities

$$0 \leq J_{t+1} \leq bA_t, \quad 0 \leq A_{t+1} \leq sJ_t$$

and an induction show

$$0 \leq J_t \leq x_t, \quad 0 \leq A_t \leq y_t$$

where x_t, y_t solve the linear system equations

$$x_{t+1} = by_t, \quad y_{t+1} = sx_t$$

with initial condition $(x_0, y_0) = (J_0, A_0)$. Since $n < 1$ implies (x_t, t_t) approaches $(0, 0)$ as $t \to +\infty$, it follows that (J_t, A_t) approaches $(0, 0)$ as $t \to +\infty$.

If an equilibrium is LAS and if all orbits with initial conditions lying in a set S tend to the equilibrium, then we say the equilibrium is *globally asymptotically stable* (GAS) on S. Thus, if $n < 1$ in the juvenile–adult model (3), then the origin is GAS on the closed cone $\bar{R}_+^2$.

On the other hand, if $n > 1$ then (3) is uniformly persistent (permanent) with respect to the origin.[†] This follows from Theorem 3 in [22] once it is noted that (3) is dissipative (all solutions in $\bar{R}_+^2$ satisfy $0 \leq J_t \leq b$ and $0 \leq A_t \leq sc^{-1}$ after one time step) and $\bar{R}_+^2/\{(0, 0)\}$ is forward invariant (also see [21]). Moreover, if $n > 1$ there exists a unique nontrivial equilibrium, i.e. an equilibrium lying in $R_+^2/\{(0, 0)\}$, namely

$$(J, A) = \left(\frac{n-1}{ds+1}, \frac{n-1}{d+b} \right). \tag{4}$$

This equilibrium is LAS (the eigenvalues of the Jacobian at the equilibrium are $\pm n^{-1/2}$). Moreover, it is GAS on the positive cone R_+^2. To see this, we consider the subsequence extracted from a solution at even time steps. This subsequence satisfies the *uncoupled* equations

$$J_{t+2} = n \frac{1}{1 + (1 + ds)J_t} J_t$$

$$A_{t+2} = n_1 \frac{1}{1 + (d + b)A_t} A_t$$

each of which has the form of the discrete logistic (1). Therefore, for an initial condition $(j_0, A_0) \in R_+^2$ each component of the even-step subsequence approaches an equilibrium. Specifically, the subsequence (J_{2t}, A_{2t}) approaches the equilibrium (4). It then follows from (3) that the odd-step subsequence approaches the same equilibrium.

If, on the other hand, a nontrivial initial condition (J_0, A_0) lies on the boundary of the cone, i.e. if $(J_0, A_0) \in \partial R_+^2/\{(0, 0)\}$, then the solution of (3) approaches a 2-cycle. This is because one, but not both, of the components (J_0, A_0) equals 0 and hence that component equals 0 at all even time steps, while the other component equilibrates. From the equations (3) we see that at odd time steps the former component equilibrates while the latter tends to 0. This means the solution approaches a so-called *synchronous* (or single class) 2-cycle [23] in which, at each time, one life stage is absent. For example, $(J_0, A_0) = (0, A_0)$ implies the solution approaches the 2-cycle that alternates between the two points $(0, (n - 1)(d + b)^{-1})$ and $((n - 1)(ds + 1)^{-1}, 0)$ lying on the boundary of the cone. In the other case $(J_0, A_0) = (J_0, 0)$, the solution tends to the phase shift of this same 2-cycle.

[†]This means there exists a constant $\alpha > 0$ (that does not depend on the initial conditions) such that $(J_0, A_0) \in \bar{R}_+^2/\{(0, 0)\}$ implies $\liminf_{t \to +\infty}(|J_t| + |A_t|) \geq \alpha$.

THEOREM 2.1 *If $n \triangleq bs < 1$, all solutions of the juvenile–adult model* (3) *converge to the origin*:

$$\lim_{t \to +\infty} (J_t, A_t) = (0, 0).$$

If $n > 1$, then (3) *is uniformly persistent with respect to the origin. Moreover, the equilibrium* (4) *is GAS on R_+^2. However, if $(J_0, A_0) \in \partial R_+^2 / \{(0, 0)\}$ then the solution of* (3) *tends to the (synchronous or single class) 2-cycle defined by the two consecutive points*

$$\left(0, \frac{n-1}{d+b} \right) \longleftrightarrow \left(\frac{n-1}{ds+1}, 0 \right)$$

lying on the boundary ∂R_+^2 of R_+^2.

See [23] for more concerning the existence and bifurcation of synchronous cycles in semelparous population models.

Consider two species, each of whose dynamics are governed by a juvenile–adult model of the form (3) in the absence of the other and whose juveniles (the feeding/growing stage) compete when placed together. If we denote the two species by J, A and j, a, then we have a stage structured Leslie-Gower model

$$J_{t+1} = b_1 \frac{1}{1 + d_1 A_t} A_t$$

$$A_{t+1} = s_1 \frac{1}{1 + J_t + c_1 j_t} J_t$$

$$j_{t+1} = b_2 \frac{1}{1 + d_2 a_t} a_t$$

$$a_{t+1} = s_2 \frac{1}{1 + c_2 J_t + j_t} j_t \tag{5}$$

where the coefficients $c_i > 0$ measure the intensity of the inter-specific competition between the juveniles class. We assume each species, in the absence of the other, is viable, that is to say, we assume

$$n_1 > 1, \quad n_2 > 1$$

where $n_i \triangleq b_i s_i$ are the inherent net reproductive numbers for each species.

The nontrivial equilibria (J, A, j, a) of the competition model (5) are

$$(J_e, A_e, 0, 0), \quad (0, 0, j_e, a_e), \quad (J^*, A^*, j^*, a^*)$$

where

$$J_e \triangleq \frac{n_1 - 1}{1 + d_1 s_1}, \quad A_e \triangleq \frac{n_1 - 1}{d_1 + b_1}, \quad j_e \triangleq \frac{n_2 - 1}{1 + d_2 s_2}, \quad a_e \triangleq \frac{n_2 - 1}{d_2 + b_2}$$

$$J^* \triangleq \frac{(1 + d_2 s_2)(n_1 - 1) - c_1(n_2 - 1)}{(1 + d_1 s_1)(1 + d_2 s_2) - c_1 c_2}, \quad A^* \triangleq s_1 \frac{1}{1 + J^* + c_1 j^*} J^* \tag{6}$$

$$j^* \triangleq \frac{(1 + d_1 s_1)(n_2 - 1) - c_2(n_1 - 1)}{(1 + d_1 s_1)(1 + d_2 s_2) - c_1 c_2}, \quad a^* \triangleq s_2 \frac{1}{1 + c_2 J^* + j^*} j^*.$$

We refer to the first two equilibria (which lie on the boundary ∂R_+^4 of the positive cone R_+^4) as *exclusion equilibria*. We refer to the third equilibrium as the *coexistence equilibrium*, provided it lies in the positive cone R_+^4.

The following theorem accounts for the stability properties of all nontrivial equilibria of (5). We distinguish four cases for the inter-specific competition coefficients:

$$\text{(a) } c_1 < (1 + d_2 s_2)\frac{n_1 - 1}{n_2 - 1}, \quad c_2 < (1 + d_1 s_1)\frac{n_2 - 1}{n_1 - 1}$$

$$\text{(b) } c_1 < (1 + d_2 s_2)\frac{n_1 - 1}{n_2 - 1}, \quad c_2 > (1 + d_1 s_1)\frac{n_2 - 1}{n_1 - 1}$$

$$\text{(c) } c_1 > (1 + d_2 s_2)\frac{n_1 - 1}{n_2 - 1}, \quad c_2 < (1 + d_1 s_1)\frac{n_2 - 1}{n_1 - 1}$$

$$\text{(d) } c_1 > (1 + d_2 s_2)\frac{n_1 - 1}{n_2 - 1}, \quad c_2 > (1 + d_1 s_1)\frac{n_2 - 1}{n_1 - 1} \tag{7}$$

THEOREM 2.2 *Assume* $n_i \triangleq b_i s_i > 1$ *in the competition mode* (5).

In case (7a) *the coexistence equilibrium is GAS on* R_+^4.
In case (7b) *the exclusion equilibrium* $(J_e, A_e, 0, 0)$ *is GAS on* R_+^4.
In case (7c) *the exclusion equilibrium* $(0, 0, j_e, a_e)$ *is GAS on* R_+^4.
In case (7d) *exclusion equilibria are LAS and the coexistence equilibrium* $(J^*, A^*, j^*, a^*) \in R_+^4$ *is a saddle.*

The proof of this theorem, which appears in Appendix A2, is based on the composite equations

$$J_{t+2} = n_1 \frac{1}{1 + (1 + d_1 s_1) J_t + c_1 j_t} J_t$$

$$A_{t+2} = n_1 \frac{1}{1 + (d_1 + b_1)A_t + c_1 b_2 a_t (1 + d_1 A_t)/(1 + d_2 a_t)} A_t$$

$$j_{t+2} = n_2 \frac{1}{1 + c_2 J_t + (1 + d_2 s_2) j_t} j_t$$

$$a_{t+2} = n_2 \frac{1}{1 + c_2 b_1 A_t (1 + d_2 a_t)/(1 + d_1 A_t) + (d_2 + b_2)a_t} a_t \tag{8}$$

which are satisfied by both the even and odd step subsequences $(J_{2t}, A_{2t}, j_{2t}, a_{2t})$ and $(J_{2t+1}, A_{2t+1}, j_{2t+1}, a_{2t+1})$ of any solution sequence of (5). Note that the juvenile components (J_t, j_t) of these subsequences satisfy uncoupled equations that have the form of the Leslie–Gower equations (2), namely

$$x_{t+1} = n_1 \frac{1}{1 + (1 + d_1 s_1)x_t + c_1 y_t} x_t$$

$$y_{t+1} = n_2 \frac{1}{1 + c_2 x_t + (1 + d_2 s_2) y_t} y_t. \tag{9}$$

The four global stability options for the Leslie–Gower model appear in Appendix A1.

As far as equilibria of the juvenile–adult competition model (5) are concerned, the four dynamic scenarios in Theorem 2.2 match those of classic Lotka–Volterra competition theory. They predict competitive exclusion of one species unless the inter-specific competition coefficients c_i are sufficiently small (case (7a)). Notice, however, that unlike Lotka–Volterra theory, case (7d) does not describe the global dynamics of the model, as do cases (7a–c). This is because it turns out in the saddle case (7d) that there is a non-equilibrium coexistence

attractor, as Theorem 2.4 below shows. Thus, in contradistinction to Lotka–Volterra theory, the competition model (5) does not necessarily predict competitive exclusion when inter-specific competition coefficients c_i are large.

As we will see, a coexistence 2-cycle (a non-equilibrium, periodic solution of period 2 in which both species are present) plays a prominent role in the global dynamics of the competition model (5) in the saddle case (7d). The two points making a 2-cycle are equilibria of the composite equations (8). Consequently, we can account for all possible 2-cycles by means of the equilibria of the uncoupled equations (9), which are equilibria for the even and the odd step subsequences of the juvenile components.

The Leslie–Gower model (9) can have four equilibria in the closed cone $\bar{R}_+^2$ when, $n_i > 1$, namely, $(0, 0)$, $(J_e, 0)$, $(0, j_e)$ and (J^*, j^*). By pairing equilibria, one for the even step sub-sequence (J_{2t}, j_{2t}) with one for the odd step subsequences (J_{2t+1}, j_{2t+1}), we get 2-cycle sequences for (J_t, j_t). When extended by use of the second and fourth equations in the competition system (5) to include the sequence of adult stages, these 2-cycle sequences of juveniles yield 2-cycle solutions (J_t, A_t, j_t, a_t) of (5).

There are 16 possible pairings of the four equilibria of (9), although these include the four equilibria (when an equilibrium is paired with itself). This leaves 12 2-cycles that are not equilibria, although this count includes phase shifts of the 2-cycles. Modulo phase shifts there are six 2-cycle sequences (J_t, j_t) which yield the following 2-cycle solutions of (5):

$$
\begin{aligned}
C_1 &: \ (J_e, 0, 0, a_e) \rightleftarrows (0, A_e, j_e, 0) \\
C_2 &: \ (0, 0, 0, a_e) \rightleftarrows (0, 0, j_e, 0) \\
C_3 &: \ (0, A_e, 0, 0) \rightleftarrows (J_e, 0, 0, 0) \\
C_4 &: \ (0, A^*, 0, a^*) \rightleftarrows (J^*, 0, j^*, 0) \\
C_5 &: \ (J_e, A^*, 0, a^*) \rightleftarrows (J^*, A_e, j^*, 0) \\
C_6 &: \ (0, A^*, j_e, a^*) \rightleftarrows (J^*, 0, j^*, a_e).
\end{aligned}
\tag{10}
$$

In cases (7a,d) these six 2-cycles are the only 2-cycles lying in $\bar{R}_+^4$. In cases (7b, c), C_1, C_2 and C_3 are the only 2-cycles lying in $\bar{R}_+^4$.

THEOREM 2.3 *Assume* $n_i \triangleq b_i s_i > 1$ *in the competition model* (5).

In case (7a) *the only 2-cycles in* $\bar{R}_+^4$ *are the six cycles* C_i *in* (10) *and they are all unstable.*
In cases (7b) *and* (7c) *the only 2-cycles in* $\bar{R}_+^4$ *are* C_1, C_2, C_3 *and they are all unstable.*
In case (7d) *the only 2-cycles in* $\bar{R}_+^4$ *are the six cycles* C_i *in* (10) *and* C_2, C_3, C_4, C_5, C_6 *are unstable.*

The proof of this theorem involves, for each 2-cycle (10), an investigation of the eigenvalues of the Jacobian of the composite map or equivalently of the product of the Jacobian of (5) (denoted by $M(J, A, j, a)$) evaluated at each of the points of the cycle. For example, for the stability of cycle C_1, we examine the product $M(J_e, 0, 0, a_e) \, M(0, A_e, j_e, 0)$. The details are given in Appendix A3.

To describe the global dynamics in the saddle case (7d) we introduce the basin B_J and B_j of attraction of the two equilibria $(x, y) = (J_e, 0)$ and $(0, j_e)$ of the Leslie–Gower model (9). In the saddle case these open sets of R_+^2 have the property that

$$
R_+^2 = B_J \cup B_j \cup W_{J_j}^s
$$

where $W_{J_j}^s$ is the stable manifold of the saddle equilibrium (J^*, j^*). This stable manifold is the graph of a strictly increasing continuously differentiable function. The sets are open, connected and invariant. See [13, 24].

Consider an initial condition $(J_0, A_0, j_0, a_0) \in R_+^4$ for the competition model (5). If $(J_0, j_0) \in B_J$ then (J_{2t}, j_{2t}) approaches $(J_e, 0)$ as $t \to +\infty$. The fate of the odd step subsequence (J_{2t+1}, j_{2t+1}) is determined by their initial condition (J_1, j_1). If $(J_1, j_1) \in B_J$ then (J_{2t+1}, j_{2t+1}) approaches $(J_e, 0)$ as $t \to +\infty$, which then results in

$$\lim_{t \to +\infty} (J_t, A_t, j_t, a_t) = (J_e, A_e, 0, 0).$$

If, on the other hand, $(J_1, j_1) \in B_j$ then (J_{2t+1}, j_{2t+1}) approaches $(0, j_e)$ as $t \to +\infty$. This means (J_t, A_t, j_t, a_t) approaches the 2-cycle C_1 as $t \to +\infty$.

The map

$$F: (A, a) \longrightarrow \left(b_1 \frac{1}{1 + d_1 A} A, b_2 \frac{1}{1 + d_2 a} a \right)$$

is a one-to-one, onto, bicontinuous map of R_+^2 onto the rectangle

$$\Omega \triangleq \{ (J, j) \in R_+^2 : 0 < J < b_1/d_1, 0 < j < b_2/d_2 \}.$$

Define the open, connected, and disjoint sets

$$B_A \triangleq F^{-1}(\Omega \cap B_J), \quad B_a \triangleq F^{-1}(\Omega \cap B_j).$$

Then

$$R_+^2 = B_A \cup B_a \cup W_{Aa}^s$$

where $W_{Aa}^s \triangleq F^{-1}(W_{Jj}^s)$ is the graph of a curve in the plane (and hence has measure zero). Define the sets

$$B_{c_1} \triangleq \{ (J, A, j, a) \in R_+^4 \mid (J, j) \in B_J, \ (A, a) \in B_a \}$$
$$\cup \{ (J, A, j, a) \in R_+^4 \mid (J, j) \in B_j, \ (A, a) \in B_A \}$$
$$B_{JA} \triangleq \{ (J, A, j, a) \in R_+^4 \mid (J, j) \in B_J, \ (A, a) \in B_A \}$$
$$B_{ja} \triangleq \{ (J, A, j, a) \in R_+^4 \mid (J, j) \in B_j, \ (A, a) \in B_a \}.$$

These are open, disjoint sets in R_+^4 and, by the properties of B_J, B_A, B_j and B_a, the set $R_+^4/\{B_{C_1} \cup B_{JA} \cup B_{ja}\}$ has measure zero. By construction

$$(J_0, A_0, j_0, a_0) \in B_{C_1} \Longrightarrow (J_t, A_t, j_t, a_t) \text{ tends to the 2-cycle } C_1$$
$$(J_0, A_0, j_0, a_0) \in B_{JA} \Longrightarrow (J_t, A_t, j_t, a_t) \text{ tends to } (J_e, A_e, 0, 0)$$
$$(J_0, A_0, j_0, a_0) \in B_{ja} \Longrightarrow (J_t, A_t, j_t, a_t) \text{ tends to } (0, 0, j_e, a_e).$$

We have characterized the basins of attraction of the two exclusion equilibria and the coexistence 2-cycle in terms of the basins of attraction of the Leslie–Gower model (9). The global asymptotic dynamics of saddle case (7d) is described (up to a set of measure zero) by the following theorem.

THEOREM 2.4 *Assume* $n_i \triangleq b_i s_i > 1$ *in the competition model* (5) *and that the inequalities* (7d) *hold. All 2-cycles* (10) *are unstable except the coexistence 2-cycle* C_1 *which is LAS.*

The basin of attraction of the 2-*cycle* C_1 *is* B_{C_1}, *the basin of attraction of the exclusion equilibrium* $(J_e, A_e, 0, 0)$ *is* B_{JA}, *and the basin of attraction of the exclusion equilibrium* $(0, 0, j_a, a_e)$ *is* B_{ja}.

Proof All that remains to prove is the local asymptotic stability of the 2-cycle C_1. A calculation shows that the product $M(J_e, 0, 0, a_e)M(0, A_e, j_e, 0)$ is

$$
\begin{pmatrix}
\dfrac{n_1}{c_1 j_e + 1} & 0 & 0 & 0 \\[2ex]
0 & \dfrac{n_1}{(J_e + 1)^2(d_1 A_e + 1)^2} & 0 & -\dfrac{b_2 s_1 c_1 J_e}{(J_e + 1)^2} \\[2ex]
-\dfrac{n_2 c_2 j_e}{(j_e + 1)^2(d_2 a_e + 1)^2} & 0 & \dfrac{n_2}{(j_e + 1)^2(d_2 a_e + 1)^2} & 0 \\[2ex]
0 & 0 & 0 & \dfrac{n_2}{c_2 J_e + 1}
\end{pmatrix}
$$

and that the four eigenvalues of this matrix are

$$
\lambda_1 = \frac{n_1}{c_1 j_e + 1}, \quad \lambda_2 = \frac{n_1}{(J_e + 1)^2(d_1 A_e + 1)^2}
$$

$$
\lambda_3 = \frac{n_2}{(j_e + 1)^2(d_2 a_e + 1)^2}, \quad \lambda_4 = \frac{n_2}{c_2 J_e + 1}
$$

all of which are real and positive. From the formulas (6) we find that

$$
\lambda_1 = \frac{n_1(1 + d_2 s_2)}{(n_2 - 1)c_1 + 1 + d_2 s_2}, \quad \lambda_2 = \frac{1}{n_1}
$$

$$
\lambda_3 = \frac{1}{n_2}, \quad \lambda_4 = \frac{n_2(1 + d_1 s_1)}{(n_1 - 1)c_2 + 1 + d_1 s_1}. \tag{11}
$$

The inequalities in case (7d) and $n_i > 1$ imply all four eigenvalues are less than one. $\blacksquare$

Figures 1 and 2 illustrate the dynamic scenarios for the stage structured Leslie–Gower model (5) described in Theorems 2.3 and 2.4. In the sequence of graphs appearing in figure 1 we see, for fixed initial conditions, the competitive outcome begin with coexistence, then pass to global exclusion (of species *j, a*), and finally arrive at cyclic coexistence as the inter-specific competition coefficients c_1 and c_2 increase. In the case of cyclic coexistence in figure 1(c), figure 2 illustrates the triple attractor scenario of Theorem 2.4 by showing that competitive exclusion of either species can also result if initial conditions are changed.

In the next section we show that this triple attractor scenario for strong inter-specific competition described in Theorem 2.4 is not restricted to the stage structured Leslie–Gower model (5), but occurs in a general class of stage-structured competition models.

3. A general stage-structured competition model

The system

$$
\begin{aligned}
J_{t+1} &= b_1 f_1(A_t)A_t \\
A_{t+1} &= s_1 g_1(J_t + c_1 j_t)J_t \\
j_{t+1} &= b_2 f_2(a_t)a_t \\
a_{t+1} &= s_2 g_2(c_2 J_t + j_t)j_t
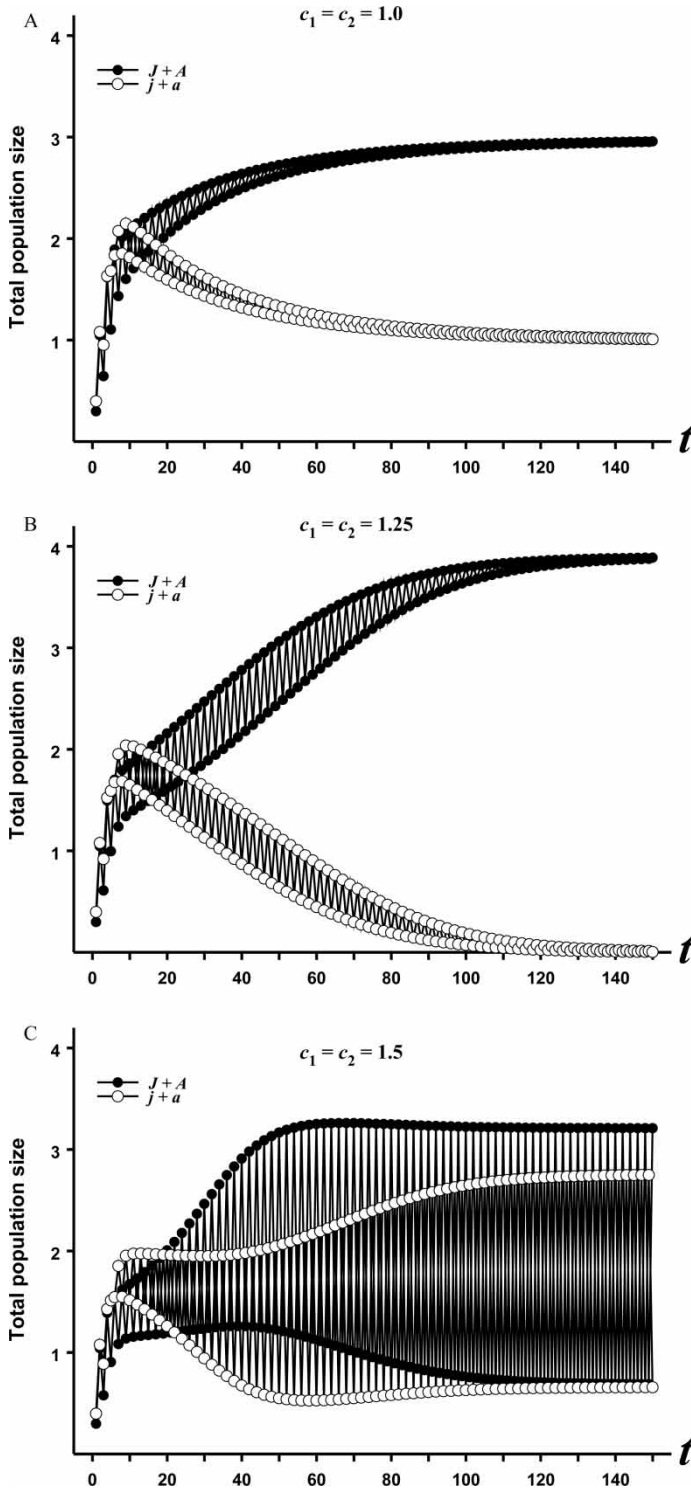\end{aligned} \tag{12}
$$

Figure 1. Graphs (a), (b), and (c) show total population sizes $J_t + A_t$ and $j_t + a_t$ for solutions of the competition model (5) as the inter-specific competition coefficients $c_1 = c_2$ increase. Other parameter values are fixed at $b_1 = b_2 = 5$, $s_1 = s_2 = 0.9$, $d_1 = 0.1$, $d_2 = 0.3$. The initial condition in all cases is $(J_0, A_0, j_0, a_0) = (0.1, 0.2, 0.2, 0.2)$. Coexistence is attained for both small and large values of $c_1 = c_2$.
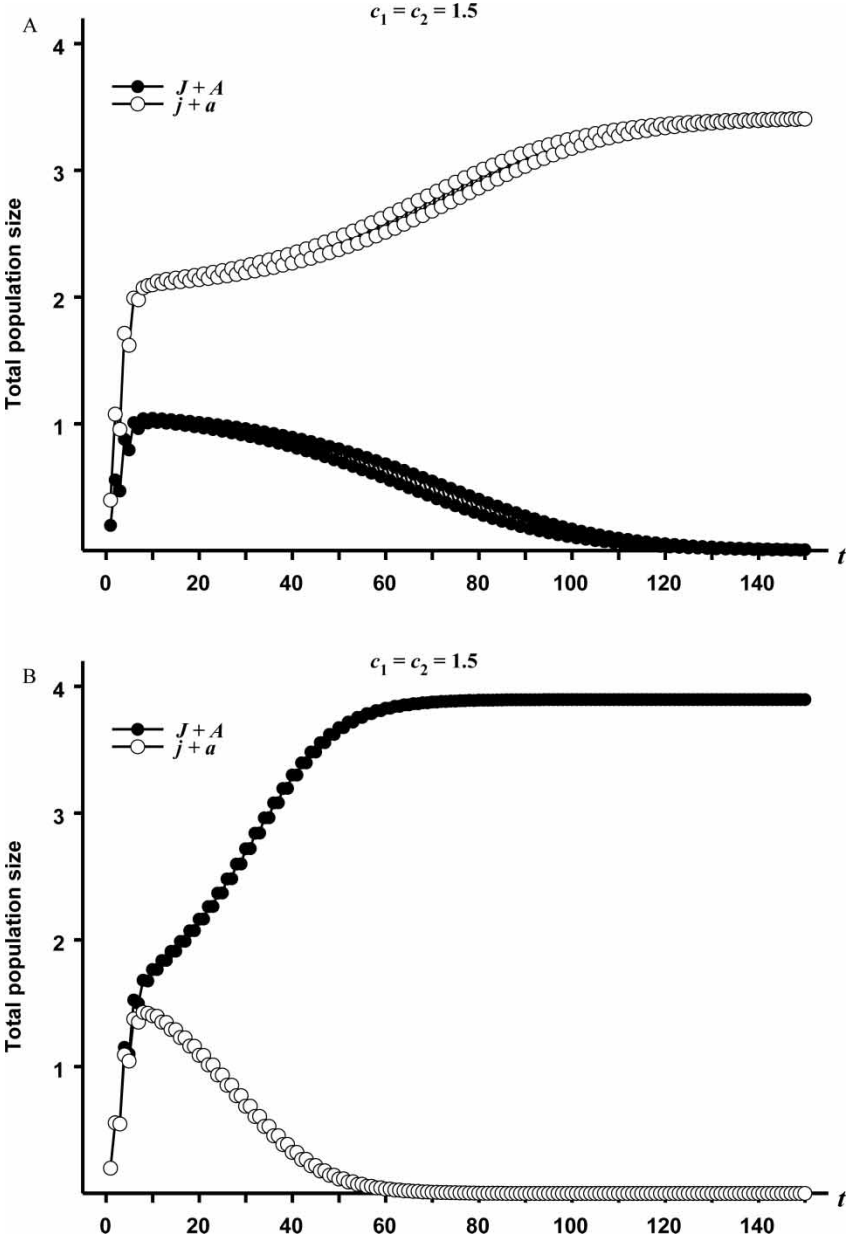
Figure 2. The graphs show plots of the total population sizes $J_t + A_t$ and $j_t + a_t$ for solutions of the competition model (5) with the same parameter values used in figure 1(c). In figure 1(c) the initial condition $(J_0, A_0, j_0, a_0) = (0.1, 0.2, 0.2, 0.2)$ result in (oscillatory) coexistence. Here the initial conditions in (a), $(J_0, A_0, j_0, a_0) = (0.1, 0.1, 0.2, 0.2)$ and in (b), $(J_0, A_0, j_0, a_0) = (0.1, 0.1, 0.1, 0.1)$, lead to the competitive exclusion of one species.

is a generalization of the stage-structured Leslie–Gower competition model (5). We assume that the density-related functions f_i and g_i satisfy the following conditions on an interval $I_\delta = \{x: -\delta < x < +\infty\}$ for some $\delta > 0$:

$$f_i \in C^2(I_\delta, R_+^1), \quad f_i' < 0, \quad f_i(0) = 1$$

$$g_i \in C^1(I_\delta, R_+^1), \quad g_i' < 0, \quad g_i(0) = 1, \quad g_i(+\infty) = 0$$

$$h_i(x) \triangleq f_i(x)x \text{ and } k_i(x) \triangleq g_i(x)x \text{ are bounded}$$
$$h'_i > 0, \quad k'_i > 0. \tag{13}$$

The coefficients satisfy

$$b_i, c_i > 0, \quad 0 < s_i < 1.$$

The coefficient b_i is the inherent fecundity of adults and s_i the inherent juvenile survivorship. The competition coefficients c_i measure the intensity of competition between the juvenile classes of the two species.

Our goal is to show that the triple-attractor scenario of Theorem 2.4 occurs for the system (12) when both inter-specific competition coefficients c_i are sufficiently large. To do this in a mathematically convenient way, we fix the ratio ρ between the competition coefficients and study how the dynamics of the system depends on a single parameter c, i.e. we substitute

$$c_1 = c, \quad c_2 = \rho c$$

into (12) and consider the system

$$
\begin{aligned}
J_{t+1} &= b_1 f_1(A_t) A_t \\
A_{t+1} &= s_1 g_1(J_t + c j_t) J_t \\
j_{t+1} &= b_2 f_2(a_t) a_t \\
a_{t+1} &= s_2 g_2(\rho c J_t + j_t) j_t
\end{aligned}
\tag{14}
$$

for large values of c. We will show that for c sufficiently large, this system has two stable competitively exclusion equilibria as well as a stable coexistence 2-cycle.

To begin, we need to understand the dynamics of each species in the absence of the other. Toward this end we consider the juvenile–adult model

$$
\begin{aligned}
J_{t+1} &= b f(A_t) A_t \\
A_{t+1} &= s g(J_t) J_t.
\end{aligned}
\tag{15}
$$

This is an example of a semelparous model of the type studied in [23]. Note that R^2_+ and its boundary ∂R^2_+ are forward invariant. The proof of the following theorem appears in Appendix A4.

THEOREM 3.1 *Consider* (15) *under the assumptions*

$$
\begin{aligned}
f &\in C^1(I_\delta, R^1_+), \quad f' < 0, \quad f(0) = 1 \\
g &\in C^1(I_\delta, R^1_+), \quad g' < 0, \quad g(0) = 1, \quad g(+\infty) = 0 \\
h(x) &\triangleq f(x)x \text{ and } k(x) \triangleq g(x)x \text{ are bounded} \\
h' &> 0, \quad k' > 0.
\end{aligned}
$$

If $n \triangleq bs > 1$ then there exists a GAS equilibrium in R^2_+. There also exists a 2-cycle on ∂R^2_+ that is GAS on $\partial R^2_+ / \{(0, 0)\}$.

As a result of this theorem, the competition model (14) has two competitive exclusion equilibria

$$(J, A, j, a) = (J_e, A_e, 0, 0) \text{ and } (0, 0, j_e, a_e)$$

where $(J_e, A_e) \in R^2_+$ is the equilibrium of (14) with $f = f_1, g = g_1, b = b_1$ and $s = s_1$ and $(j_e, a_e) \in R^2_+$ is the equilibrium of (14) with $f = f_2, g = g_2, b = b_2$ and $s = s_2$.

The Jacobian of (14) evaluated at the equilibrium $(J_e, A_e, 0, 0)$

$$
\begin{pmatrix}
0 & b_1 h_1'(A_e) & 0 & 0 \\
s_1 g_1(J_e) + s_1 g_1'(J_e) J_e & 0 & c s_1 J_e g_1'(J_e) & 0 \\
0 & 0 & 0 & b_2 \\
0 & 0 & s_2 g_2(\rho c J_e) & 0
\end{pmatrix}
$$

is block diagonal. The 2×2 in the upper left corner is the Jacobian of the single-species model (15) with $f = f_1$, $g = g_1$, $b = b_1$ and $s = s_1$ evaluated at its equilibrium (J_e, A_e). According to Theorem 3.1, the eigenvalues of this block are less than one in magnitude if $b_1 s_1 > 1$. The remaining two eigenvalues of the Jacobian are those of the 2×2 block in the lower right corner, which satisfy $\lambda^2 = n_2 g_2(\rho c J_e)$. Since J_e is independent of c, we have by (13) that $|n_2 g_2(\rho c J_e)| > 1$ for c sufficiently small and $|n_2 g_2(\rho c J_e)| < 1$ for c sufficiently large. Thus, the equilibrium $(J, A, j, a) = (J_e, A_e, 0, 0)$ of the competition model (14) is unstable for c small and LAS for c large. An analogous proof shows that the equilibrium $(J, A, j, a) = (0, 0, j_e, a_e)$ of the competition model (14) is also unstable for c small and LAS for c large.

For $c = 0$ the uncoupled model (14) has a GAS equilibrium $(J_e, A_e, j_e, a_e) \in R_+^4$. A straightforward application of the implicit function theorem shows that there exists an equilibrium in R_+^4 for c small. A continuity argument implies that this equilibrium is LAS. We summarize these conclusions in parts (a)–(c) of the following theorem. Proofs of parts (d) and (e) appear in Appendix A6.

THEOREM 3.2 *Assume the competition model* (14) *satisfies* (13).

For c sufficiently small
(a) *the exclusion equilibria $(J_e, A_e, 0, 0)$ and $(0, 0, j_e, a_e)$ are unstable and*
(b) *there exists LAS coexistence equilibrium $(J^*, A^*, j^*, a^*) \in R_+^4$.*

For c sufficiently large
(c) *the exclusion equilibria $(J_e, A_e, 0, 0)$ and $(0, 0, j_e, a_e)$ are LAS,*
(d) *there exists unique coexistence equilibrium $(J^*, A^*, j^*, a^*) \in R_+^4$ and*
(e) *the equilibrium $(J^*, A^*, j^*, a^*) \in R_+^4$ is a saddle.*

The even and odd time step sub-sequences of solutions of (14) satisfy the composite equations

$$
\begin{aligned}
J_{t+2} &= n_1 f_1(s_1 g_1(J_t + c j_t) J_t) g_1(J_t + c j_t) J_t \\
j_{t+2} &= n_2 f_2(s_2 g_2(c \rho J_t + j_t) j_t) g_2(c \rho J_t + j_t) j_t \\
A_{t+2} &= n_1 g_1(b_1 f_1(A_t) A_t + c b_2 f_2(a_t) a_t) f_1(A_t) A_t \\
a_{t+2} &= n_2 g_2(c \rho b_1 f_1(A_t) A_t + b_2 f_2(a_t) a_t) f_2(a_t) a_t.
\end{aligned}
$$

Note that the two equations for the juveniles uncouple from the two equations for the adults. Thus, both even and odd time step sub-sequences of solutions of (14) satisfy the uncoupled systems (with $(x_t, y_t) = (J_t, j_t)$ and $(z_t, w_t) = (A_t, a_t)$)

$$
\begin{aligned}
(a) \quad & x_{t+1} = b_1 h_1(s_1 g_1(x_t + c y_t) x_t) \\
(b) \quad & y_{t+1} = b_2 h_2(s_2 g_2(c \rho x_t + y_t) y_t)
\end{aligned}
$$

$$(c) \qquad z_{t+1} = s_1 g_1(b_1 h_1(z_t) + cb_2 h_2(w_t))b_1 h_1(z_t)$$

$$(d) \qquad w_{t+1} = s_2 g_2(c\rho b_1 h_1(z_t) + b_2 h_2(w_t))b_2 h_2(w_t). \tag{16}$$

Equilibria of the composite equations (16) give rise to equilibria or 2-cycles of (14). One equilibrium is $(x, y, z, w) = (J_e, 0, 0, a_e)$. This equilibrium gives rise to the (non-equilibrium) 2-cycle

$$(J_e, 0, 0, a_e) \leftrightarrows (0, A_e, j_e, 0) \tag{17}$$

of the competition model (14). For sufficiently large values of c another equilibrium is $(x, y, z, w) = (J^*, j^*, A^*, a^*)$, which corresponds to the equilibrium $(J, A, j, a) = (J^*, A^*, j^*, a^*)$ of the competition model (14). A proof that this equilibrium is stable is found in Appendix A5.

THEOREM 3.3 *Assume the competition model* (14) *satisfies* (13). *For c sufficiently large the coexistence* 2-*cycle* (17) *is LAS.*

Theorems 3.2 and 3.3 together imply that for large inter-specific competition coefficients c and ρc in (14) three possible asymptotic outcomes are possible. Depending on initial conditions, the competitive outcome can asymptotically result in the elimination of one species or the other, by approaching one of the two stable exclusion equilibria $(J, A, j, a) = (J_e, A_e, 0, 0)$ or $(0, 0, j_e, a_e)$, or result in non-equilibrium coexistence by approaching the 2-cycle (17).

By applying recent results of Kulenović and Merino [24] for planar strongly monotone maps (Theorem 4.1 in Appendix A7) we can give a global description of the basins of attraction of these three attractors. Define the partial ordering on R^2 by $u = (u_1, u_2) \leq (v_1, v_2) = v \Leftrightarrow u_1 \leq v_1$ and $u_2 \geq v_2$. Define $u < v$ to mean $u \leq v$ and $u \neq v$. Also define $u \ll v$ to mean $u \leq v$ and $u_1 \neq v_1, u_2 \neq v_2$. A map (continuous function) $T : R^2_+ \to R^2_+$ is strongly monotone if $u < v$ implies $T(u) \ll T(v)$ for all $u, v \in R^2_+$. A C^2 planar map is strongly monotone on R^2_+ if the Jacobian $J(x, y)$ has the sign structure [24]

$$\begin{pmatrix} + & - \\ - & + \end{pmatrix}. \tag{18}$$

For the planar map defined by equations (16 a, b) we have from (13) that

$$\frac{\mathrm{d}}{\mathrm{d}x}(f_i(x+c)x) = \frac{\mathrm{d}}{\mathrm{d}x}(h_i(x+c) - f_i(x+c)c)$$

$$= h_i'(x+c) - f_i'(x+c)c > 0$$

$$\frac{\mathrm{d}}{\mathrm{d}x}(g_i(x+c)x) = \frac{\mathrm{d}}{\mathrm{d}x}(k_i(x+c) - g_i(x+c)c)$$

$$= k_i'(x+c) - g_i'(x+c)c > 0$$

for $c \geq 0$. These imply the sign conditions (18) and consequently this map is strongly monotone on R^2_+. (Similar calculations show the map defined by the equations (16c, d) is also strongly monotone on R^2_+.) If we assume

$$(16a, b) \text{ has no (non-equilibrium) 2-cycle in } R^2_+ \tag{19}$$

then the hypotheses of the Theorem 4.1 in Appendix A7 (see [24]) are satisfied for monotone maps defined by equations (16a, b) and (16c, d) provided c is sufficiently large. That theorem implies the stable manifold W^s_{xy} of the equilibrium $x = J^*$, $y = j^*$ is the graph of a continuous

and strictly increasing function whose endpoints lie on ∂R_+^2 and the basins of attraction B_x and B_y of the two exclusion equilibria $(x, w) = (J_e, 0)$ and $(x, y) = (0, j_e)$, respectively, are open, invariant, disjoint, and connected sets that satisfy

$$R_+^2 / W_{xy}^s = B_x \cup B_y.$$

Similarly the stable manifold W_{zw}^s of the equilibrium $z = A^*$, $w = a^*$ is the graph of a continuous and strictly increasing function whose endpoints lie on ∂R_+^2 and the basins of attraction B_z and B_w of the two exclusion equilibria $(z, w) = (A_e, 0)$ and $(z, w) = (0, a_e)$, respectively, are open, invariant, disjoint, and connected sets that satisfy

$$R_+^2 / W_{zw}^s = B_z \cup B_w.$$

Using the sets B_x, B_y, B_z and B_w we can describe the basins of attraction of the stable equilibrium and 2-cycle given in Theorems 3.2(c) and 3.3 for the competition model (14). Define the open sets

$$B_{JA} \triangleq \{(J, A, j, a) \in R_+^4 : (J, j) \in B_x \text{ and } (A, a) \in B_z\}$$
$$B_{ja} \triangleq \{(J, A, j, a) \in R_+^4 : (J, j) \in B_y \text{ and } (A, a) \in B_w\}$$
$$B_{Ja} \triangleq \{(J, A, j, a) \in R_+^4 : (J, j) \in B_x \text{ and } (A, a) \in B_w\}$$
$$B_{jA} \triangleq \{(J, A, j, a) \in R_+^4 : (J, j) \in B_y \text{ and } (A, a) \in B_z\} \tag{20}$$

in R_+^4. Note that $R_+^4 / (B_{JA} \cup B_{ja} \cup B_{Ja} \cup B_{jA})$ has measure zero. In fact, a point in R_+^4 not in this set must have an associated pair (J, j) or (A, a) that lies on a boundary of B_x or B_y.

THEOREM 3.4 *Assume* (13) *and* (19). *For c sufficiently large, solution sequences in R_+^4 of the competition model* (14) *with initial conditions lying in $B_{JA} \cup B_{ja} \cup B_{Ja} \cup B_{jA}$ satisfy the following alternatives as $t \to +\infty$:*

Competitive exclusion

$$(J_0, A_0, j_0, a_0) \in B_{JA} \Rightarrow (J_t, A_t, j_t, a_t) \longrightarrow (J_e, A_e, 0, 0)$$
$$(J_0, A_0, j_0, a_0) \in B_{Ja} \Rightarrow (J_t, A_t, j_t, a_t) \longrightarrow (0, 0, j_e, a_e)$$

Competitive (2-cycle) coexistence

$$(J_0, A_0, j_0, a_0) \in B_{Ja} \Rightarrow \begin{cases} (J_{2t}, A_{2t}, j_{2t}, a_{2t}) \longrightarrow (J_e, 0, 0, a_e) \\ (J_{2t+1}, A_{2t+1}, j_{2t+1}, a_{2t+1}) \longrightarrow (0, A_e, j_e, 0) \end{cases}$$

$$(J_0, A_0, j_0, a_0) \in B_{jA} \Rightarrow \begin{cases} (J_{2t}, A_{2t}, j_{2t}, a_{2t}) \longrightarrow (0, A_e, j_e, 0) \\ (J_{2t+1}, A_{2t+1}, j_{2t+1}, a_{2t+1}) \longrightarrow (J_e, 0, 0, a_e). \end{cases}$$

4. Discussion

The triple-attractor case in Theorem 2.4 (and 3.4), in which both coexistence and exclusion attractors are represented, is unusual in competition models. Even more unusual is that this case occurs when the inter-specific competition coefficients are large. In the stage-structured Leslie–Gower model global competitive exclusion occurs only for intermediate levels of inter-specific competition (where global exclusion occurs in cases (7b, c) in Theorem 2.4). From an

initial condition where one species competitively excludes the other, the model allows the two species to attain coexistence by either a decrease or an *increase* of the competition coefficients. This result seemingly contradicts the classic competitive exclusion principle, at least when that principle is expressed by the assertion that in order to coexist two species must *decrease* the intensity of their inter-specific competition.

There is a reconciliation, however, and that lies in the observation that the juvenile classes are never simultaneously present in the 2-cycle coexistence attractor in Theorem 2.4 (and 3.4). Therefore, after arriving at this attractor no competition occurs between the species. Large values of the competition coefficients in a model represent the potential for strong competitive interactions, should such interactions take place. In the stage-structured competition models (5) and (12) it is possible for the species to avoid inter-specific competition by synchronizing their life cycle stages. This observation shows that there would be no contradiction to the competitive exclusion principle if this principle were stated slightly differently (as it often is in the ecological literature): in order to survive a species must find a way to minimize or avoid competition from other species (i.e. find its 'niche'). What our results show is that the competition coefficients in a model might not relate in a straightforward way (e.g. by means of their magnitudes) to this form of the competitive exclusion principle. However, the model (5) also questions this formulation competitive exclusion principle. This is because the 'avoidance' coexistence 2-cycle in Theorems 2.4 and 3.4 in fact exists for all values of the competition coefficients, including small values where global equilibrium coexistence occurs. In this case rather than seeking to avoid competition in order to coexist (by tending to the avoidance 2-cycle), the two species coexistence in equilibrium where competition is not avoided.

Appendices

A1   *The Leslie–Gower model*

To analyze the stability properties of these equilibria we will use the following facts about the Leslie–Gower competition model (2) [13, 18, 24]:

$$x_{t+1} = b_1 \frac{1}{1 + c_{11}x_t + c_{12}y_t} x_t$$

$$y_{t+1} = b_2 \frac{1}{1 + c_{21}x_t + c_{22}y_t} y_t.$$

There exist three nontrivial equilibria, namely,

$$(x, y) = (x_e, 0), \quad (0, y_e), \quad (x^*, y^*) \tag{A1}$$

where

$$x_e \triangleq \frac{b_1 - 1}{c_{11}}, \quad y_e \triangleq \frac{b_2 - 1}{c_{22}}$$

$$x^* \triangleq \frac{c_{22}(b_1 - 1) - (b_2 - 1)c_{12}}{c_{11}c_{22} - c_{12}c_{21}}, \quad y^* \triangleq \frac{c_{11}(b_2 - 1) - c_{21}(b_1 - 1)}{c_{11}c_{22} - c_{12}c_{21}}.$$

Assuming $b_i > 1$, then

$$\left.\begin{array}{l} c_{12} < c_{22}\dfrac{b_2 - 1}{b_1 - 1} \\[3mm] c_{21} < c_{11}\dfrac{b_1 - 1}{b_2 - 1} \end{array}\right\} \implies (x^*, y^*) \text{ is GAS on } R_+^2 \tag{A2a}$$

$$\left.\begin{array}{l} c_{12} < c_{22}\dfrac{b_2 - 1}{b_1 - 1} \\[3mm] c_{21} > c_{11}\dfrac{b_1 - 1}{b_2 - 1} \end{array}\right\} \implies (x_e, 0) \text{ is GAS on } R_+^2 \tag{A2b}$$

$$\left.\begin{array}{l} c_{12} > c_{22}\dfrac{b_2 - 1}{b_1 - 1} \\[3mm] c_{21} < c_{11}\dfrac{b_1 - 1}{b_2 - 1} \end{array}\right\} \implies (0, y_e) \text{ is GAS on } R_+^2 \tag{A2c}$$

$$\left.\begin{array}{l} c_{12} > c_{22}\dfrac{b_2 - 1}{b_1 - 1} \\[3mm] c_{21} > c_{11}\dfrac{b_1 - 1}{b_2 - 1} \end{array}\right\} \implies (x_e, 0), (0, y_e) \text{ are LAS and } (x^*, y^*) \text{ is a saddle.} \tag{A2d}$$

In the latter case, the stable manifold W^s of (x^*, y^*) lies on the graph of a strictly increasing, continuously differentiable function and $R_+^2 = B_x \cup B_y \cup W^s$ where B_x and B_y are the open, disjoint and connected basins of attraction of $(x_e, 0)$ and $(0, y_e)$, respectively (Theorems 5 and 6 in [24]).

A2 Proof of theorem 2.2

Case (a). The inequalities concerning the coefficients in this case correspond to the option (A2a) in the Leslie–Gower system (9) for the subsequences of juvenile components. Given an initial condition $(J_0, A_0, j_0, a_0) \in R_+^4$, and hence an initial condition $(x_0, y_0) = (J_0, j_0) \in R_+^2$ for the even step subsequence, it follows from Appendix A1 that the juvenile components (J_{2t}, j_{2t}) of the even step subsequence converge to (J^*, j^*). (See (A1).) Since $(J_0, A_0, j_0, a_0) \in R_+^4$ implies $(J_1, A_1, j_1, a_1) \in R_+^4$, the initial condition $(x_0, y_0) = (J_1, j_1) \in R_+^2$ and the odd subsequence of the juvenile components (J_{2t+1}, j_{2t+1}) also converge to (J^*, j^*). It follows that the time series of juvenile components (J_t, j_t) converges to (J^*, j^*). From this conclusion equations (5) imply

$$\lim_{t\to\infty} A_{t+1} = s_1 \frac{1}{1 + J^* + c_1 j^*} J^* = A^*$$

$$\lim_{t\to\infty} a_{t+1} = s_2 \frac{1}{1 + c_2 J^* + j^*} j^* = a^*.$$

To complete the proof that the coexistence equilibrium (J^*, j^*, A^*, a^*) is GAS on R_+^4 we need to show that it is LAS.

The characteristic polynomial $p(\lambda)$ of the Jacobian

$$M(J, A, j, a) = \begin{pmatrix} 0 & \dfrac{b_1}{(Ad_1 + 1)^2} & 0 & 0 \\[3mm] \dfrac{s_1(jc_1 + 1)}{(J + jc_1 + 1)^2} & 0 & -\dfrac{s_1 c_1 J}{(J + jc_1 + 1)^2} & 0 \\[3mm] 0 & 0 & 0 & \dfrac{b_2}{(ad_2 + 1)^2} \\[3mm] -\dfrac{s_2 c_2 j}{(j + Jc_2 + 1)^2} & 0 & \dfrac{s_2(Jc_2 + 1)}{(j + Jc_2 + 1)^2} & 0 \end{pmatrix}$$

of (5) is quadratic in λ^2. Specifically, $p(\lambda) = q(\lambda^2)$ where

$$q(z) \triangleq z^2 - a_1 z + a_2$$

$$a_1 \triangleq n_1 \frac{1 + c_1 j}{(1 + d_1 A)^2 (1 + J + c_1 j)^2} + n_2 \frac{1 + c_2 J}{(1 + d_2 a)^2 (1 + c_2 J + j)^2}$$

$$a_2 \triangleq n_1 n_2 \frac{1 + c_2 J + c_1 j}{(1 + d_1 A)^2 (1 + d_2 a)^2 (1 + J + c_1 j)^2 (1 + c_2 J + j)^2}.$$

The roots λ of p have magnitude less than 1 if and only if the roots z of q do. Since $a_i > 0$ the roots of z of the quadratic q have magnitude less than 1 if and only if the Jury conditions[†] hold if (and only if)

$$1 - a_1 + a_2 > 0, \quad a_2 < 1. \tag{A3}$$

If (at least) one of these inequalities is reversed, then there is a root λ of magnitude greater than 1. To establish the local stability of an equilibrium by means of the linearization principle we need to evaluate a_i at the equilibrium and investigate the two inequalities (A3).

Consider the coexistence equilibrium (J^*, j^*, A^*, a^*). Multiplying together the first two equilibrium equations and then the last two equilibrium equations, we find that

$$n_1 = (1 + d_1 A^*)(1 + J^* + c_1 j^*)$$

$$n_2 = (1 + d_2 a^*)(1 + j^* + c_2 J^*) \tag{A4}$$

and hence

$$n_1 n_2 = (1 + d_1 A^*)(1 + d_2 a^*)(1 + J^* + c_1 j^*)(1 + j^* + c_2 J^*).$$

It follows that

$$a_2 = \frac{1}{1 + d_1 A^*} \frac{1}{1 + d_2 a^*} \frac{1 + c_2 J^* + c_1 j^*}{(1 + J^* + c_1 j^*)(1 + j^* + c_2 J^*)}$$

is less than 1 (because each factor is). It also follows that

$$1 - a_1 + a_2 = 1 - \left(\frac{1 + c_1 j^*}{n_1} + \frac{1 + c_2 J^*}{n_2} \right) + \frac{1 + c_2 J^* + c_1 j^*}{n_1 n_2}$$

$$= \frac{(n_1 - 1)(n_2 - 1)}{n_1 n_2} \left(1 - \frac{1}{n_2 - 1} c_2 J^* - \frac{1}{n_1 - 1} c_1 j^* \right).$$

The formulas for J^* and j^* yield, after some algebra,

$$1 - a_1 + a_2 = \frac{(1 + d_1 s_1)(1 + d_2 s_2) - c_1 c_2}{n_1 n_2} J^* j^*.$$

The inequalities in case (a) imply this expression is positive.

[†]The roots of the quadratic $z^2 + \beta z + \alpha$ satisfy $|z| < 1$ if and only if $|\alpha| < 1$ and $|\beta| < 1 + \alpha$. If one of these inequalities is reversed, there is a root satisfying $|z| > 1$.

Case (b). The inequalities concerning the coefficients in this case correspond to the option (A2b) in the Leslie–Gower system (9) for the subsequences of juvenile components. Given an initial condition $(J_0, A_0, j_0, a_0) \in R_+^4$, and hence an initial condition $(x_0, y_0) = (J_0, j_0) \in R_+^2$ for the even step subsequence, it follows from Appendix A1 that the juvenile components of the even step subsequence (J_{2t}, j_{2t}) converge to $(J_e, 0)$ (See (Al).) Since $(J_0, A_0, j_0, a_0) \in R_+^4$ implies $(J_1, A_1, j_1, a_1) \in R_+^4$, the initial condition $(x_0, y_0) = (J_1, j_1) \in R_+^2$ and the odd subsequence of the juvenile components (J_{2t+1}, j_{2t+1}) also converges to $(J_e, 0)$. It follows that the time series of juvenile components (J_t, j_t) converges to $(J_e, 0)$. From this conclusion the equations (5) imply

$$\lim_{t \to +\infty} A_{t+1} = s_1 \frac{1}{1 + J_e} J_e = A_e$$

$$\lim_{t \to +\infty} a_{t+1} = 0.$$

To complete the proof that the coexistence equilibrium $(J_e, A_e, 0, 0)$ is GAS on R_+^4 we need to show that it is LAS. The Jacobian

$$M(J_e, A_e, 0, 0) = \begin{pmatrix} M_{11} & M_{12} \\ 0 & M_{22} \end{pmatrix}$$

is block triangular with

$$M_{22} = \begin{pmatrix} 0 & b_2 \\ \dfrac{s_2(1 + d_1 s_1)}{c_2(n_1 - 1) + 1 + d_1 s_1} & 0 \end{pmatrix}.$$

The eigenvalues of M_{11} are less than one in magnitude since this matrix is the Jacobian of the J, A single species model (2.1) and $n_1 > 1$. The remaining eigenvalues of $M(J_e, A_e, 0, 0)$ are those of M_{22}, which are

$$\lambda = \pm \sqrt{\frac{n_2(1 + d_1 s_1)}{c_2(n_1 - 1) + (1 + d_1 s_1)}}$$

and hence, under the assumptions of case (b), are less than one in magnitude.

Case (c). This case is proved analogously to Case (b).

Case (d). The proof that $(J_e, A_e, 0, 0)$ is LAS is the same as the proof in Case (b). An analogous proof shows $(0, 0, j_e, a_e)$ is LAS. From the calculations in the proof of Case (a), we find in this case that the coefficients a_i that define the characteristic polynomial $p(\lambda) = q(\lambda^2)$ of the Jacobin associated with coexistence equilibrium (J^*, j^*, A^*, a^*) satisfy

$$a_i > 0, 1 - a_1 + a_2 < 0 \text{ and } a_2 < 1.$$

It follows that $q(z) = z^2 - a_1 z + a_2$ has two positive real roots $0 < z_1 < 1 < z_2$ and that two eigenvalues $\lambda = \pm \sqrt{z_1}$ are less than one in magnitude and two eigenvalues $\lambda = \pm \sqrt{z_2}$ are greater than one in magnitude. Therefore, (J^*, j^*, A^*, a^*) is a saddle, with two-dimensional stable and unstable manifolds.

A3 *Proof of theorem 2.3*

We investigate the stability of each of the six 2-cycles (10) consecutively. By the linearization principle, a 2-cycle that oscillates between points (J_0, j_0, A_0, a_0) and (J_1, A_1, j_1, a_1) is LAS

if the eigenvalues of the product $M(J_0, j_0, A_0, a_0) M(J_1, A_1, j_1, a_1)$ are less than one in magnitude. If one eigenvalue has magnitude greater than one, the 2-cycle is unstable.

In the proof of Theorem 2.4 we calculated the eigenvalues (11) of the product $M(J_e, 0, 0, a_e) M(0, A_e, j_e, 0)$. In cases (7a,b,c) at least one of the eigenvalues λ_2 or λ_3 is greater than one. Therefore, the 2-cycle C_1 is unstable in these cases.

Calculations show that the matrices

$$M(0, 0, 0, a_e)M(0, 0, j_e, 0)$$

$$M(0, A_e, 0, 0)M(J_e, 0, 0, 0)$$

are, respectively,

$$
\begin{pmatrix}
\dfrac{n_1}{c_1 j_e + 1} & 0 & 0 & 0 \\[3mm]
0 & n_1 & 0 & 0 \\[3mm]
-\dfrac{n_2 c_2 j_e}{(j_e + 1)^2 (d_2 a_e + 1)^2} & 0 & \dfrac{n_2}{(j_e + 1)^2 (d_2 a_e + 1)^2} & 0 \\[3mm]
0 & 0 & 0 & n_2
\end{pmatrix}
$$

$$
\begin{pmatrix}
\dfrac{n_1}{(J_e + 1)^2 (d_1 A_e + 1)^2} & 0 & -\dfrac{n_1 c_1 J_e}{(J_e + 1)^2 (d_1 A_e + 1)^2} & 0 \\[3mm]
0 & n_1 & 0 & 0 \\[3mm]
0 & 0 & \dfrac{n_2}{c_2 J_e + 1} & 0 \\[3mm]
0 & 0 & 0 & n_2
\end{pmatrix}.
$$

Both of these matrices have eigenvalues $n_i > 1$ and, as a result, the 2-cycles C_2 and C_3 are unstable in all cases (7).

In Cases (7a,d) the 2-cycles C_4, C_5 and C_6 lie in $\bar{R}_+^4$. A calculation shows $M(0, A^*, 0, a^*)M(J^*, 0, j^*, 0)$ equals

$$
\begin{pmatrix}
\dfrac{n_1(c_1 j^* + 1)}{(d_1 A^* + 1)^2 (J^* + c_1 j^* + 1)^2} & 0 & -\dfrac{n_1 c_1 J^*}{(d_1 A^* + 1)^2 (J^* + c_1 j^* + 1)^2} & 0 \\[3mm]
0 & n_1 & 0 & 0 \\[3mm]
-\dfrac{n_2 c_2 j^*}{(d_2 a^* + 1)^2 (j^* + c_2 J^* + 1)^2} & 0 & \dfrac{n_2(c_2 J^* + 1)}{(d_2 a^* + 1)^2 (j^* + c_2 J^* + 1)^2} & 0 \\[3mm]
0 & 0 & 0 & n_2
\end{pmatrix}.
$$

This matrix has eigenvalues $n_i > 1$ and consequently the 2-cycle C_4 is unstable.

To investigate 2-cycle C_5 we calculate the product of the two Jacobians $M(J_e, A^*, 0, a^*)$ and $M(J^*, A_e, j^*, 0)$, which turns out to be

$$
\begin{pmatrix}
\dfrac{n_1(c_1 j^* + 1)}{(d_1 A^* + 1)^2 (J^* + c_1 j^* + 1)^2} & 0 & -\dfrac{n_1 c_1 J^*}{(d_1 A^* + 1)^2 (J^* + c_1 j^* + 1)^2} & 0 \\[3mm]
0 & \dfrac{n_1}{(J_e + 1)^2 (d_1 A_e + 1)^2} & 0 & -\dfrac{b_2 s_1 c_1 J_e}{(J_e + 1)^2} \\[3mm]
-\dfrac{n_2 c_2 j^*}{(d_2 a^* + 1)^2 (j^* + c_2 J^* + 1)^2} & 0 & \dfrac{n_2(c_2 J^* + 1)}{(d_2 a^* + 1)^2 (j^* + c_2 J^* + 1)^2} & 0 \\[3mm]
0 & 0 & 0 & \dfrac{n_2}{c_2 J_e + 1}
\end{pmatrix}.
$$

which, by formulas (6) and (4), reduces to

$$
\begin{pmatrix}
\dfrac{c_1 j^* + 1}{n_1} & 0 & -\dfrac{c_1 J^*}{n_1} & 0 \\[3mm]
0 & \dfrac{1}{n_1} & 0 & -\dfrac{b_2 c_1 s_1 J_e}{(J_e + 1)^2} \\[3mm]
-\dfrac{c_2 j^*}{n_2} & 0 & \dfrac{c_2 J^* + 1}{n_2} & 0 \\[3mm]
0 & 0 & 0 & \dfrac{n_2}{c_2 J_e + 1}
\end{pmatrix}.
$$

One eigenvalue of this matrix is $\lambda_1 = n_1^{-1} < 1$. Another eigenvalue

$$
\lambda_2 = \frac{n_2}{c_2 J_e + 1} = \frac{n_2(1 + d_1 s_1)}{c_2(n_1 - 1) + (1 + d_1 s_1)}
$$

is greater than one in case (7a), but less than one in case (7d). To investigate the latter case, we factor the characteristic polynomial

$$
p(\lambda) = (\lambda - \lambda_1)(\lambda - \lambda_2)\left(\lambda_2 - \frac{n_2 + n_1 + c_2 n_1 J^* + c_1 n_2 j^*}{n_1 n_2} \lambda + \frac{1 + c_2 J^* + c_1 j^*}{n_1 n_2} \right)
$$

and consider the two roots of the quadratic polynomial

$$
\lambda^2 - \frac{n_2 + n_1 + c_2 n_1 J^* + c_1 n_2 j^*}{n_1 n_2} \lambda + \frac{1 + c_2 J^* + c_1 j^*}{n_1 n_2}.
$$

In case (7d) the first Jury inequality (A3) for stability is reversed for this polynomial and hence it has a root larger than one in magnitude. This follows from a calculation that shows

$$
\begin{aligned}
1 - a_1 + a_2 &= 1 - \frac{n_2 + n_1 + c_2 n_1 J^* + c_1 n_2 j^*}{n_1 n_2} + \frac{1 + c_2 J^* + c_1 j^*}{n_1 n_2} \\[2mm]
&= \frac{(c_1(n_2 - 1) - (1 + d_2 s_2)(n_1 - 1))(c_2(n_1 - 1) - (1 + d_1 s_1)(n_2 - 1))}{n_1 n_2((1 + d_1 s_1)(1 + d_2 s_2) - c_1 c_2)}
\end{aligned}
$$

and hence $1 - a_1 + a_2 < 0$ in both cases (7a, d). We conclude that the cycle C_5 is unstable.

The analysis of the 2-cycle C_6, based on the eigenvalues of $M(0, A^*, j_e, a^*) M(J^*, 0, j^*, a_e)$ is analogous to that of C_5.

A4 *Proof of theorem 3.1*

Solving the equilibrium equations

$$J = bf(A)A, \quad A = sg(J)J$$

is equivalent, for nontrivial equilibria, to solving the equation

$$bf(sg(J)J)sg(J) = 1$$

for $J > 0$ and then letting $A = sg(J)J$. The left side of the equation, namely $bf(sg(J)J)sg(J)$, is strictly decreasing in $J \geq 0$, equals $n > 1$ at $J = 0$, and approaches 0 as $J \to +\infty$. As a result there exists a unique root $J_e > 0$ of the equation and a unique positive equilibrium $(J_e, A_e) = (J_e, sg(J_e)J_e)$. The eigenvalues of the Jacobian evaluated at this equilibrium

$$\begin{pmatrix} 0 & bh'(A_e) \\ sk'(J_e) & 0 \end{pmatrix}$$

satisfy the characteristic equation $\lambda^2 = bh'(A_e)sk'(J_e) > 0$. Since

$$0 < bh'(A_e) = bf(A_e) + bf'(A_e)A_e = \frac{J_e}{A_e} + bf'(A_e)A_e < \frac{J_e}{A_e}$$

$$0 < sk'(J_e) = sg(J_e) + sg'(J_e)J_e = \frac{A_e}{J_e} + sg'(J_e)J_e < \frac{A_e}{J_e} \tag{A5}$$

it follows that $\lambda^2 < 1$ and the equilibrium is LAS.

To see that the equilibrium (J_e, A_e) is GAS on R_2^+ we consider the odd and even time step subsequences (J_{2t+1}, A_{2t+1}) and (J_{2t}, A_{2t}) of a solution (J_t, A_t) sequence, both of which satisfy the uncoupled system

$$\begin{aligned} (a) & \quad x_{t+1} = bh(sk(x_t)) \\ (b) & \quad y_{t+1} = sk(bh(y_t)). \end{aligned} \tag{A6}$$

These equations define one dimensional, bounded, monotone maps and hence their solution sequences are monotone and convergent. The origin 0 is unstable for both equations (the linearization at 0 has coefficient $n > 1$), and no solution with positive initial condition can approach it. Each has a unique positive equilibrium ($x = J_e$ and $y = A_e$ respectively), which, therefore, is approached by all solutions with positive initial conditions.

If $J_0 > 0$ and $A_0 > 0$, then both odd and even subsequences (J_{2t+1}, A_{2t+1}) and (J_{2t}, A_{2t}), and hence the solution sequence (J_t, A_t) itself, converge to (J_e, A_e). This shows (J_e, A_e) is GAS on R_+^2.

If, on the other hand, either $J_0 > 0$ and $A_0 = 0$ or $J_0 = 0$ and $A_0 > 0$ then the odd and even subsequences converge to different limits, one to a positive limit (J_e or A_e, respectively) and the other to 0. This means the sequence (J_t, A_t) converges to one of the phases of the 2-cycle whose points are $(J_e, 0)$ and $(0, A_e)$. The 2-cycle is LAS because, as (A5) shows, J_e and A_e are LAS fixed points of (A6a) and (A6b), respectively. ∎

A5 *Proof of theorem 3.3*

The 2-cycle (17) is stable if the equilibrium $(x, y, z, w,) = (J_e, 0, 0, a_e)$ of the composite system (16) is stable. The Jacobian of (16) is block diagonal

$$M(x, y, z, w) = \begin{pmatrix} D_1(x, y) & 0_{2\times 2} \\ 0_{2\times 2} & D_2(z, w) \end{pmatrix}$$

where the 2×2 matrix $D_1(x, y)$ is the Jacobian of equations (16a, b) and the 2×2 matrix $D_2(z, w)$ is the Jacobian of equations (16c, d). ($0_{2\times 2}$ is the 2×2 zero matrix.) The eigenvalues of the Jacobian at the equilibrium $(x, y, z, w) = (J_e, 0, 0, a_e)$ are the eigenvalues of $D_1(J_e, 0)$ and $D_2(0, a_e)$.

A calculation shows the eigenvalues of

$$D_1(J_e, 0) = \begin{pmatrix} n_1 h_1'(A_e)k_1'(J_e) & n_1 c h_1'(A_e)g_1'(J_e)J_e \\ 0 & n_2 g_2(c\rho J_e) \end{pmatrix}$$

are

$$\lambda_1 = b_1 h_1'(A_e)s_1 k_1'(J_e) > 0$$
$$\lambda_2 = n_2 g_2(c\rho J_e) > 0$$

Now

$$0 < b_1 h_1'(A_e) = b_1 f_1(A_e) + b_1 f_1'(A_e)A_e = \frac{Je}{A_e} + b_1 f_1'(A_e)A_e < \frac{J_e}{A_e}$$
$$0 < s_1 k_1'(J_e) = s_1 g_1'(J_e) + s_1 g_1'(J_e)J_e = \frac{A_e}{J_e} + s_1 g_1'(J_e)J_e < \frac{A_e}{J_e}$$

and hence $0 < \lambda_1 < 1$. The second eigenvalue λ_2 approaches 0 as $c \to +\infty$ and hence $0 < \lambda_2 < 1$ for c sufficiently large.

The remaining two eigenvalues of $M(J_e, 0, 0, a_e)$ are those of $D_2(0, a_e)$. A calculation shows

$$D_2(0, a_e) = \begin{pmatrix} n_1 g_1(c j_e) & 0 \\ s_2 c\rho b_1 g_2'(j_e)j_e & n_2 h_2'(a_e)k_2'(j_e) \end{pmatrix}$$

whose eigenvalues are

$$\lambda_3 = n_1 g_1(c j_e) > 0$$
$$\lambda_4 = n_2 h_2'(a_e)k_2'(j_e) > 0.$$

Since λ_3 approaches 0 as $c \to +\infty$, it follows that $0 < \lambda_3 < 1$ for c sufficiently large. An argument similar to that used to study λ_2 shows $0 < \lambda_4 < 1$. Thus, the eigenvalues of $D_2(0, a_e)$ also satisfy $0 < \lambda_3, \lambda_4 < 1$ for c sufficiently large.   ∎

A6. *Proof of Theorem 3.2d, e*

Part (d). The equilibrium equations

$$J = b_1 f_1(A)A$$
$$A = s_1 g_1(J + c_j)J$$
$$j = b_2 f_2(a)a$$
$$a = s_2 g_2(\rho c J + j)j$$

of (14) are equivalent to the equations

$$J = b_1 f_1(s_1 g_1(J + cj)J)s_1 g_1(J + cj)J$$
$$j = b_2 f_2(s_2 g_2(c\rho J + j)j)s_2 g_2(c\rho J + j)j$$
$$A = s_1 g_1(J + cj)J$$
$$a = s_2 g_2(c\rho J + j)j. \tag{A7}$$

To solve these equations for positive J, j, A, a is equivalent to solving the first two equations for $(J, j) \in R_+^2$ and using the second two equations to define positive A, a. Rewriting the first two equations as

$$J = b_1 h_1(s_1 g_1(J + cj)J)$$
$$j = b_2 h_2(s_2 g_2(c\rho J + j)j) \tag{A8}$$

we see that any positive solutions (J, j) must lie in the open, bounded set $r_1 \times r_2$ where

$$r_i \triangleq]b_i h_i(-\delta), \ b_i h_i(\infty)[.$$

On $r_1 \times r_2$ the equations (A8) are in turn equivalent to the equations

$$g_1(J + cj) = s_1^{-1} h_1^{-1}(b_1^{-1}J)J^{-1}$$
$$g_2(c\rho J + j) = s_2^{-1} h_2^{-1}(b_2^{-1}j)j^{-1}.$$

Since the range of g_1 is the unit interval $[0, 1[$, for any positive solution the right hand sides of these equations must lie in $]0, 1[$. Thus, these equations are equivalent to

$$J + cj = g_1^{-1}(s_1^{-1} h_1^{-1}(b_1^{-1}J)J^{-1})$$
$$c\rho J + j = g_2^{-1}(s_2^{-1} h_2^{-1}(b_2^{-1}j)j^{-1}) \tag{A9}$$

for $(J, j) \in \hat{r}_1 \times \hat{r}_2$ where the sets

$$\hat{r}_1 \triangleq \{J \in r_1 : s_1^{-1} h_1^{-1}(b_1^{-1}J)J^{-1} < 1\} \subset R_+^1$$
$$\hat{r}_2 \triangleq \{j \in r_2 : s_2^{-1} h_2^{-1}(b_2^{-1}j)j^{-1} < 1\} \subset R_+^1$$

are open. Under assumptions (13) h_i and hence h_i^{-1} are twice continuously differentiable. Since $h_i^{-1}(0) = 0$, it follows that $h_i^{-1}(b_i^{-1}J)J^{-1}$ is continuously differentiable on r_i. As a result, the

right hand sides of equations (A9) are continuously differentiable on $\hat{r}_i$. Calculations show

$$\lim_{J \to 0} s_1^{-1} h_1^{-1}(b_1^{-1}J)J^{-1} = n_1^{-1} < 1$$

$$\lim_{j \to 0} s_2^{-1} h_2^{-1}(b_2^{-1}j)j^{-1} = n_2^{-1} < 1$$

and hence $0 \in \hat{r}_i$. Rewrite (A9) equivalently as

$$\hat{\xi} = c^{-1}\hat{F}(\hat{\xi}) \tag{A10}$$

where $\hat{\xi} \triangleq (J, j) \in \hat{r}_1 \times \hat{r}_2$ and where $\hat{F}(\hat{\xi}) = (F_1(j), F_2(J))$ is defined by

$$F_1(j) \triangleq \rho^{-1}(-j + g_2^{-1}(s_2^{-1}h_2^{-1}(b_2^{-1}j)j^{-1}))$$

$$F_2(J) \triangleq -J + g_1^{-1}(s_1^{-1}h_1^{-1}(b_1^{-1}J)J^{-1}).$$

Note that $\hat{F} \in C^1(\hat{r}_1 \times \hat{r}_2, R_+^2)$.

Choose $\varepsilon > 0$ so small that

$$D(\varepsilon) \triangleq [0, \varepsilon] \times [0, \varepsilon] \subset \hat{r}_1 \times \hat{r}_2.$$

For c sufficiently large, $c^{-1}\hat{F} : D(\varepsilon) \to D(\varepsilon)$. Since the first order derivatives of F_i are bounded on $[-\varepsilon, \varepsilon]$ it follows that for each c sufficiently large $c^{-1}\hat{F}$ is a contraction and therefore has a unique fixed point $(J^*, j^*) = (J^*(c), j^*(c)) \in D(\varepsilon)$.

Since

$$F_1(0) = \rho^{-1}g_2^{-1}(n_2^{-1}) \neq 0$$

$$F_2(0) = g_1^{-1}(n_1^{-1}) \neq 0$$

it follows that $J^*(c) > 0$ and $j^*(c) > 0$. This positive fixed point yields the positive equilibrium $(J^*(c), A^*(c), j^*(c), a^*(c))$ of (14) where

$$A^*(c) = s_1 g_1(J^*(c) + cj^*(c))J^*(c)$$

$$a^*(c) = s_2 g_2(c\rho J^*(c) + j^*(c))j^*(c).$$

Part (e). We begin by noting that from

$$h_i^{-1}(\theta) = \frac{1}{h_i'(0)}\theta + O(\theta^2)$$

and $h_i'(0) = 1$ we have

$$\lim_{\theta \to 0} h_i^{-1}(\theta)\theta^{-1} = 1.$$

Both $F_1(j)$ and $F_2(J)$ are bounded for $(J, j) \in D(\epsilon)$ and it follows from (A10), i.e. from the equations

$$J^*(c) = c^{-1}F_1(j^*(c))$$

$$j^*(c) = c^{-1}F_2(J^*(c)),$$

that

$$\lim_{c \to \infty} J^*(c) = \lim_{c \to \infty} j^*(c) = 0$$

and

$$\lim_{c\to\infty} cJ^*(c) = \lim_{c\to\infty} F_1(j^*(c))$$

$$= \lim_{\theta\to 0} \rho^{-1}(-b_2\theta + g_2^{-1}(s_2^{-1}b_2^{-1}h_2^{-1}(\theta)\theta^{-1}))$$

$$= \rho^{-1}g_2^{-1}\left(b_2^{-1}s_2^{-1}\lim_{\theta\to 0} h_2^{-1}(\theta)\theta^{-1}\right)$$

or

$$\lim_{c\to\infty} cJ^*(c) = \rho^{-1}g_2^{-1}(n_2^{-1}).$$

A similar calculation shows

$$\lim_{c\to\infty} cj^*(c) = g_1^{-1}(n_1^{-1}).$$

Using these limits, we can calculate the limit, as $c \to +\infty$, of the Jacobian of (14) evaluated at the equilibrium $(J^*(c), A^*(c), j^*(c), a^*(c))$ and obtain

$$\begin{pmatrix} 0 & b_1 & 0 & 0 \\ b_1^{-1} & 0 & \rho^{-1}s_1 g_1'(g_1^{-1}(n_1^{-1}))g_2^{-1}(n_2^{-1}) & 0 \\ 0 & 0 & 0 & b_2 \\ \rho s_2 g_2'(g_2^{-1}(n_2^{-1}))g_1^{-1}(n_1^{-1}) & 0 & b_2^{-1} & 0 \end{pmatrix}.$$

The characteristic polynomial of this matrix is $\lambda^4 - 2\lambda^2 + (1 - \mathrm{p})$ where

$$p \triangleq [n_1 g_1'(g_1^{-1}(n_1^{-1}))g_1^{-1}(n_1^{-1})][n_2 g_2'(g_2^{-1}(n_2^{-1}))g_2^{-1}(n_2^{-1})].$$

Thus $\lambda^2 = z_\pm$ where

$$z_\pm \triangleq +1 \pm \sqrt{[n_1 g_1'(g_1^{-1}(n_1^{-1}))g_1^{-1}(n_1^{-1})][n_2 g_2'(g_2^{-1}(n_2^{-1}))(g_2^{-1}(n_2^{-1})].}$$

Note that $n_i > 1$ implies

$$n_i g_i'(g_i^{-1}(n_i^{-1}))g_i^{-1}(n_i^{-1}) > -1.$$

This follows from (13) because

$$\frac{1}{g_i(x)}g_i'(x)x > -1$$

$$\Longleftrightarrow g_i'(x)x + g_i(x) > 0$$

$$\Longleftrightarrow k_i'(x) > 0.$$

It follows that

$$[n_1 g_1'(g_1^{-1}(n_1^{-1}))g_1^{-1}(n_1^{-1})][n_2 g_2'(g_2^{-1}(n_2^{-1})g_2^{-1}(n_2^{-1})] < 1$$

and hence

$$0 < z_- < 1 < z_+ < 2.$$

Hence, for c sufficiently large, the four eigenvalues λ of the Jacobian are real and satisfy

$$-\sqrt{2} < \lambda_1 < -1 < \lambda_2 < 0 < \lambda_3 < 1 < \lambda_4 < \sqrt{2}.$$

Thus the equilibrium is a saddle (with, locally, a two-dimensional stable manifold and a two-dimensional unstable manifold).

A7.   *Proof of Theorem 3.4*

The theorem below is a corollary of Theorems 5 and 6 in [24]. Denote two of the quadrants determined by a point (x_1, y_1) by

$$Q_1(x_1, y_1) \triangleq \{(x, y) : x_1 \leq x, \; y_2 \leq y\}$$

$$Q_3(x_1, y_1) \triangleq \{(x, y) : x_1 \geq x, \; y_2 \geq y\}.$$

THEOREM 4.1   [24] *Suppose* $T : R_+^2 \to R_+^2$ *is strongly monotone. Assume*

(a) *T has a unique fixed point* $(x^*, y^*) \in R_+^2$
(b) (x^*, y^*) *is a saddle*
(c) *either*
   (i) *det* $J(x^*, y^*) > 0$ *and* $T(x, y) = (x^*, y^*) \Rightarrow (x, y) = (x^*, y^*)$
   (ii) *T has no prime period two orbits in* $Q_1(x^*, y^*) \cup Q_3(x^*, y^*)$.

The global stable manifold $W^s = W^s(x^*, y^*)$ *is the graph of a continuous and strictly increasing function whose endpoints lie on* ∂R_+^2. *Let*

$$B_x = \{(x, y) \in R_+^2 / W^s : \exists (x_1, y_1) \in W^s \; such \, that \; x < x_1, y > y_1\}$$

$$B_y = \{(x, y) \in R_+^2 / W^s : \exists (x_1, y_1) \in W^s \; such \, that \; x > x_1, y < y_1\}.$$

Then B_x *and* B_y *are open, invariant, disjoint, and connected and satisfy*

$$R_+^2 / W^2 = B_x \cup B_y.$$

Suppose further that $T = (T_1, T_2)$ *has a unique fixed point* $(x_e, 0)$ *on the positive x-axis such that* $x > x_e$ *implies* $T_1(x, 0) < x$. *Then* B_x *is the basin of attraction for* $(x_e, 0)$ *Suppose* $T = (T_1, T_2)$ *has a unique fixed point* $(0, y_e)$ *on the positive y-axis such that* $y > y_e$ *implies* $T_2(0, y) < y$. *Then* B_y *is the basin of attraction for* $(0, y_e)$.

Let $T: R_+^2 \to R_+^2$ be the strongly monotone map defined by the equations (16a, b). For c sufficiently large we apply Theorem 4.1 to obtain the sets B_x and B_y. Define the open sets (20) in R_+^4.

Recall the even and odd step subsequences of any solution of the competition model (14) satisfy the equations (16a, b). In the following lemma we refer to pairs (J, A) and (j, a) as associated components of $(J, A, j, a) \in R_+^4$.

LEMMA 4.1   *Assume* (13) *for the competition model* (14). *If the even-step* (*or odd-step*) *subsequence of a solution sequence in* R_+^4 *converges to a point which has a 0 component, then the odd-step* (*respectively even-step*) *subsequence of the orbit cannot approach a point in which the corresponding associated component is nonnegative.*

Proof   We prove the lemma for the even-step subsequence of a convergent solution sequence. The proof for the odd-step subsequence is analogous.

Let $(J_t, A_t, j_t, a_t) \in R_+^4$ be any solution sequence of (14) and suppose the J component of the even-step subsequence converges to 0:

$$\lim_{t \to +\infty} (J_{2t}, A_{2t}, j_{2t}, a_{2t}) \longrightarrow (0, A^e, j^e, a^e).$$

The proofs are similar should any one of the other three components converge to 0. For the purposes of contradiction, assume

$$\lim_{t \to +\infty} (J_{2t+1}, A_{2t+1}, j_{2t+1}, a_{2t+1}) \longrightarrow (J^o, A^o, j^o, a^o), \quad A^o > 0.$$

If we choose $t > 0$ so large that

$$0 \le J_{2t} \le \frac{1}{3s_1} A^o \text{ and } A_{2t+1} \ge \frac{2}{3} A^o$$

then from the second equation in (14) we arrive at the contradiction

$$A_{2t+1} = s_1 g_1(J_{2t} + c j_{2t}) J_{2t} \le s_1 J_{2t} \le \frac{1}{3} A^o.$$

∎

LEMMA 4.2 *Assume* (13) *for the competition model* (14). *For the map T defined by the competition system* (14) *we have*

$$T : B_{JA} \longrightarrow B_{JA}, \quad T : B_{ja} \longrightarrow B_{ja}$$
$$T : B_{Ja} \longrightarrow B_{jA}, \quad T : B_{jA} \longrightarrow B_{Ja}.$$

Proof We'll give the proof for $T : B_{JA} \to B_{JA}$. The proofs for the other three cases are similar. Assume $(J_o, A_o, j_o, a_o) \in B_{JA}$. By the definition (20) of B_{JA} it follows that

$$\lim_{t \to +\infty} (J_{2t}, A_{2t}, j_{2t}, a_{2t}) = (J_e, A_e, 0, 0). \tag{A11}$$

If $(J_1, A_1, j_1, a_1) \in B_{ja}$ then by the definition (20) of B_{ja} it would follow that

$$\lim_{t \to +\infty} (J_{2t+1}, A_{2t+1}, j_{2t+1}, a_{2t+1}) = (0, 0, j_e, a_e),$$

which together with (A11) yields a contradiction to Lemma 4.1. If $(J_1, A_1, j_1, a_1) \in B_{jA}$ then by the definition (20) of B_{jA} it would follow that

$$\lim_{t \to +\infty} (J_{2t+1}, A_{2t+1}, j_{2t+1}, a_{2t+1}) = (0, A_e, j_e, 0)$$

which together with (A11) yields a contradiction to Lemma 4.1. Similarly, a contradiction arises if $(J_1, A_1, j_1, a_1) \in B_{Ja}$. Finally, if

$$(J_1, A_1, j_1, a_1) \in R_+^4 / (B_{JA} \cup B_{ja} \cup B_{Ja} \cup B_{jA}),$$

then (J_1, j_1) and/or (A_1, a_1) would lie on the boundary of a basin and hence on the stable manifold of the positive equilibrium (J^*, j^*) and/or (A^*, a^*). In this case, (J_{2t+1}, j_{2t+1}) and/or (A_{2t+1}, a_{2t+1}) would tend to the positive equilibrium (J^*, j^*) and/or (A^*, a^*). Either case, together with (A11), is a contradiction to Lemma 4.1. The only alternative left is that $(J_1, A_1, j_1, a_1,) \in B_{JA}$. ∎

Proof of Theorem 3.4. We can now enumerate the possibilities for all orbits with initial conditions in $B_{JA} \cup B_{ja} \cup B_{Ja} \cup B_{jA}$ (i.e. all orbits in R_+^4 except for a set of measure zero). This is done by interlacing the asymptotic dynamics of the even and odd step subsequences of the solution sequence. We illustrate with one case. The other cases are similar. Suppose $(J_o, A_o, j_o, a_o) \in B_{JA}$. Then by the definition (3.9) of B_{JA} we have $(J_o, j_o) \in B_x$ and $(A_o, a_o) \in B_z$. Hence, the even step subsequences (J_{2t}, j_{2t}) and (A_{2t}, a_{2t}) approach $(J_e, 0)$ and $(A_e, 0)$, respectively. Lemma 4.2 implies $(J_1, A_1, j_1, a_1) \in B_{JA}$ and hence the odd step subsequences (J_{2t+1}, j_{2t+1}) and (A_{2t+1}, a_{2t+1}) approach the same limits. Consequently, the solution sequence (J_t, A_t, j_t, a_t) approaches $(J_e, A_e, 0, 0)$.

Acknowledgements

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