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Global stability of discrete-time competitive population models

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Abstract We develop practical tests for the global stability of interior fixed points for discrete-time competitive population models. Our method constitutes the extension to maps of the Split Lyapunov method developed for differential equations. We give ecologically-motivated sufficient conditions for global stability of an interior fixed point of a competitive map of Kolmogorov form, and show how these conditions can simplify when a carrying simplex is known to exist. We introduce the concept of a principal reproductive mode, which is linked to a left eigenvector for the dominant eigenvalue of a positive matrix, which in turn is linked to a normal vector, at an interior fixed point, to a hypersurface of vanishing weighted-average growth, and also to a normal to the carrying simplex when present. A connection with permanence is also discussed. As examples of applications, we first take two well-understood planar models, namely the Leslie-Gower and the May-Oster models, where our method confirms global stability results that have previously been established, through, for example, properties of monotone maps. We also apply our methods to establish new global stability results for 3-species competitive systems of May-Leonard type, giving detailed descriptions of the parameter ranges for which the models have globally stable interior fixed points.

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1 Introduction

There is a large body of literature describing mathematical techniques for identifying global stability of fixed points of differential equation models of interacting populations, but the corresponding literature for discrete-time models is significantly smaller. Here we describe a general test for *global stability* of a coexistence state that can be successfully applied to a wide range of discrete-time competitive population models, and we provide examples of the application of the test to some standard models, including some whose global stability properties are unresolved.

We restrict our attention to population models described by Kolmogorov systems, which includes the vast majority of classic population models. These Kolmogorov systems are defined by per-capita growth rates that are at least bounded and continuous for non-negative populations. As a consequence, if a species is initially absent then it remains so for all time; immigration or emmigration is not modelled.

Thus, let us assume that the model has N interacting species with population densities $x_i \geq 0$ for $i \in I_N := \{1, 2, \ldots, N\}$ and write $\mathbf{x} = (x_1, \ldots, x_N)^\mathsf{T}$ (a column vector). We set $\mathcal{C} = \mathbb{R}_+^N$ for the nonnegative first orthant, where $\mathbb{R}_+ = [0, \infty)$. We use the natural numbers $\mathbb{N} = \{0, 1, \ldots\}$ for the model time units. Let $\mathbf{f} = (f_1, \ldots, f_N)^\mathsf{T} : \mathcal{C} \to \mathbb{R}^N$ be bounded and continuous in each N components. Then the Kolmogorov model that we consider is

$$x_i(t+1) = T_i(\mathbf{x}(t)) = x_i(t) f_i(\mathbf{x}(t)), \; i \in I_N, \quad t \in \mathbb{N}. \tag{1}$$

For each initial state $\mathbf{x} \in \mathcal{C}$, equation (1) generates a forward orbit $O^+(\mathbf{x}) = \{\mathbf{x}(t)\}_{t \in \mathbb{N}}$ with $\mathbf{x}(t)$ denoting the population state reached from the initial state $\mathbf{x} = \mathbf{x}(0)$ after t time steps. Thus our models are restricted to those where the growth or decline does not impact back on the environment, and those for which the environment is constant, and not, for example, subject to seasonal changes or random disturbances.

As with many studies of the global dynamics of population models, our approach is based upon a Lyapunov function. In fact, the Lyapunov function that we choose has been previously as an entropic asymmetric distance function in continuous-time population models [16,43], and also as part of average Lyapunov function in the study of permanence of population models [19,20]. We recall that a population model is said to exhibit *permanence* if all populations remain bounded and whenever all populations are present, they remain present for all future time with densities eventually above some positive number. In some respects, our method extends the average Lyapunov function approach, a technique which is usually applied only over a finite time interval, and extends it over all forward time to extract long term properties of a permanent system.

The framework that we use is as follows. The model (1) is assumed to have a unique interior fixed point: $\mathbf{p} \in \mathring{\mathcal{C}} = (0,\infty)^N$. Let $\mathbf{v}$ be a given positive vector and $V(\mathbf{x}) = \prod_{i=1}^N x_i^{v_i}$; this is the Lyapunov function we employ that has also been widely used as an average Lyapunov function [20, 15]. The vector $\mathbf{v}$ is similar to that identified as Reproductive Value in classic Leslie matrix models (e.g. [7, 39]) in that it is a left eigenvector associated with the dominant eigenvalue of an irreducible nonnegative matrix. Then for $\mathbf{x}(0) = \mathbf{x}$, and $\mathbf{x}(t) \in O^+(\mathbf{x})$,

$$V(\mathbf{x}(t)) = \Lambda(t,\mathbf{x})V(\mathbf{x}),$$

where $\Lambda(t,\mathbf{x}) = \exp\left(\mathbf{v}^\mathsf{T} \sum_{k=0}^t \ln(\mathbf{x}(k))\right)$. Notice that $\Lambda(t,\mathbf{x})$ is nondecreasing along the forward orbit $O^+(\mathbf{x})$ when the sum

$$\Theta(t,\mathbf{x}) = \sum_{k=0}^{t} \mathbf{v}^\mathsf{T} \ln(\mathbf{x}(k))$$

is nondecreasing. Thus a necessary and sufficient condition for V to be nondecreasing along $O^+(\mathbf{x})$ is that $\mathbf{v}^\mathsf{T} \ln(\mathbf{x}(t)) \geq 0$ for each $t \in \mathbb{N}$. Consequently, knowledge of the omega limit set of a point $\mathbf{x} \in \mathring{\mathcal{C}}$ under (1) can be obtained by studying the scalar function $\Theta(t,\mathbf{x})$. An important feature of the expression $\Theta(t,\mathbf{x})$, is the weighting in the sum by the vector $\mathbf{v}$, and an ecologically-motivated choice of $\mathbf{v}$ is the key to the method's success, as we explain later.

The key property that our models satisfy is:

Property 1: Given any $\mathbf{x} \in \mathcal{C}$ and $O^+(\mathbf{x}) = \{\mathbf{x}(t)\}_{t\in\mathbb{N}}$ there exists a t' (which may depend on $\mathbf{x}$) such that $\mathbf{v}^\mathsf{T} \ln(\mathbf{x}(t)) \geq 0$ for all $t \geq t'$.

Property 1 states that an orbit eventually enters a certain region of phase space where the Lyapunov function V then is nondecreasing. As we shall demonstrate, such a property can often be used to determine omega limit sets of interior orbits and even global convergence to an interior fixed point. A major part of this paper is developing sufficient conditions for Property 1 above to hold. Defining $\boldsymbol{\alpha} = D[\mathbf{p}]^{-1}\mathbf{v}$, the vector $\boldsymbol{\alpha}$ will be called by us the principal reproductive mode. The function $\varphi(\mathbf{x}) := \mathbf{v}^\mathsf{T} \ln \mathbf{f}(\mathbf{x}) = \boldsymbol{\alpha}^\mathsf{T} D[\mathbf{p}] \ln \mathbf{f}(\mathbf{x})$ appearing in Property 1 will be called by us the *principal component of the reproductive rate* since it is a scalar that provides a measure of the component of the per-capita growth of the whole population in the direction of the dominant mode $\boldsymbol{\alpha}$. As we will also show, for competitive Kolmogorov systems that possess a carrying simplex (a manifold of codimension 1 that attracts all nonzero orbits, as described in section 7 below), the principal reproductive mode points in the same direction of the normal to the carrying simplex at the interior fixed point.

From a practical point of view, our results say the following principle:

> For a bounded population model with unique coexistence state $\mathbf{p}$, if the principal component of the reproductive rate is eventually positive, the population converges to $\mathbf{p}$.

The positiveness of the principal reproductive mode $\boldsymbol{\alpha}$ is guaranteed when the model is strongly competitive (as are all the models studied here), but it is in principle possible to have models where $\boldsymbol{\alpha}$ has negative components to reflect that some species may sometimes be detrimental to overall population growth. The price to be paid for this generalisation is that permanence of the system (1) also has to be proved before the Lyapunov function V can be used (see [4] for the continuous-time Lotka-Volterra case). When there is a carrying simplex that lies entirely in a region where the principal component of the reproductive rate is positive except at the interior fixed point where it is zero, all nonzero orbits converge to the unique interior fixed point. This motivates that the normal to the carrying simplex at the fixed point should be parallel to the normal to the hypersurface of zero principal component of the reproductive rate which is in turn parallel to a weighted eigenvector $\boldsymbol{\alpha}$ by the interior fixed point associated with the dominant eigenvalue of the inverse of the linearisation of the model at the fixed point. A summary of the geometry of our method is shown in figure 1.

It is worth noting here also that a system of the form $\mathbf{x}(t+1) = \mathbf{F}(\mathbf{x}(t))$ which is also permanent in the first orthant could also be treated by our methods here by defining $f_i(\mathbf{x}) = F_i(\mathbf{x})/x_i$ for $x_i > 0$. This observation opens our method up to other application areas such as mathematical genetics where many of the well-known models contain terms that are not entirely per-capita rates, such as for genetic recombination.

What is quite surprising to us is the sheer number of discrete-time population models to which our method can be successfully applied to show global attractiveness of the interior fixed point. The principle does not depend upon a particular form for the per-capita growth functions, although some models (e.g. those with exponential functions) inevitably give rise to principal component of the reproductive rate that are easier to work with. The principle cannot be applied as it stands when there are periodic orbits present in the system, and this would include chaotic systems.

As practical demonstrations of their wide applicability to population models, we apply our methods to establish global stability in the case of 3 species for two well-known competitive models, namely the Leslie-Gower model and the May-Oster models. These take the form

$$x_i' = \frac{bx_i}{1 + (\mathbf{A}\mathbf{x})_i} \quad (i = 1, 2, 3) \quad \text{(Leslie-Gower)}$$

$$x_i' = x_i \exp(r(1 - (\mathbf{A}\mathbf{x})_i)) \quad (i = 1, 2, 3) \quad \text{(May-Oster)}.$$

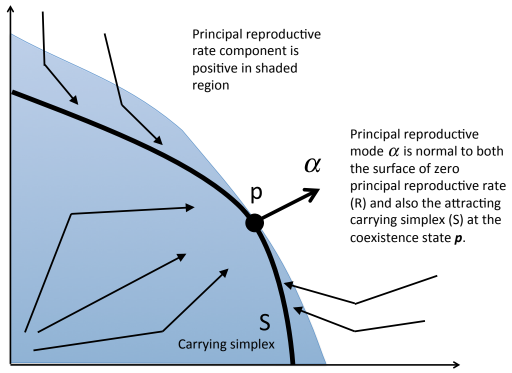

Fig. 1 A summary of our method. All trajectories eventually end up in the shaded region where the principal reproductive rate component is positive, and then converge to the coexistence fixed point $\mathbf{p}$. Both the surface of zero principal reproductive rate and the carrying simplex (when it exists) have a outward normal at $\mathbf{p}$ that points along the vector $\boldsymbol{\alpha}$, the principal reproductive mode.

where x_i, x_i' are the current and next generation population densities of species i respectively, $r, b > 0$ constants and $\mathbf{A}$ is a positive 3×3 matrix given by $\mathbf{A} = \begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix}$, and $\alpha, \beta > 0$ reflect the strength of competition.

For these models we establish:

Theorem 1 (Global stability for the 3-species May-Leonard Leslie-Gower model) *Suppose that $b > 1$, $0 < \alpha + \beta < 2$ and either*

$$b\left(4\alpha^2 + 4\beta^2 - 4\alpha - 4\beta - \alpha\beta + 1\right) < 3\left(\alpha^2 + \beta^2 - \alpha - \beta - \alpha\beta + 1\right),$$

or

$$3b(1 - 2\alpha - 2\beta + 3\alpha\beta) \geq 5(1 - \alpha - \beta) + 7\alpha\beta - \alpha^2 - \beta^2.$$

Then the Leslie-Gower model has a unique fixed point that is globally asymptotically stable in the interior of the first orthant.

Theorem 2 (Global stability for the 3-species May-Oster model) *Suppose that $r \in (0, 1)$, $\alpha + \beta < 2$ and either*

$$3r(1 + \alpha^2 + \beta^2 - \alpha - \beta - \alpha\beta) < (2 - \alpha - \beta)(1 + \alpha + \beta),$$

or

$$r(5 - \alpha^2 - \beta^2 - 5(\alpha + \beta) + 7\alpha\beta) \geq (2 - \alpha - \beta)(1 + \alpha + \beta).$$

Then the May-Oster model has a unique fixed point that is globally asymptotically stable in the interior of the first orthant.

Local asymptotic stability of interior fixed points in these models (indeed their $N-$species versions) were studied by Roeger in a series of papers [34,33,32] and recently global stability of the $N-$species periodic Leslie-Gower model was studied [37] using contraction mapping techniques and also the planar May-Oster in [38]. An advantage of our approach is that it yields a detailed description of parameter values sufficient for global stability. A disadvantage over [37] is that our method cannot directly deal with periodic orbits. However, it might be possible to overcome this shortcoming by working with powers of the map $\mathbf{T}$.

2 Notation and previous results

2.1 Notation and standing assumptions

Let $\mathcal{X}$ be a metric space and $\mathbf{T}:\mathcal{X}\to\mathcal{X}$ be continuous. For a given $\mathbf{x}\in\mathcal{X}$ one typically studies the sequence $O^+(\mathbf{x}) := \{\mathbf{T}^t(\mathbf{x}) : t\in\mathbb{N}\}$ ($\mathbb{N}=\{0,1,2,\ldots\}$) which is referred to as the *forward orbit* of $\mathbf{T}$ through $\mathbf{x}$. A set $\mathcal{A}\subset\mathcal{X}$ is $\mathbf{T}-$invariant if $\mathbf{T}(\mathcal{A})=\mathcal{A}$. The set of fixed points of $\mathbf{T}$ is $\text{Fix}(\mathbf{T})=\{\mathbf{x}\in\mathcal{X}: \mathbf{T}(\mathbf{x})=\mathbf{x}\}$. For a given set $\mathcal{W}\subset\mathcal{X}$ let $\omega(\mathcal{W}) := \bigcap_{n=0}^{\infty}\left(\overline{\bigcup_{k=n}^{\infty}\mathbf{T}^k(\mathcal{W})}\right)$ denote the *omega limit set* of $\mathcal{W}$. When $O^+(\mathbf{x})$ has compact closure in $\mathcal{X}$, $\omega(\mathbf{x})$ is a nonempty, compact and invariant set. An invariant set $\mathcal{A}\subset\mathcal{X}$ is said to be an *attractor* if there exists an open $\mathcal{U}\supset\mathcal{A}$ for which $\omega(\mathcal{U})=\mathcal{A}$. A compact invariant set $\mathcal{R}\subset\mathcal{X}$ is said to be a *repellor* if there exists a $\mathcal{U}\supset\mathcal{R}$ such that for all $\mathbf{x}\notin\mathcal{R}$ there exists an integer $n_0(\mathbf{x})>0$ such that $\mathbf{T}^k(\mathbf{x})\notin\mathcal{U}$ for all $k\geq n_0(\mathbf{x})$. If $\mathcal{A}\subset\mathcal{X}$ and $\mathcal{U}\supset\mathcal{A}$ is open, we say that $\mathcal{A}$ is *absorbing* for $\mathcal{U}$ if for any bounded set $\mathcal{B}\subset\mathcal{U}$, there exists an ℓ (which may depend on $\mathcal{B}$) such that $\mathbf{T}^k(\mathcal{B})\subseteq\mathcal{A}$ for all $k\geq\ell$.

Definition 1 The model (1) is called dissipative if there exists a compact attractor for $\mathbf{T}$, whose basin of attraction is $\mathbb{R}^N_+$.

Let $\mathbb{R}_+=[0,\infty)$, $\mathcal{C}=\mathbb{R}^N_+$ denote the nonnegative orthant, with the integer N representing the number of species, and $\mathring{\mathcal{C}}$ denote the interior of $\mathcal{C}$ in $\mathbb{R}^N$. Here we focus on a special class of *Kolmogorov maps* of the form $\mathbf{T}(\mathbf{x})=D[\mathbf{x}]\mathbf{f}(\mathbf{x})$ where $D[\mathbf{x}]$ denotes the diagonal matrix whose elements are $x_i\delta_{ij}$ for $i,j\in I_N:=\{1,\ldots,N\}$. Thus the discrete-time model we study is

$$\mathbf{x}(t+1)=\mathbf{T}(\mathbf{x}(t))=D[\mathbf{x}(t)]\mathbf{f}(\mathbf{x}(t)),\quad t\in\mathbb{N}. \tag{2}$$

We will often use the following partial ordering for vectors $\mathbf{u}\in\mathbb{R}^N$: (a) $\mathbf{u}\leq\mathbf{v}$ if $u_i\leq v_i$ for $i\in I_N$, (b) $\mathbf{u}<\mathbf{v}$ if $\mathbf{u}\leq\mathbf{v}$ but $\mathbf{u}\neq\mathbf{v}$, and (c) $\mathbf{u}\ll\mathbf{v}$ if $\mathbf{v}-\mathbf{u}\in\mathring{\mathcal{C}}$. Similar orderings are used for matrices, so that, for example, for a given matrix $\mathbf{A}$, $\mathbf{A}>0$ means that each element of $\mathbf{A}$ is nonnegative, and at least one element is positive.

We will use the following definition for a competitive map.

Definition 2 (Competitive map) A continuous map $\mathbf{T} : \mathcal{C} \to \mathcal{C}$ is *competitive* if $\mathbf{T}(\mathbf{x}) < \mathbf{T}(\mathbf{y}) \Rightarrow \mathbf{x} < \mathbf{y}$ for each $\mathbf{x}, \mathbf{y} \in \mathcal{C}$.

Definition 3 (Strongly Competitive map) A continuous map $\mathbf{T} : \mathcal{C} \to \mathcal{C}$ is *strongly competitive* if $\mathbf{T}(\mathbf{x}) < \mathbf{T}(\mathbf{y}) \Rightarrow \mathbf{x} \ll \mathbf{y}$ for each $\mathbf{x}, \mathbf{y} \in \mathcal{C}$.

A sufficient condition for $\mathbf{T}$ to be strongly competitive on a set Ω is that $D\mathbf{T}^{-1}(\mathbf{x}) \gg 0$ for $\mathbf{x} \in \Omega$.

We place the following standing assumptions on the map $\mathbf{f}$:

1. **Assumption A1** $\mathbf{f} : \mathcal{C} \to \mathring{\mathcal{C}}$ is of class at least C^2.
2. **Assumption A2** For each $i \in I_N$, $f_i(\lambda e_i) = 1$ has a unique solution $\lambda_i^* > 0$.

   Thus if there is only one extant species i, its equilibrium density is λ_i^*.
3. **Assumption A3** There is a unique interior fixed point $\mathbf{p}$.

   Here we only study stability of coexistence states. The stability of boundary fixed points have been studied in [11–14,30,29,31,35] and will also be considered by us in future work.

2.2 Previous work

For planar competitive discrete-time (and continuous-time) models (i.e. two species models, $N = 2$), there is a standard approach to the study of stability that does not rely (directly, at least) upon a global Lyapunov function, namely monotone systems theory. It turns out that planar competitive systems are monotone systems when a non-standard orthant ordering is used. By exploiting this monotonicity, many authors, and in particular Smith [42,6], have been able to establish global stability results for both coexistence and partial extinction states of well-known planar competitive models including the planar Leslie-Gower and May-Oster models. Since there does not appear to be a suitable ordering to render 3-species discrete-time competitive models monotone, it seems likely that a similar approach will not lend itself to general discrete-time competitive models and alternatives need to be found.

Some earlier ideas appeared in a little-cited 1977 paper, where Fisher and Goh [9] present a Lyapnuov function approach to global stability of discrete-time population models. The method described by us here has some similarities with Fisher and Goh's approach, particularly that they determine absorbing sets based upon the sign of the difference ΔV between successive values of a specific Lyapunov function V which is the sum of polynomial and logarithmic terms.

They do not use injectivity of the flow map, but are still able to determine absorbing sets Y which are the union of level sets of the Lyapunov function, and on which $\Delta V \leq 0$, so that V is nonincreasing on Y. Here we develop a similar approach, but with a different Lyapunov function and using that the flow map is injective on our chosen sets.

Perhaps the most promising geometrical approaches to (2) have been developed by Franke and Yakubu in a series of papers [10,13,12], and also by Kon in [30]. We first mention the work of Franke and Yakubu, which is primarily concerned with exclusion principles for discrete-time population models. In [10] the authors study global attractors of 2-species discrete-time competitive models, and in particular establish an ecological principle for mutual exclusion of species through the introduction of dominance of one species by the other. Subsequent papers [12] extended these ideas to more species with the introduction of the notions of weak and strong dominance.

In a similar, but distinct geometrical approach, Ryusuke Kon has studied permanence and mutual exclusion principles in discrete-time competitive population models [29–31]. In [30] Kon uncovers a very nice geometrically-derived exclusion principle based upon the convexity or concavity of the per-capita growth rate functions. These papers contain sums similar to Θ, but with equal weights $v_i = 1$ for $i \in I_N$, and utilised in quite a distinct fashion.

More recently Riuz-Herrera has used the carrying simplex often found in competitive systems to study exclusion principles [35]. The carrying simplex is a codimension-one invariant manifold [18,28,8] that attracts all nonzero points in the first orthant. One of its appeals is that it contains all limit sets other than the origin and hence stability or repulsion need only be checked on the carrying simplex. In [35], the author provides proofs of results stated in [18] and uses these to examine the equivalence for 3 species between non-existence of interior fixed points and exclusion of a species (a form of the Poincaré-Bendixson theorem on the 2-dimensional carrying simplex). For the latest results on carrying simplicies for discrete-time systems see [27].

Employing an approach that has found success for continuous-time Lotka-Volterra models, Wang and Zhengyi [46] assume diagonal dominance of the interaction matrix and use a Lyapunov function to show global stability of an N-species non autonomous May-Oster model under the assumption of strong persistence. In particular, they deduce from known permanence results for the 2-species autonomous case, sufficient conditions for global stability (these have also been shown by many other authors, e.g. [5,6,42], and are also derived here as an application of our own methods in examples 1 and 2 later).

Recently Sacker [37] used dynamical reduction to demonstrate global stability in a multi-species periodic Leslie-Gower model. Theorem 3.5 in [37] confirms that in the autonomous case, the Leslie-Gower model with sufficiently weak competition (to ensure that the mapping that he constructs is a contraction) globally attracts the interior of the first orthant. Other models, including those of May-Oster type are also considered in an earlier paper [38].

For differential equations, recent geometrical approaches include the Split-Lyapunov method introduced by Zeeman and Zeeman [47] for competitive systems and extended to more general Lotka-Volterra systems in [22, 4].

The main objective of this paper is to link the geometrical ideas of those applied by Franke, Yakube, Kon and others, while also placing emphasis on injectivity of maps, with the method of the Split Lyapunov function for continuous-time Kolmogorov systems developed by E. C. Zeeman, M. L. Zeeman in [47], Hou and Baigent [22, 4, 23]. A secondary objective is to demonstrate how existence of a carrying simplex, plus some knowledge of its geometry, can be used to identify globally stable fixed points.

3 Forward invariance of sets under maps

For a continuous-time dynamical system generated by a smooth differential equation on $\mathbb{R}^N$ forward invariance of a compact set $\mathcal{B} \subset \mathbb{R}^N$ is often obtained by showing that the vector field points outwards nowhere on $\partial\mathcal{B}$, so that points on the boundary $\partial\mathcal{B}$ either stay in $\partial\mathcal{B}$ or move into $\mathring{\mathcal{B}}$ and stay there for all subsequent times. In discrete-time systems, even if the map T maps all boundary points into $\mathring{\mathcal{B}}$, then some points in $\mathring{\mathcal{B}}$ may be mapped outside of $\mathcal{B}$, and then $\mathcal{B}$ is not forward invariant. For example, for the one-dimensional model $x' = T(x) = 16(x-1)^2(x-2)^2 + \frac{3}{2}$ and $\mathcal{B} = [1, 2] \subset \mathbb{R}_+$. Then $T(1) = 3/2 \in \mathring{\mathcal{B}}$, $T(2) = 3/2 \in \mathring{\mathcal{B}}$ but $T(3/2) = 5/2 \notin \mathcal{B}$.

The following theorem is fundamental [24] (Lemma 2.1). Here $\mathcal{X}$ is a metric space, and $\mathbf{T} : \mathcal{X} \to \mathcal{X}$ is continuous.

Theorem 3 *Let $\mathcal{U} \subset \mathcal{X}$ be an open set with compact closure and suppose that $\mathcal{V} \subset \mathcal{X}$ is open and forward invariant under $\mathbf{T}$, and $\overline{\mathcal{U}} \subset \mathcal{V}$. If $O^+(\mathbf{x}) \cap \mathcal{U} \neq \emptyset$ for every $\mathbf{x} \in \mathcal{V}$, then $O^+(\overline{\mathcal{U}})$ is compact, forward invariant and absorbing for $\mathcal{V}$.*

As pointed out by Kon [29], this gives a test for dissipativity of $\mathbf{T}$. Here, we may take $\mathcal{V} = \mathcal{C}$. If there is a compact set $\mathcal{K} \subset \mathcal{C}$ such that $O^+(\mathbf{x}) \cap \mathring{\mathcal{K}} \neq \emptyset$ for every $\mathbf{x} \in \mathcal{C}$ then $O^+(\mathcal{K})$ is compact and absorbing for $\mathcal{C}$ and hence $\mathbf{T}$ is dissipative. Thus, if $\mathcal{B} \subset \mathbb{R}^N$ is a compact set for which $\mathbf{T}(\partial\mathcal{B}) \subset \mathcal{B}$ then $\mathcal{B}$ may itself not be forward invariant, but the typically larger compact set $\Omega = O^+(\mathcal{B})$ certainly is. Theorem 3 is certainly useful for showing that a discrete dynamical system is dissipative, but it is not always straightforward to determine explicitly the absorbing set $\Omega = O^+(\mathcal{B})$. To obtain forward invariance based upon movement of boundary points, which is typically much more practical to implement, we will appeal to the recent result of Sacker [36] which shows that injectivity of the map (which is immediate for the time-1 flow map of continuous-time systems) is what is missing:

Theorem 4 (Sacker) *Let $\mathcal{D} \subset \mathbb{R}^n$ be a bounded subset and $\mathbf{T} : \overline{\mathcal{D}} \to \mathbb{R}^n$ be continuous. Suppose that $\mathbf{T} : \mathring{\mathcal{D}} \to \mathbb{R}^n$ is injective and $\mathbf{T}(\partial\mathcal{D}) \subset \overline{D}$. If $\overline{\mathcal{D}}^C = \mathbb{R}^n \setminus \overline{\mathcal{D}}$ has no bounded components then $\mathbf{T}(\overline{\mathcal{D}}) \subset \overline{\mathcal{D}}$.*

Our strategy will be to utilise theorem 4 to determine explicitly a compact set $\mathcal{K}$ that absorbs $\mathcal{C}$. Properties of omega limit sets will then be examined via a Lyapunov function restricted to $\mathcal{K}$.

For an effective application of theorem 4, we need sufficient conditions for $\mathbf{T}$ to be injective. From the general results of Wang and Jiang (Theorem 4.1 in [45]) we know that if $\mathbf{T} : \mathcal{C} \to \mathcal{C}$ is competitive and a local homeomorphism on $\mathcal{U} \subseteq \mathcal{C}$ then $\mathbf{T} : \mathcal{U} \to T(\mathcal{U})$ is a global homeomorphism from $\mathcal{U}$ onto $\mathbf{T}(\mathcal{U})$. Thus for competitive maps $\mathbf{T}$ we need only check that $\det D\mathbf{T}(\mathbf{x}) \neq 0$ for $\mathbf{x} \in \mathcal{U}$ to conclude that $\mathbf{T}$ is injective on $\mathcal{U}$.

Note that the injective condition is very restrictive. Our next result removes this restriction and the boundedness requirement of $\mathcal{D}$.

Theorem 5 *Let $\mathcal{D} \subset \mathbb{R}^n$ with $\mathring{\mathcal{D}}$ a connected set and $\overline{\mathring{\mathcal{D}}} = \overline{\mathcal{D}}$. Let $\mathbf{T} : \overline{\mathcal{D}} \to \mathbb{R}^n$ be continuous. Assume that there is a $\mathbf{p}_0 \in \mathring{\mathcal{D}}$ such that $\mathbf{T}(\mathbf{p}_0) \in \mathring{\mathcal{D}}$ and no interior points of $\mathcal{D}$ are mapped to the boundary of $\mathcal{D}$ under $\mathbf{T}$:*

$$\forall \mathbf{x} \in \partial\mathcal{D},\ \mathbf{T}^{-1}(\mathbf{x}) = \{\mathbf{y} \in \overline{\mathcal{D}} : \mathbf{T}(\mathbf{y}) = \mathbf{x}\} \cap \mathring{\mathcal{D}} = \emptyset. \tag{3}$$

Then $\mathbf{T}(\overline{\mathcal{D}}) \subset \overline{\mathcal{D}}$ and $\mathbf{T}(\mathring{\mathcal{D}}) \subset \mathring{\mathcal{D}}$.

Proof Suppose $\mathbf{T}(\overline{\mathcal{D}}) \not\subset \overline{\mathcal{D}}$. Then there is a $\mathbf{q} \in \overline{\mathcal{D}}$ such that $\mathbf{T}(\mathbf{q}) \notin \overline{\mathcal{D}}$. If $\mathbf{q} \notin \mathring{\mathcal{D}}$, by $\overline{\mathring{\mathcal{D}}} = \overline{\mathcal{D}}$ and the continuity of $\mathbf{T}$, we can always choose a point $\mathbf{q}' \in \mathring{\mathcal{D}}$ such that both $\|\mathbf{q}' - \mathbf{q}\|$ and $\|\mathbf{T}(\mathbf{q}') - \mathbf{T}(\mathbf{q})\|$ are sufficiently small so that $\mathbf{T}(\mathbf{q}') \notin \overline{\mathcal{D}}$. Without loss of generality, we assume that $\mathbf{q} \in \mathring{\mathcal{D}}$ with $\mathbf{T}(\mathbf{q}) \notin \overline{\mathcal{D}}$. Since $\mathring{\mathcal{D}}$ is connected, there is a continuous curve $\mathbf{c} \subset \mathring{\mathcal{D}}$ connecting $\mathbf{p}_0$ to $\mathbf{q}$. Since $\mathbf{T}(\mathbf{p}_0) \in \mathring{\mathcal{D}}$ but $\mathbf{T}(\mathbf{q}) \notin \overline{\mathcal{D}}$, by continuity of $\mathbf{c}$ and $\mathbf{T}$ there is $\mathbf{r} \in \mathbf{c} \subset \mathring{\mathcal{D}}$ such that $\mathbf{T}(\mathbf{r}) \in \partial\mathcal{D}$. This contradicts (3). Therefore, we must have $\mathbf{T}(\overline{\mathcal{D}}) \subset \overline{\mathcal{D}}$.

As $\mathbf{T}(\mathring{\mathcal{D}}) \subset \mathbf{T}(\overline{\mathcal{D}}) \subset \overline{\mathcal{D}}$, if $\mathbf{T}(\mathring{\mathcal{D}}) \not\subset \mathring{\mathcal{D}}$ then there is $\mathbf{y} \in \mathring{\mathcal{D}}$ such that $\mathbf{x} = \mathbf{T}(\mathbf{y}) \in \partial\mathcal{D}$ so $\mathbf{T}^{-1}(\mathbf{x}) \cap \mathring{\mathcal{D}} \neq \emptyset$, a contradiction to (3). Hence, we also have $\mathbf{T}(\mathring{\mathcal{D}}) \subset \mathring{\mathcal{D}}$.

4 Population Permanence

A key question in demographic studies is which, and how many, species can coexist in a community. This does not ask for convergence to a steady population state, but rather that the population avoids the boundary of $\mathcal{C}$, thus allowing for more complicated dynamical attractors, such as attracting limit cycles or deterministic chaos. A popular way of modelling this survival of all species is to introduce the notion of permanence:

Definition 4 The system (1) is said to be *permanent* if it is dissipative and if $\mathbf{T}$ has an attractor contained in $\mathring{\mathcal{C}}$.

Thus for a permanent population model, the boundary $\partial\mathcal{C}$ is repelling. This repulsion leads to the well-known fact that a permanent system must have an interior fixed point $\mathbf{p}$.

Studies of permanence are wide-ranging, and include non-autonomous and stochastic population models [41, 21, 40, 1].

Focussing on relations to our method, we highlight [20] where the authors study the permanence of difference equations of the form $\mathbf{x}' = D[\mathbf{x}]\exp(\mathbf{f})$. The average Lyapunov function used in [20] is the same as that used here to show global stability, namely $V(\mathbf{x}) = \prod_{i=1}^{N} x_i^{v_i}$ with suitably chosen $\mathbf{v}$. The authors show

$$V(\mathbf{T}^m(\mathbf{x})) = \alpha(m, \mathbf{x})V(\mathbf{x})$$

where $\alpha(m, \mathbf{x}) = \exp\left(\sum_{j=0}^{m-1} \mathbf{v}^\mathsf{T}\mathbf{f}(\mathbf{T}^j(\mathbf{x})\right)$. Since our $\mathbf{f}$ corresponds to $\exp(\mathbf{f}(\mathbf{x}))$ we may equate $\alpha(m, \mathbf{x}) = \Theta(m, \mathbf{x})$. Using the average Lyapunov approach, the authors in [20] show that if

$$\sup_{m\geq 1} \frac{V(\mathbf{T}^m(\mathbf{x}))}{V(\mathbf{x}))} = \sup_{m\geq 1} \exp\left(\sum_{j=0}^{m-1} \mathbf{v}^\mathsf{T}\mathbf{f}(\mathbf{T}^j(\mathbf{x}))\right) > 1$$

for each $\mathbf{x} \in S := \mathcal{K} \cap \partial\mathcal{C}$ then the system $\mathbf{x}' = D[\mathbf{x}]\exp(\mathbf{f})$ is permanent. In fact, using results from Hutson and Moran [24], Hofbauer et al. note that $\beta(\mathbf{x}) > 1$ need only be checked for each $\mathbf{x} \in \cup_{s\in S}\omega(s)$. Hence we note that permanence requires only properties on the boundary of $\mathcal{C}$, but to prove global convergence to interior fixed points later (which of course implies permanence), we will need to utilise properties of the Lyapunov function on all of the compact attractor $\mathcal{K}$ and for all sufficiently large time. That the properties of $\mathbf{T}$ on $S = \mathcal{K} \cap \partial\mathcal{C}$ are enough to show permanence follows from the fact that boundary regularity allows boundary properties to partially extended into the interior.

Not dealt with in [20] or it seems the related literature is how a choice of the vector $\mathbf{v}$ might be motivated by the ecology. Our analysis below suggests that a good candidate for $\mathbf{v}$ is $D[\mathbf{p}]\boldsymbol{\alpha}$ where $\boldsymbol{\alpha}$ is the principal reproductive mode.

5 Global attraction of interior fixed points

Fix $\mathbf{v} \gg 0$ and define $V(\mathbf{x}) := \prod_{i=1}^{N} x_i^{v_i}$, $\psi(\mathbf{x}) := V(\mathbf{f}(\mathbf{x}))$. For an orbit $O^+(\mathbf{x}) \ni \mathbf{x}(t)$ we will use the shorthand $V_t := V(\mathbf{x}(t))$ and $\psi_t = \psi(\mathbf{x}(t))$ so that $V_{t+1} = \psi_t V_t$. Note that $V \geq 0$ with equality only on the boundary $\partial\mathcal{C}$ and that $V_{t+1} > V_t$ when $\psi_t > 1$. For any vector $\mathbf{u} = (u_1, \ldots, u_N)^\mathsf{T} \in \mathring{\mathcal{C}}$, we shall use the shorthand $\ln \mathbf{u}$ for $(\ln u_1, \ldots, \ln u_N)^\mathsf{T}$. We will find it more convenient to work with $\varphi(\mathbf{x}) := \ln \psi(\mathbf{x})$ so that $V_{t+1} > V_t$ when $\varphi_t > 0$. Let us take some $\mathbf{x} \in \mathring{\mathcal{C}}$ and suppose that $O^+(\mathbf{x})$ is bounded, so that the numbers V_t, ψ_t are also bounded. The following theorem, an elaboration of LaSalle's invariance theorem, provides a test for global convergence to an interior fixed point $\mathbf{p}$. It does not require the results of section 3 for application.

Theorem 6 *Under the general assumptions A1-A3 for system (2), assume that the following conditions hold.*

(i) There is a compact set $\mathcal{K} \subset \mathcal{C}$ *such that*

$$\forall \mathbf{x}(0) = \mathbf{x} \in \mathring{\mathcal{C}},\ \exists t_1 \geq 0,\ \forall t \geq t_1,\ \mathbf{x}(t) \in \mathcal{K}.$$

(ii) There is a $\mathbf{v} \in \mathring{\mathcal{C}}$ *such that either*

$$\forall \mathbf{x} \in \mathcal{K},\ \varphi(\mathbf{x}) = \mathbf{v}^\mathsf{T} \ln(\mathbf{x}) \geq \mathbf{0} \tag{4}$$

or

$$\forall \mathbf{x} \in \mathcal{K},\ \varphi(\mathbf{x}) = \mathbf{v}^\mathsf{T} \ln(\mathbf{x}) \leq \mathbf{0}. \tag{5}$$

(iii) Under (5) the set $S = \{\mathbf{x} \in \partial\mathcal{C} : \varphi(\mathbf{x}) \leq 0\}$ *contains no invariant set.*

Then for each $\mathbf{x} \in \mathring{\mathcal{C}}$*, there is a constant* $c > 0$ *such that*

$$\omega(\mathbf{x}) \subseteq \mathcal{K} \cap \varphi^{-1}(0) \cap V^{-1}(c).$$

In addition, if $\mathbf{x} \in \mathcal{K} \cap (\varphi^{-1}(0) \setminus \{\mathbf{p}\})$ *implies* $\mathbf{T}(\mathbf{x}) \notin \varphi^{-1}(0) \setminus \{\mathbf{p}\}$*, then the interior fixed point* $\mathbf{p}$ *is globally attracting.*

Proof With $V(\mathbf{x}) = \prod_{i=1}^{N} x_i^{v_i}$, $\psi(\mathbf{x}) = V(\mathbf{f}(\mathbf{x}))$, $V_t = V(\mathbf{x}(t))$ and $\psi_t = \psi(\mathbf{x}(t))$, we have $V_0 = V(\mathbf{x}(0)) = V(\mathbf{x})$, $\psi_0 = \psi(\mathbf{x}(0)) = \psi(\mathbf{x})$ and $V_{t+1} = \psi_t V_t$ and $V_t = \left(\prod_{k=0}^{t} \psi_k\right) V_0 = \exp\left(\sum_{k=0}^{t} \varphi(x_k)\right) V_0$. Suppose (4) holds. Then V_k is monotone nondecreasing with k. By the boundedness of $O^+(\mathbf{x})$, V_k is bounded for $k \in \mathbb{N}$. Therefore, $\lim_{k\to\infty} V_k = c$ for some $c > 0$. Let $\mathbf{y} \in \omega(\mathbf{x})$ so that $\mathbf{x}_{t_k} \to \mathbf{y}$ as $k \to \infty$ for some sequence $t_k \to \infty$ as $k \to \infty$. Since $\lim_{k\to\infty} V_{t_k} = c$ (all subsequences of the nondecreasing sequence V_k have the same limit c), continuity of V shows that $V(\mathbf{y}) = c$. This shows that $\omega(\mathbf{x}) \subset V^{-1}(c)$. Now let $O^+(\mathbf{y})$ be the forward orbit through $\mathbf{y}$. Since $\omega(\mathbf{x})$ is invariant, $c = V(\mathbf{y}(t+1)) = \psi(\mathbf{y}(t))V(\mathbf{y}(t)) = \psi(\mathbf{y}(t))c$, so that since

$c > 0$, $\psi(\mathbf{y}(t)) = 1$ for each $t \in \mathbb{N}$. This shows that $\mathbf{y} \in \varphi^{-1}(0)$ and hence $\omega(\mathbf{x}) \subset \varphi^{-1}(0)$. Thus $\omega(\mathbf{x}) \subset \varphi^{-1}(0) \cap V^{-1}(c)$.

Alternatively suppose (5) holds. Now V_k is monotone nonincreasing in k so there is a $c \geq 0$ such that $\lim_{k\to\infty} V_k = c$ and so $\omega(\mathbf{x}) \subset V^{-1}(c)$. If $c = 0$, then by the definition of V, $V^{-1}(c) = \partial\mathcal{C}$ so $\omega(\mathbf{x}) \subset \partial\mathcal{C}$ and since $\psi_k \leq 1$ for $k \geq 0$ we see that $\psi(\mathbf{y}) \leq 1$, i.e. $\varphi(\mathbf{y}) \leq 0$ for all $\mathbf{y} \in \omega(\mathbf{x})$. This leads to $\omega(\mathbf{x}) \subset S = \{\mathbf{x} \in \partial\mathcal{C} : \varphi(\mathbf{x}) \leq 0\}$, a contradiction to condition (iii) as $\omega(\mathbf{x})$ is invariant. Therefore, we must have $c > 0$. Then by the same reasoning as before, we have $\omega(\mathbf{x}) \subset \mathcal{K} \cap \varphi^{-1}(0) \cap V^{-1}(c)$.

Now suppose $\mathbf{y} \in \varphi^{-1}(0) \setminus \{\mathbf{p}\}$ implies $\mathbf{T}(\mathbf{y}) \notin \varphi^{-1}(0) \setminus \{\mathbf{p}\}$. We show that $\omega(\mathbf{x}) = \{\mathbf{p}\}$, so that $\lim_{t\to\infty} \mathbf{x}(t) = \mathbf{p}$. Assume $\omega(\mathbf{x}) \neq \{\mathbf{p}\}$ and let $\mathbf{y} \in \omega(\mathbf{x}) \setminus \{\mathbf{p}\}$. Then, as $\omega(\mathbf{x}) \subset \varphi^{-1}(0) \cap V^{-1}(c) \subset \varphi^{-1}(0)$, we have $\mathbf{y} \in \varphi^{-1}(0) \setminus \{\mathbf{p}\}$ so $\mathbf{T}(\mathbf{y}) \notin \varphi^{-1}(0) \setminus \{\mathbf{p}\}$. On the other hand, however, the invariance of $\omega(\mathbf{x})$ ensures that $\mathbf{T}(\mathbf{y}) \in \omega(\mathbf{x}) \subset \varphi^{-1}(0)$. Thus, we must have $\mathbf{T}(\mathbf{y}) = \mathbf{p}$. This shows that $\omega(\mathbf{x}) = \mathbf{T}(\omega(\mathbf{x})) = \{\mathbf{p}\}$, a contradiction to our supposition. Therefore, $\omega(\mathbf{x}) = \{\mathbf{p}\}$.

6 Split-Lyapunov stability of interior fixed points

Up to now, and in particular for theorem 6, we have not specified how the vector $\mathbf{v}$ used to construct the Lyapunov function V is to be chosen. Now we turn to the discrete-time version of the Split Lyapunov method which is a method for choosing $\mathbf{v}$ introduced for competitive Lotka-Volterra differential equations in [47] and developed further for general Lotka-Volterra systems in [22,4] and for general Kolmogorov differential equations in [23].

Since we deal with strongly competitive models we may utilise the Frobnius-Perron theorem for positive matrices such as $D\mathbf{T}(\mathbf{p})^{-1} \gg 0$. Let $\mathbf{u}_0$ be a positive left eigenvector in the 1-dimensional eigenspace associated with the eigenvalue of $D\mathbf{T}(\mathbf{p})^{-1}$ of largest modulus $\mu_0 > 0$ say.

Recall the last condition ensuring convergence of theorem 6, namely that if $T(\mathcal{D}_0 \setminus \{\mathbf{p}\}) \subset \mathring{\mathcal{D}}_+$ then $\varphi(\mathbf{T}(\mathbf{x})) \geq 0$ for $\mathbf{x} \in \varphi^{-1}(0)$ with equality only if $\mathbf{x} = \mathbf{p}$. Hence $\varphi \circ \mathbf{T}$ is minimised on $\varphi^{-1}(0)$ at $\mathbf{x} = \mathbf{p}$ which implies that there is a $\kappa \in \mathbb{R}$ such that $\kappa \nabla\varphi(\mathbf{p}) + D\mathbf{T}(\mathbf{p})^T \nabla\varphi(\mathbf{p}) = 0$. Thus for stationarity the normal $\nabla\varphi(\mathbf{p})$ must be a left eigenvector of $D\mathbf{T}(\mathbf{p})$. Note that since $\varphi(\mathbf{x}) = \mathbf{v}^\mathsf{T} \ln \mathbf{f}(\mathbf{x})$, $\mathcal{D}_0 = \varphi^{-1}(0)$ in theorem 7 is an $(N-1)$-dimensional surface with $\mathbf{p} \in \mathcal{D}_0$. At $\mathbf{p}$, we compute a normal to this surfaces at $\mathbf{p}$:

$$\nabla\varphi(\mathbf{p}) = \sum_{i=1}^{N} v_i \frac{\nabla f_i(\mathbf{p})}{f_i(p)} = \mathbf{v}^\mathsf{T} D\mathbf{f}(\mathbf{p}) = \boldsymbol{\alpha}^\mathsf{T}(D\mathbf{T}(\mathbf{p}) - I),$$

where $\mathbf{v} = D[\mathbf{p}]\boldsymbol{\alpha}$. Hence if the last condition ensuring convergence of theorem 6 is to be obtained, we must take $\mathbf{v} = D[\mathbf{p}]\boldsymbol{\alpha}$ where $\boldsymbol{\alpha}$ is a left eigenvector of

$D\mathbf{T}(\mathbf{p})$; $\boldsymbol{\alpha}$ is then also normal to $\mathcal{D}_0 = \varphi^{-1}(0)$ at $\mathbf{p}$. This provides a useful constraint on practical choices of $\mathbf{v}$. However, it does not suggest which of the eigenvectors of $D\mathbf{T}(\mathbf{p})$ should be chosen. In section 7 we show that a suitable choice for strongly competitive maps, at least in the case where there is a carrying simplex, is that $\boldsymbol{\alpha}$ should coincide with the normal to the carrying simplex at the interior fixed point $\mathbf{p}$, which in turn corresponds to an eigenvector in the 1-dimensional eigenspace associated with the dominant eigenvector of $D\mathbf{T}(\mathbf{p})^{-1}$.

For the choice $\mathbf{v} = D[\mathbf{p}]\boldsymbol{\alpha}$ we define V, ψ, φ as above and take $\mathcal{D}_+ = \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) > 0\}$. The aim is to apply forward invariance theorems with $\mathcal{D} = \mathcal{D}_+$ to establish that $\overline{\mathcal{D}}_+$ is forward invariant. First, for Sacker's theorem, we require (i) $\mathcal{D}$ to be bounded and $\mathbf{T}$ to be injective on $\mathring{\mathcal{D}}_+$. Next (ii) the set $\mathcal{C} \setminus \mathcal{D}_+$, i.e. $\{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) \leq 0\}$, must have no bounded components. Finally, perhaps the most difficult part we must show that (iii) $\mathbf{T}(\partial\mathcal{D}_+) \subset \overline{\mathcal{D}}_+$. If (i)-(iii) hold true then by theorem 4 the set $\overline{\mathcal{D}}_+$ is forward invariant, and if $\varphi(\mathbf{x}) \geq 0$ then $\varphi(\mathbf{T}^n\mathbf{x}) \geq 0$ for all $n \in \mathbb{N}$.

Theorem 7 *Under the general assumptions A1-A3 for system (2), suppose that $\mathbf{T}$ is dissipative. Let $\mathbf{p}$ be an interior fixed point of $\mathbf{T}$ and $\boldsymbol{\alpha}$ a positive left eigenvector of $D\mathbf{T}(\mathbf{p})$ associated with a real eigenvalue $\mu \neq 0$. Define the function $\varphi : \mathcal{C} \to \mathbb{R}$ by $\varphi(\mathbf{x}) := \boldsymbol{\alpha}^\mathsf{T} D[\mathbf{p}] \ln \mathbf{f}(\mathbf{x})$ and the sets $\mathcal{D}_+ := \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) > 0\}$, $\mathcal{D}_- := \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) < 0\}$ and $\mathcal{D}_0 := \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) = 0\}$. Suppose that (i) $\overline{\mathcal{D}}_+$ is bounded and $\mathbf{T}$ is injective on $\mathring{\mathcal{D}}_+$, (ii) $\overline{\mathcal{D}}_-$ has no bounded components in $\mathcal{C}$, (iii) $\mathbf{T}(\mathcal{D}_0 \cup (\overline{\mathcal{D}}_+ \cap \partial\mathcal{C})) \subset \overline{\mathcal{D}}_+$, and (iv) $\mathbf{T}$ has no invariant set in $\partial\mathcal{C} \cap \overline{\mathcal{D}}_-$.*

Then for each $\mathbf{x} \in \mathring{\mathcal{C}}$, $\omega(\mathbf{x}) \subseteq \mathcal{D}_0 \cap V^{-1}(c)$ for some $c > 0$.

Moreover, if $\mathbf{T}(\mathcal{D}_0 \setminus \{\mathbf{p}\}) \subset \mathring{\mathcal{D}}_+$ then $\omega(\mathbf{x}) = \{\mathbf{p}\}$ for all $\mathbf{x} \in \mathring{\mathcal{C}}$.

Proof Let $\mathcal{K} = \overline{\mathcal{D}}_+$. Then, by conditions (i)–(iii) in theorem 4 and the conclusions of theorem 4, $\mathcal{K}$ is forward invariant. Given any $\mathbf{x} \in \mathring{\mathcal{C}}$, there are two possibilities: (a) $\mathbf{x}(t) = \mathbf{T}^t(\mathbf{x}) \notin \mathcal{K}$ for any $t \in \mathbb{N}$ or (b) $\mathbf{x}(\tau + t) \in \mathcal{K}$ for some $\tau \in \mathbb{N}$ and all $t \in \mathbb{N}$.

In case (b) we immediately have $\varphi(\mathbf{x}(t)) > 0$. Thus by theorem 6, $\omega(\mathbf{x}) \subset \mathcal{D}_0 \cap V^{-1}(c)$. In case (a) we have $\varphi(\mathbf{x}(t)) < 0$ for all $t \in \mathbb{N}$, so that by theorem 6 $\omega(\mathbf{x}) \subset \mathcal{D}_0 \cap V^{-1}(c)$. Finally, if $T(\mathcal{D}_0 \setminus \{\mathbf{p}\}) \subset \mathring{\mathcal{D}}_+$, then since $\omega(\mathbf{x}) \subseteq \mathcal{D}_0$ is an invariant set and $T(\mathcal{D}_0 \setminus \{\mathbf{p}\}) \cap D_0 = \emptyset$, we must have $\omega(\mathbf{x}) = \{\mathbf{p}\}$.

Remark 1 Note that the choice of nonzero eigenvalues of $D\mathbf{T}(\mathbf{p})$ is irrelevant to the proof of theorem 7 as long as it has a corresponding positive left eigenvector $\boldsymbol{\alpha}$. However, if we are aiming at global stability of $\mathbf{p}$, we implicitly require a real eigenvalue μ of $D\mathbf{T}(\mathbf{p})$ to satisfy $0 < |\mu| < 1$. Since $D\mathbf{T}(\mathbf{p}) = I + D[\mathbf{p}]D\mathbf{f}(\mathbf{p})$, if $\boldsymbol{\alpha}$ is a positive left eigenvector of $D\mathbf{T}(\mathbf{p})$ associated with an eigenvalue μ then it is also a positive left eigenvector of $D[\mathbf{p}]D\mathbf{f}(\mathbf{p})$ associated with the eigenvalue $\mu - 1$. Moreover, for $\mathbf{p}$ to be stable, we must have $\mu - 1 \in (-2, 0)$. This remark applies to all the onward results.

Next, we apply theorem 5 for global attraction to an interior fixed point.

Theorem 8 *Under the general assumptions A1-A3 for system (2), suppose that* $\mathbf{T}$ *is dissipative. Let* $\mathbf{p}$ *be an interior fixed point of* $\mathbf{T}$ *and* $\boldsymbol{\alpha}$ *a positive left eigenvector of* $D\mathbf{T}(\mathbf{p})$ *associated with a real eigenvalue* $\mu \neq 0$*. Define the function* $\varphi : \mathcal{C} \to \mathbb{R}$ *by* $\varphi(x) := \boldsymbol{\alpha}^\mathsf{T} D[\mathbf{p}] \ln \mathbf{f}(\mathbf{x})$ *and the sets* $\mathcal{D}_+ := \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) > 0\}$, $\mathcal{D}_- := \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) < 0\}$, $\mathcal{D}_0 := \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) = 0\}$ *and* $\mathcal{D} = \mathring{\mathcal{C}} \cap \mathcal{D}_+$*. Suppose that (i)* $\mathcal{D}$ *is connected, (ii)* $\mathbf{T}(\mathcal{D}) \cap \mathcal{D} \neq \emptyset$*, (iii) for each* $\mathbf{x} \in \mathcal{D}_0$, $\{\mathbf{y} \in \mathcal{C} : \mathbf{T}(\mathbf{y})) = \mathbf{x}\} \cap \mathcal{D} = \emptyset$*, and (iv)* $\mathbf{T}$ *has no invariant set in* $\partial\mathcal{C} \cap \overline{\mathcal{D}}_-$*.*

Then for each $\mathbf{x} \in \mathring{\mathcal{C}}$, $\omega(\mathbf{x}) \subseteq \mathcal{D}_0 \cap V^{-1}(c)$ *for some* $c > 0$*.*

Moreover, if $\mathbf{T}(\mathcal{D}_0 \setminus \{\mathbf{p}\}) \subset \mathring{\mathcal{D}}_+$ *then* $\omega(\mathbf{x}) = \{\mathbf{p}\}$ *for all* $\mathbf{x} \in \mathring{\mathcal{C}}$*.*

Proof Let $\mathcal{K} = \overline{\mathcal{D}}$. Then, by conditions (i)–(iii) and theorem 5, $\mathcal{K}$ is forward invariant. The rest of the proof is the same as that of theorem 7.

In addition, the the conditions of the following theorem that uses a tangent hyperplane approximation to the carrying simplex are sometimes easier to satisfy.

Theorem 9 *Suppose that* $\mathbf{p}$ *is an interior fixed point of* $\mathbf{T}$, $\boldsymbol{\alpha}$ *is a positive left eigenvector of* $D\mathbf{T}(\mathbf{p})$ *associated with a real eigenvalue* $\mu \neq 0$*, and the function* $\varphi(\mathbf{x}) = \boldsymbol{\alpha}^\mathsf{T} D[\mathbf{p}] \ln \mathbf{f}(\mathbf{x})$ *is convex. Let* $\xi(\mathbf{x}) = \boldsymbol{\alpha}^\mathsf{T}(\mathbf{x} - \mathbf{p})$ *and* $\mathcal{K} = \{\mathbf{x} \in \mathcal{C} : \xi(\mathbf{x}) \leq 0\}$*. Then if* $\mathbf{T}(\mathcal{K}) \subset \mathcal{K}$ *and* $\xi(\mathbf{T}(\mathbf{x})) < \xi(\mathbf{x})$ *for all* $\mathbf{x} \in \mathcal{C} \setminus \{\mathbf{p}\}$ *with* $\xi(\mathbf{x}) \geq 0$*, the fixed point* $\mathbf{p}$ *globally attracts* $\mathring{\mathcal{C}}$*.*

Proof We first claim that $\omega(\mathbf{x}) \subset \mathcal{K}$ for all $\mathbf{x} \in \mathcal{C}$. As a matter of fact, this is obvious for $\mathbf{x} \in \mathcal{K}$ since $\mathbf{T}(\mathcal{K}) \subset \mathcal{K}$. For $\mathbf{x} \in \mathcal{C} \setminus \mathcal{K}$, we have $\xi(\mathbf{x}) > 0$ so $\xi(\mathbf{T}(\mathbf{x})) < \xi(\mathbf{x})$. If there is an integer $m > 0$ such that $\xi(\mathbf{T}^m(x)) \leq 0$, then $\mathbf{T}^m(\mathbf{x}) \in \mathcal{K}$ and the positive invariance of $\mathcal{K}$ implies that $\mathbf{T}^k(\mathbf{x}) \in \mathcal{K}$ for all $k \geq m$ so $\omega(\mathbf{x}) \subset \mathcal{K}$. Otherwise, we have $\xi(T^m(\mathbf{x})) > 0$ for all $m > 0$ so that $\xi(T^m(\mathbf{x}))$ is decreasing. Then there is a $c \geq 0$ such that $\lim_{m\to\infty} \xi(\mathbf{T}^m(\mathbf{x})) = c$, i.e. $\omega(\mathbf{x}) \subset \xi^{-1}(c)$. If $c > 0$ then for any $\mathbf{y} \in \omega(\mathbf{x})$, we have $\xi(\mathbf{y}) = c > 0$ so $\xi(\mathbf{T}(\mathbf{y})) < \xi(\mathbf{y}) = c$. But the invariance of $\omega(\mathbf{x})$ implies that $\mathbf{T}(\mathbf{y}) \in \omega(\mathbf{x})$ so $\xi(\mathbf{T}(\mathbf{y})) = \xi(\omega(\mathbf{x})) = c$, a contradiction. Therefore, $c = 0$ so $\omega(\mathbf{x}) \subset \xi^{-1}(0) \subset \mathcal{K}$.

Next, we show that $\omega(\mathbf{x}) = \{\mathbf{p}\}$ for all $\mathbf{x} \in \mathring{\mathcal{C}}$. Suppose $\omega(\mathbf{x}) \neq \{\mathbf{p}\}$ for some $\mathbf{x} \in \mathring{\mathcal{C}}$. Then $\omega(\mathbf{x}) \setminus \{\mathbf{p}\} \neq \emptyset$. Taking $\mathbf{y} \in \omega(\mathbf{x}) \setminus \{\mathbf{p}\} \subset \mathcal{K}$, we have $\xi(\mathbf{y}) \leq 0$ so either $\xi(\mathbf{y}) < 0$ or $\xi(\mathbf{T}(\mathbf{y})) < \xi(\mathbf{y}) = 0$. As both $\mathbf{y}$ and $\mathbf{T}(\mathbf{y})$ are in $\omega(\mathbf{x})$, we can always find an integer $m > 0$ such that $\mathbf{T}^m(\mathbf{x})$ is close enough to $\mathbf{y}$ or $\mathbf{T}(\mathbf{y})$ so that $\xi(\mathbf{T}^m(\mathbf{x})) \leq 0$, i.e. $\mathbf{T}^m(\mathbf{x}) \in \mathcal{K}$. By the positive invariance of $\mathcal{K}$

we have $\mathbf{T}^k(\mathbf{x}) \in \mathcal{K}$ for all $k \geq m$. Since the function $\varphi(\mathbf{x})$ is convex, the set $\overline{\mathcal{D}}_- = \mathcal{D}_- \cup \mathcal{D}_0$ is also convex. As the plane defined by $\xi(\mathbf{x}) = 0$ is the tangent plane of $\mathcal{D}_0$ at $\mathbf{p}$, we must have $\mathcal{K} \setminus \{\mathbf{p}\} \subset \mathcal{D}_+$. Then, from theorem 6 (ii), we obtain $\omega(\mathbf{x}) \subset \mathcal{K} \cap \mathcal{D}_0 = \{\mathbf{p}\}$, a contradiction to the supposition $\omega(\mathbf{x}) \neq \{\mathbf{p}\}$. Hence, $\omega(\mathbf{x}) = \{\mathbf{p}\}$ for all $\mathbf{x} \in \mathring{\mathcal{C}}$.

Based on theorem 7, theorem 8 or theorem 9, we are now in a position to deal with the global asymptotic stability of $\mathbf{p}$, i.e. $\omega(\mathbf{x}) = \{\mathbf{p}\}$ for all $\mathbf{x} \in \mathring{\mathcal{C}}$ and

$$\forall \varepsilon > 0,\ \exists \delta > 0,\ \forall \mathbf{x} \in \mathcal{B}_\delta(\mathbf{p}) \cap \mathring{\mathcal{C}},\ \forall n \geq 1,\ \mathbf{T}^n(\mathbf{x}) \in \mathcal{B}_\varepsilon(\mathbf{p}).$$

Here $\mathcal{B}_r(p)$ is the open ball centred at p with a radius $r > 0$.

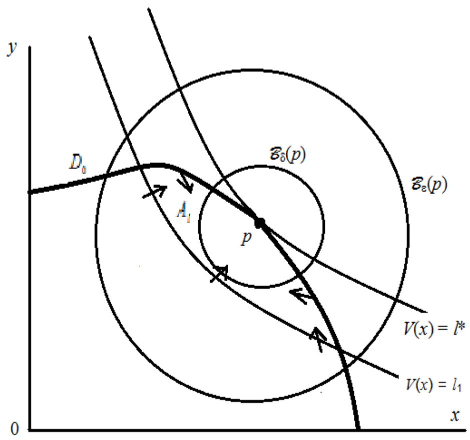

Fig. 2 An illustration of the asymptotic stability argument in theorem 10 of the interior fixed point $\mathbf{p}$.

Theorem 10 (Split Lyapunov Stability) *Assume that* $\mathbf{p}$ *is globally attracting by theorem 7, theorem 8 or theorem 9. Then* $\mathbf{p}$ *is globally asymptotically stable if one of the following conditions is met:*

(a) Each eigenvalue μ *of* $D\mathbf{T}(\mathbf{p})$ *satisfies* $|\mu| < 1$.

(b) Under the conditions of theorem 7 or theorem 8, there exist $\rho > 0$ *and an integer* $m > 0$ *such that* $T^m\mathcal{B}_\rho(\mathbf{p}) \subseteq \mathcal{D}_+ \cup \mathcal{D}_0$.

(c) Under the conditions of theorem 9, there exist $\rho > 0$ *and an integer* $m > 0$ *such that* $T^m\mathcal{B}_\rho(\mathbf{p}) \subseteq \mathcal{K}$.

Proof Under condition (a), $\mathbf{p}$ is locally stable. Then the conclusion follows from this and the global attraction of $\mathbf{p}$.

Now suppose condition (b) holds. We need only show the local stability of p. Restricted to a small open ball centred at $\mathbf{p}$, $\mathcal{D}_0$ and $V^{-1}(\ell) = \{\mathbf{x} \in \mathring{\mathcal{C}} : V(\mathbf{x}) = \ell\}$ for any $\ell > 0$ close to $V(\mathbf{p})$ are $(N-1)$-dimensional surfaces (see figure 2). From the proof of theorem 7 or theorem 8 we know that $\overline{\mathcal{D}}_+ \cap \mathring{\mathcal{C}}$ is forward invariant. Thus, $\mathbf{x} \in \overline{\mathcal{D}}_+ \cap \mathring{\mathcal{C}}$ implies $\mathbf{x}(t) = \mathbf{T}^t(\mathbf{x}) \in \overline{\mathcal{D}}_+ \cap \mathring{\mathcal{C}}$ for all $t \in \mathbb{N}$ so that $V_{t+1}(\mathbf{x}) = \psi_t V_t(\mathbf{x}) \geq V_t(\mathbf{x})$, $V_t(\mathbf{x})$ tends to $V(\mathbf{p}) = \ell^*$ monotonically (since $\mathbf{x}(t) \to \mathbf{p}$) as $t \to \infty$. If $\mathbf{x} \in \overline{\mathcal{D}}_+ \cap \mathring{\mathcal{C}}$ but $\mathbf{x} \neq \mathbf{p}$, the condition $\mathbf{T}(\mathcal{D}_0 \setminus \{\mathbf{p}\}) \subset \mathcal{D}_+$ implies that $V_t(x)$ strictly increases to ℓ^* as $t \to \infty$. This shows that $\mathcal{D}_0 \cap V^{-1}(\ell^*) = \{\mathbf{p}\}$. Moreover, for any $\ell \in (0, \ell^*)$ close enough to ℓ^*, the two surfaces $\mathcal{D}_0$ and $V^{-1}(\ell)$ intersect with each other near $\mathbf{p}$ so that the closed set $A_\ell = \{\mathbf{x} \in \mathring{\mathcal{C}} : \varphi(\mathbf{x}) \geq 0, V(\mathbf{x}) \geq \ell\}$ is forward invariant. Now for any given $\varepsilon > 0$, we can choose $\ell \in (0, \ell^*)$ close enough to ℓ^* so that $A_\ell \subset \mathcal{B}_\varepsilon(\mathbf{p})$ (see figure 2). Then, by (ii) and continuity of $\mathbf{T}$, we can choose $\delta \in (0, \min\{\rho, \varepsilon\})$ sufficiently small such that

$$\forall t \in I_m,\ \mathbf{T}^t \mathcal{B}_\delta(\mathbf{p}) \subset \mathcal{B}_\varepsilon(\mathbf{p});\ \mathbf{T}^m \mathcal{B}_\delta(\mathbf{p}) \subset A_\ell.$$

Hence, by forward invariance of A_ℓ, we have $\mathbf{T}^t \mathcal{B}_\delta(\mathbf{p}) \subset \mathcal{B}_\varepsilon(\mathbf{p})$ for all $t = 1, 2, \dots$ so $\mathbf{p}$ is stable.

Suppose (c) holds. Then, since $(\mathcal{K} \cap \mathring{\mathcal{C}}) \subset (\mathcal{D}_+ \cup \{\mathbf{p}\})$ and $\mathbf{T}(\mathcal{K}) \subset \mathcal{K}$, the above reasoning under (b) is still valid after the replacement of $\overline{\mathcal{D}}_+$ by $\mathcal{K}$.

6.1 Ultra-bounded population models

Some models of Kolmogorov form satisfy

$$T_k(\mathbf{x}) = x_k f_k(\mathbf{x}) \to 0 \text{ for each } k \text{ as } |\mathbf{x}|_1 \to \infty \text{ in } \mathcal{C}. \tag{6}$$

Definition 5 We will call a map $\mathbf{T} : \mathcal{C} \to \mathring{\mathcal{C}}$ satisfying (6) *ultra-bounded.*

An example is the May-Oster model $T_k(\mathbf{x}) = x_k \exp(r_k(1 - (\mathbf{A}\mathbf{x})_k)$ where $r_i > 0$ and $\mathbf{A} \geq 0$. Using simplex coordinates $R = |\mathbf{x}|_1$ and $u_k = x_k/R$ we have that $T_k(R, \mathbf{u}) = R u_k f_k(R\mathbf{u}) \to 0$ as $R \to \infty$. Thus, for each $\mathbf{u} \in \Delta$, the parameterised curve $\gamma_u = \{T(R, \mathbf{u}) : R \in [0, \infty)\}$ is a bounded and closed curve in $\mathcal{C}$. The set $\mathbf{T}\mathcal{C} = \bigcup_{\mathbf{u} \in \Delta} \gamma_u$ is, by construction, a compact absorbing set for $\mathcal{C}$. The boundary of $\mathbf{T}\mathcal{C}$ in $\mathcal{C}$ is envelope of all the curves γ_u as $\mathbf{u}$ varies over Δ and it is precisely the set of points $\mathbf{x} \in \mathcal{C}$ such that $\det D\mathbf{T}(\mathbf{x}) = 0$. The map $\mathbf{T}$ is thus an injective map from $\mathbf{T}\mathcal{C}$ into into itself.

Thus we have the following result for ultra-bounded models.

Theorem 11 *Let the model* $\mathbf{T}(\mathbf{x}) = D[\mathbf{x}]\mathbf{f}(\mathbf{x})$ *be ultra-bounded and competitive. Let* $\mathbf{p}$ *be an interior fixed point of* $\mathbf{T}$ *and* $\boldsymbol{\alpha}$ *a positive left eigenvector of* $D\mathbf{T}(\mathbf{p})$ *associated with a real eigenvalue* $\mu \neq 0$*. Define the function* $\varphi : \mathcal{C} \to \mathbb{R}$ *by* $\varphi(\mathbf{x}) = \boldsymbol{\alpha}^\mathsf{T} D[\mathbf{p}] \ln \mathbf{f}(\mathbf{x})$ *and the sets* $\mathcal{D}_+ = \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) > 0\}$

and $\mathcal{D}_0 = \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) = 0\}$*. Then* $\mathbf{p}$ *is globally asymptotically stable if one of the following conditions holds:*

(i) $\mathbf{T}\mathcal{C} \subset \mathcal{D}_+ \cup \{p\}$.

(ii) $\mathring{\mathcal{D}}_+ \cup \{\mathbf{p}\} \subset \mathbf{T}\mathcal{C}$ *is absorbing for* $\mathring{\mathcal{C}}$.

Proof Under either (i) or (ii), the conclusion follows directly from theorem 10.

We now illustrate the Split Lyapunov method with a couple of examples.

Example 1 Planar May-Oster model.

Here $\mathbf{x} = (x, y)^\mathsf{T}$ and $\mathbf{T} = (f, g)^\mathsf{T}$ where

$$\mathbf{T}(\mathbf{x})^\mathsf{T} = \left(xe^{r(1-x-\alpha y)}, ye^{s(1-\beta x-y)}\right). \tag{7}$$

This map is the class of maps studied for $0 \le r, s \le 1$ and $\alpha, \beta > 0$ by Smith [42] and also in [25]. Smith showed that (i) if $0 < \alpha < 1 < \beta$ then $\mathbf{e}_1 = (1, 0)^\mathsf{T}$ attracts all points not on the y-axis, (ii) if $\beta < 1 < \alpha$ then $\mathbf{e}_2 = (0, 1)^\mathsf{T}$ attracts all points not on the x-axis, (iii) if $\alpha, \beta < 1$ then there is a unique interior fixed point $\mathbf{p}$ that attracts the interior of $\mathbb{R}^2_+$, and (iv) if $0 < r, s < 1$ and $\alpha, \beta > 1$ then there is a C^1 separatrix Γ which partitions $\mathbb{R}^2_+$ into the basin of attractions of $\mathbf{e}_1, \mathbf{e}_2$, and $\Gamma \setminus \{0\}$ is the stable manifold of $\mathbf{p}$. In other words the situation is exactly analogous to the well-known planar differential equation competition model.

We restrict attention to $0 < r, s \le 1$.

This model is ultra-bounded and $\mathbf{T}\mathcal{C}$ is a compact absorbing set for $\mathcal{C} = \mathbb{R}^2_+$. The function φ in this model is actually linear: $\varphi(\mathbf{x}) = rv_1(1 - x - \alpha y) + sv_2(1 - y - \beta x)$. The determinant $\det D\mathbf{T}(\mathbf{x}) = 0$ when $\delta(\mathbf{x}) := (1 - rx)(1 - sy) - rs\alpha\beta xy = 0$ which has one branch in $\mathcal{C}$ when $\alpha\beta > 1$ and two branches in $\mathcal{C}$ when $\alpha\beta < 1$. When $\alpha\beta > 1$, the region $\mathcal{C} \setminus \mathbf{T}\mathcal{C}$ is convex (so that the relative boundary of $\mathbf{T}\mathcal{C}$ in $\mathcal{C}$ is the graph of a convex function). When $\alpha\beta < 1$, the region $\mathbf{T}\mathcal{C}$ is convex (its relative boundary in $\mathcal{C}$ is the lower branch of the hyperbola, which is the graph of a concave function). The set $\mathcal{D}_+$ is the triangular region below the hyperplane $\mathcal{D}_0 = \varphi^{-1}(0)$ in $\mathcal{C}$.

When $\alpha < 1$ and $\beta < 1$, the system has an interior fixed point $\mathbf{p} = \left(\frac{1-\alpha}{1-\alpha\beta}, \frac{1-\beta}{1-\alpha\beta}\right)$. As

$$D\mathbf{T}(x, y) = \begin{pmatrix} e^{r(1-x-y\alpha)}(1 - rx) & -e^{r(1-x-y\alpha)}rx\alpha \\ -e^{s(1-y-x\beta)}sy\beta & e^{s(1-y-x\beta)}(1 - sy) \end{pmatrix},$$

we have $D\mathbf{T}(\mathbf{p}) = I - \Omega$ where $\Omega = \begin{pmatrix} rp_1 & rp_1\alpha \\ sp_2\beta & sp_2 \end{pmatrix} = -D[\mathbf{p}]\frac{\partial(f,g)}{\partial(x,y)}(\mathbf{p})$. We find that $\det \Omega = rsp_1p_2(1 - \alpha\beta)$ and $\operatorname{trace} \Omega = rp_1 + sp_2$. Moreover,

$$\operatorname{trace}\Omega^2 - 4\det \Omega = (rp_1 + sp_2)^2 - 4rsp_1p_2(1 - \alpha\beta) = (rp_1 - sp_2)^2 + 4rsp_1p_2\alpha\beta > 0$$

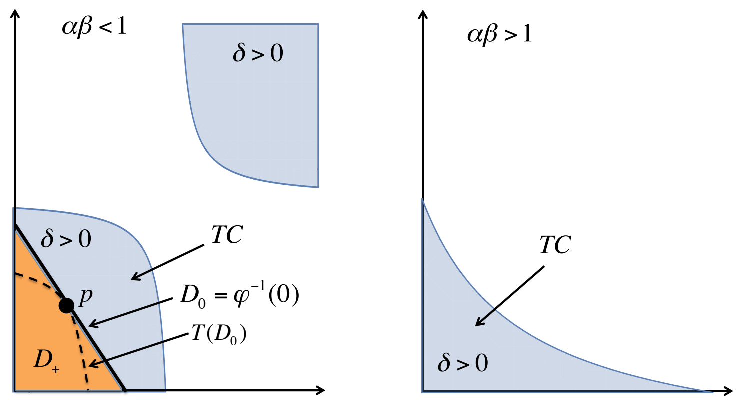

Fig. 3 The areas $\mathbf{T}\mathcal{C}$ for the model (7) when (a) $\alpha\beta < 1$ and (b) $\alpha\beta > 1$. The map $\mathbf{T}$ is injective within the absorbing set $\mathbf{T}\mathcal{C}$ and $\mathcal{D}_0 \cup \mathcal{D}_+ \subset \mathbf{T}\mathcal{C}$.

so that the eigenvalues $\lambda_\pm$ of Ω satisfy $0 < \lambda_\pm < \text{trace}\Omega < 2$. Hence the eigenvalues of $D\mathbf{T}(\mathbf{p})$, $1 - \lambda_\pm$, lie in $(-1, 1)$ when $\alpha, \beta < 1$ and we have local stability. Now we obtain global stability.

From the local stability of $\mathbf{p}$, we need only show the global attraction of $\mathbf{p}$ by theorem 7. Note that $\mathcal{D}_0$ is given by $\varphi(\mathbf{x}) = 0$, $\mathbf{v} = D[\mathbf{p}]\boldsymbol{\alpha}$ where $\boldsymbol{\alpha}$ is a positive left eigenvector of $-\Omega$ corresponding to an eigenvalue $\lambda \in (-2, 0)$, so $\boldsymbol{\alpha}$ is a normal vector of $\mathcal{D}_0$ at $\mathbf{p}$ ($\boldsymbol{\alpha} = (\alpha_1, \alpha_2)^\mathsf{T}$ should not be confused with the parameter α). Thus,

$$-r\alpha_1 p_1 - s\beta\alpha_2 p_2 = \lambda\alpha_1, \tag{8}$$

$$-r\alpha\alpha_1 p_1 - s\alpha_2 p_2 = \lambda\alpha_2, \tag{9}$$

so that eliminating the λ and writing $z = \alpha_1/\alpha_2$ we have $r\alpha p_1 z^2 + (sp_2 - rp_1)z - s\beta p_2 = 0$. There is a positive root

$$z = \frac{\sqrt{4(\alpha\beta - 1)rsp_1p_2 + (rp_1 + sp_2)^2} + rp_1 - sp_2}{2\alpha rp_1}.$$

Since $\alpha\beta < 1$ we find $z < 1/\alpha$. Similarly we find $\frac{\alpha_2}{\alpha_1} = \frac{1}{z} < \frac{1}{\beta}$ and hence

$$\beta < \frac{\alpha_1}{\alpha_2} < \frac{1}{\alpha}. \tag{10}$$

From the definition of φ, $\varphi(\mathbf{p}) = 0$, (8) and (9) we may rewrite $\varphi(\mathbf{x}) = \lambda[\alpha_1(x-p_1)+\alpha_2(y-p_2)]$.

We first show that $\mathbf{T}(\mathcal{D}_0 \setminus \{\mathbf{p}\}) \subset \mathcal{D}_+$, i.e. $\varphi(\mathbf{T}(\mathbf{x})) > 0$ for $\mathbf{x} \in \mathcal{D}_0 \setminus \{\mathbf{p}\}$. For this purpose, we use $(x, y(x))$ to parameterise $\mathcal{D}_0$ and compute

$$\begin{aligned}
\Delta(x) &= \alpha_1 x \exp\left(r(1-x-\alpha y(x))\right) + \alpha_2 y(x) \exp\left(s(1-y(x)-\beta x)\right) - \alpha_1 p_1 - \alpha_2 p_2 \\
&= \alpha_1 x \exp\left(-r((x-p_1)+\alpha(y(x)-p_2))\right) \\
&\quad + \alpha_2 y \exp\left(-s((y(x)-p_2)+\beta(x-p_1))\right) - \alpha_1 p_1 - \alpha_2 p_2 \\
&= \alpha_1 x \exp\left(-r(x-p_1)(1-\alpha\frac{\alpha_1}{\alpha_2})\right) \\
&\quad + (\alpha_1 p_1 + \alpha_2 p_2 - \alpha_1 x) \exp\left(-s(x-p_1)(\beta - \frac{\alpha_1}{\alpha_2})\right) - \alpha_1 p_1 - \alpha_2 p_2 \\
&= \alpha_1 x \exp\left(-r(x-p_1)\varpi_1\right) \\
&\quad + (\alpha_1 p_1 + \alpha_2 p_2 - \alpha_1 x) \exp\left(-s(x-p_1)\varpi_2\right) - \alpha_1 p_1 - \alpha_2 p_2
\end{aligned}$$

where $\varpi_1 = 1 - \frac{\alpha_1}{\alpha_2}\alpha$ and $\varpi_2 = \beta - \frac{\alpha_1}{\alpha_2}$. Note that $\varpi_1 > 0, \varpi_2 < 0$ from (10) and $r\alpha_1 p_1 \varpi_1 = -s\alpha_2 p_2 \varpi_2$ from (8) and (9). As $\Delta(x) = \varphi(\mathbf{T}(x, y(x)))/\lambda$, we need only show that $\Delta(x) < 0$ for $x \in [0, \frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_1}]$ with $x \neq p_1$. Differentiation of $\Delta(x)$ gives

$$\Delta'(x) = \alpha_1(1 - r\varpi_1 x)e^{-r(x-p_1)\varpi_1} - [\alpha_1 + s\varpi_2(\alpha_1 p_1 + \alpha_2 p_2 - \alpha_1 x)]e^{-s(x-p_1)\varpi_2}.$$

Then $\Delta'(p_1) = -r\alpha_1\varpi_1 p_1 - s\alpha_2\varpi_2 p_2 = 0$. Let $\ell(x) = \alpha_1(1 - r\varpi_1 x) - [\alpha_1 + s\varpi_2(\alpha_1 p_1 + \alpha_2 p_2 - \alpha_1 x)]$. Then $\ell(0) = -s\varpi_2(\alpha_1 p_1 + \alpha_2 p_2) > 0$ and $\ell(\frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_1}) = -r\varpi_1(\alpha_1 p_1 + \alpha_2 p_2) < 0$. As $\ell(x)$ is linear and $\ell(p_1) = 0$, we have $\ell(x) > 0$ for $x \in [0, p_1)$ and $\ell(x) < 0$ for $x \in (p_1, \frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_1}]$. Note also that $\alpha_1(1 - r\varpi_1 x) > 0$ for $x \in [0, p_1)$ and $-[\alpha_1 + s\varpi_2(\alpha_1 p_1 + \alpha_2 p_2 - \alpha_1 x)] < 0$ for $x \in (p_1, \frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_1}]$. Then, from the expression of $\Delta'(x)$ we obtain

$$\begin{aligned}
\Delta'(x) &> \ell(x)e^{-s(x-p_1)\varpi_2}, x \in [0, p_1), \\
\Delta'(x) &< \ell(x)e^{-r(x-p_1)\varpi_1}, x \in (p_1, \frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_1}\Big].
\end{aligned}$$

Therefore, $\Delta'(x)$ and $\ell(x)$ have the same sign for each x. This shows that $\Delta(x) < \Delta(p_1) = 0$ for all $x \in [0, \frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_1}]$ with $x \neq p_1$ so $\mathbf{T}(\mathcal{D}_0 \setminus \{p\}) \subset \mathcal{D}_+$.

Next, we assume that $1 > \alpha \geq s > 0$ and $1 > \beta \geq r > 0$. Then, as $\mathcal{D}_0$ is given by $\alpha_1(x-p_1) + \alpha_2(y-p_2) = 0$ in $\mathcal{C}$, it has end points $(\frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_1}, 0)$ and $(0, \frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_2})$. As the lower branch of the curve $\delta = 0$ in $\mathcal{C}$ has end points $(\frac{1}{r}, 0)$ and $(0, \frac{1}{s})$, from (10) we have

$$\frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_1} < p_1 + \frac{p_2}{\beta} \leq \frac{1}{r}; \quad \frac{\alpha_1 p_1 + \alpha_2 p_2}{\alpha_2} < p_2 + \frac{p_1}{\alpha} \leq \frac{1}{s}.$$

Thus, $\mathbf{T}$ is injective on $\overline{\mathcal{D}}_+$. On the x-axis, $T_1(x, 0) = xe^{r(1-x)}$ has maximum $e^{r-1}/r < 1/r$ at $x = 1/r$; on the y-axis, $T_2(0, y) = ye^{s(1-y)}$ has maximum

$e^{s-1}/s < 1/s$ at $y = 1/s$. Thus, $\mathbf{T}(\partial\overline{\mathcal{D}}_+) \subset \mathcal{D}_+$. By Sacker's theorem, $\mathbf{T}(\overline{\mathcal{D}}_+) \subset \overline{\mathcal{D}}_+$. Clearly, there is no invariant set on either x-axis with $x \geq 1/r$ or y-axis with $y \geq 1/s$. Then all the conditions of theorem 7 are met and $\mathbf{p}$ attracts $\mathring{\mathcal{C}}$.

7 Simplifications that utilise a carrying simplex

The carrying simplex Σ [17,18,35,8,28,3,26,44] is an invariant manifold that is a common feature of many continuous- and discrete-time competitive systems. Σ is a Lipschitz manifold of codimension one that attracts all nonzero orbits and is unordered in the sense that no two points in Σ may be ordered with respects to the standard ordering which use the first orthant as a cone. The most useful property of the carrying simplex for us here, and the one exploited by Zeeman and Zeeman in [47] to study global stability of interior fixed points of competitive Lotka-Volterra systems, and later in [22] for the case of boundary fixed points, is that Σ contains all limit sets of nontrivial orbits. Consequently, Σ may be used as the absorbing set $\mathcal{K}$ in the results developed above.

We recall that $\mathcal{D}_+ = \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) > 0\}$, $\mathcal{D}_- = \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) < 0\}$ and $\mathcal{D}_0 = \{\mathbf{x} \in \mathcal{C} : \varphi(\mathbf{x}) = 0\}$, where $\varphi(\mathbf{x}) = \boldsymbol{\alpha}^{\mathsf{T}} D[\mathbf{p}] \ln \mathbf{f}(\mathbf{x})$ with $\boldsymbol{\alpha}$ being a positive left eigenvector of $D\mathbf{T}(\mathbf{p})$.

We use the following definition of convexity or concavity of the carrying simplex [47]. Let Σ_+ and Σ_- denote the two components of $\mathcal{C} \setminus \Sigma$ that lie above and below Σ respectively. We call Σ convex, flat, or concave if for all $\mathbf{x}, \mathbf{y} \in \Sigma$, the interior of the line segment $\mathbf{xy}$ lies in Σ_-, Σ, or Σ_+ respectively.

Lemma 1 *Suppose that (2) has a carrying simplex Σ and $\mathbf{p} \in \Sigma$ is an interior fixed point. Let $\boldsymbol{\alpha}$ be a left eigenvector of $D\mathbf{T}(\mathbf{p})$ associated with a real eigenvalue $\mu \neq 0$ and let $\varphi(\mathbf{x}) = \mathbf{v}^{\mathsf{T}} \ln(\mathbf{f}(\mathbf{x}))$ where $\mathbf{v} = D[\mathbf{p}]\boldsymbol{\alpha}$. Then $\mathcal{D}_0 = \varphi^{-1}(0)$ is tangent to Σ at $\mathbf{p}$.*

Proof Σ globally attracts $\mathcal{C} \setminus O$. The manifold $\Delta = \{\mathbf{x} \in \mathcal{C} : \boldsymbol{\alpha}^{\mathsf{T}}(\mathbf{x} - \mathbf{p}) = 0\}$ is mapped into a sequence of manifolds $M_t = \mathbf{T}^t \Delta$, $t \in \mathbb{N}$ and $\lim_{t\to\infty} M_t = \Sigma$. For each $t \in \mathbb{N}$ let $\mathbf{n}(t)$ be normal to M_t at $\mathbf{p}$, with $\mathbf{n}(0) = \boldsymbol{\alpha}$. Then $\mathbf{n}(t+1) = \operatorname{cof}(D\mathbf{T}(\mathbf{p}))\mathbf{n}(t)$ is normal to M_{t+1} at $\mathbf{p}$ (where $\operatorname{cof}(P)$ denotes the cofactor matrix of P, and $\operatorname{cof}(P) = (\det P)P^{-1}$ when P is nonsingular). Since $\boldsymbol{\alpha}$ is a left eigenvector of $D\mathbf{T}(\mathbf{p})$ it is also a left eigenvector of $(\det D\mathbf{T}(\mathbf{p}))D\mathbf{T}(\mathbf{p})^{-1} = \operatorname{cof}(D\mathbf{T}(\mathbf{p}))$, so $\boldsymbol{\alpha}$ normal to M_t at $\mathbf{p}$ for all $t \in \mathbb{N}$. This implies that $\boldsymbol{\alpha}$ belongs to the normal cone to Σ at $\mathbf{p}$. Now we use that Σ is differentiable at $\mathbf{p}$ [26] so that the normal at $\mathbf{p}$ to Σ is in the direction of $\boldsymbol{\alpha}$.

Corollary 1 *Suppose that (2) has a carrying simplex Σ and that $\mathcal{D}_0 = \varphi^{-1}(0)$ defines a hypersurface that separates $\mathcal{D}_+$ and $\mathcal{D}_-$ in $\mathcal{C}$: $\mathcal{C} = \mathcal{D}_0 \cup \mathcal{D}_+ \cup \mathcal{D}_-$. If $\Sigma \subset \mathcal{D}_+ \cup \{\mathbf{p}\}$, then $\mathbf{p}$ attracts $\mathring{\mathcal{C}}$.*

Proof We first show that, for any $\mathbf{x} \in (\Sigma \setminus \{\mathbf{p}\}) \cap \mathring{\mathcal{C}}$, $\lim_{t\to\infty} \mathbf{T}^t(\mathbf{x}) = \mathbf{p}$ and $V(\mathbf{x}) < V(\mathbf{p})$. Indeed, since $(\Sigma \setminus \{\mathbf{p}\}) \cap \mathring{\mathcal{C}}$ is invariant and $(\Sigma \setminus \{\mathbf{p}\}) \subset \mathcal{D}_+$, we have $\mathbf{x}(t) = \mathbf{T}^t(\mathbf{x}) \in \Sigma \setminus \{\mathbf{p}\}$ so $V_{t+1}(\mathbf{x}) = \psi_t V_t > V_t(\mathbf{x})$ for all integers $t \geq 0$. As $V_t(\mathbf{x})$ is increasing and bounded, there is a $c > 0$ such that

$$\lim_{t\to\infty} V_{t+1}(\mathbf{x}) = \lim_{t\to\infty} \prod_{i=0}^{t} \psi_i V(\mathbf{x}) = c,$$

which implies $\lim_{t\to\infty} \psi_t = 1$, i.e. $\lim_{t\to\infty} \varphi(\mathbf{x}(t)) = \varphi(\omega(\mathbf{x})) = 0$, so $\omega(\mathbf{x}) \subset \mathcal{D}_0$. As $\omega(\mathbf{x}) \subset \Sigma$ and $\Sigma \cap \mathcal{D}_0 = \{\mathbf{p}\}$, we must have $\omega(\mathbf{x}) = \{\mathbf{p}\}$. Hence, $\lim_{t\to\infty} \mathbf{x}(t) = \mathbf{p}$ and $V(\mathbf{x}) < \lim_{t\to\infty} V_t(\mathbf{x}) = V(\mathbf{p})$.

Next, we show that $\lim_{t\to\infty} \mathbf{x}(t) = \mathbf{p}$ for any fixed $\mathbf{x} \in \mathring{\mathcal{C}}$. For any $\varepsilon > 0$, by continuity of $\mathbf{T}$ there is a $\delta \in (0, \varepsilon)$ such that $\mathbf{T}\mathcal{B}_\delta(\mathbf{p}) \subset \mathcal{B}_\varepsilon(\mathbf{p})$. As Σ is compact, $\mathcal{D}_+$ is open in $\mathcal{C}$ and $\Sigma \setminus \{\mathbf{p}\} \subset \mathcal{D}_+$, for this δ there is a $\rho \in (0, \delta)$ such that $\Sigma_\rho = \cup_{u\in\Sigma} \mathcal{B}_\rho(u)$ satisfies $\Sigma_\rho \cap \mathcal{D}_- \subset \mathcal{B}_\delta(p)$. Since $\omega(\mathbf{x}) \subset \Sigma$, for this ρ there is an integer $K \geq 0$ such that $\mathbf{x}(t) \in \Sigma_\rho$ for all $t \geq K$. If $\mathbf{x}(t) \in \mathcal{D}_+$ for sufficiently large t then the same reasoning as in the previous paragraph shows that $\lim_{t\to\infty} \mathbf{x}(t) = \mathbf{p}$. Otherewise, there are infinitely many $t > K$ such that $\mathbf{x}(t) \in \Sigma_\rho \cap \mathcal{D}_- \subset \mathcal{B}_\delta(\mathbf{p})$, so that $\mathbf{x}(t+1) \in \Sigma_\rho \cap \mathcal{B}_\varepsilon(\mathbf{p})$ and $V_{t+1}(\mathbf{x}) \geq \min_{u\in\overline{\mathcal{B}_\varepsilon(\mathbf{p})}} V(u) = \ell(\varepsilon)$. If $\mathbf{x}(t+1) \in \Sigma_\rho \cap \mathcal{D}_-$ then $\mathbf{x}(t+2) \in \Sigma_\rho \cap \mathcal{B}_\varepsilon(\mathbf{p})$ so $V_{t+2}(\mathbf{x}) \geq \ell(\varepsilon)$; if $\mathbf{x}(t+1) \in \Sigma \cap (\mathcal{D}_+ \cup \mathcal{D}_0)$ then $V_{t+2}(\mathbf{x}) \geq V_{t+1}(\mathbf{x}) \geq \ell(\varepsilon)$. In all cases, we derive that $V_t(\mathbf{x}) \geq \ell(\varepsilon)$ for all large t. As $\lim_{\varepsilon\to 0} \ell(\varepsilon) = V(\mathbf{p})$, by letting $t \to \infty$ and then $\varepsilon \to 0$ we see that $V(\omega(\mathbf{x})) \geq V(\mathbf{p})$. As $\omega(\mathbf{x}) \subset \Sigma$ and $V(\mathbf{y}) < V(\mathbf{p})$ for all $\mathbf{y} \in \Sigma \setminus \{\mathbf{p}\}$, we must have $\omega(\mathbf{x}) = \{\mathbf{p}\}$.

With the help of lemma 1 and corollary 1 we are able to prove the following result.

Corollary 2 *Suppose that (2) has a carrying simplex Σ, an interior fixed point $\mathbf{p}$, and that $\mathcal{D}_0 = \varphi^{-1}(0)$ defines a hypersurface that separates $\mathcal{D}_+$ and $\mathcal{D}_-$ in $\mathcal{C}$: $\mathcal{C} = \mathcal{D}_0 \cup \mathcal{D}_+ \cup \mathcal{D}_-$. If $\mathcal{D}_-$ is a convex set and the carrying simplex Σ is convex, then $\mathbf{p}$ attracts $\mathring{\mathcal{C}}$.*

Proof From the definition of φ we know that $\boldsymbol{\alpha}$ is a positive left eigenvector of $D\mathbf{T}(\mathbf{p})$ associated with a real eigenvalue $\mu = 1 + \lambda \neq 0$ and of $D[\mathbf{p}]D\mathbf{f}(\mathbf{x})$ associated with λ. Also, by lemma 1, $\nabla\varphi(\mathbf{p}) = \sum_{i=1}^{N} \alpha_i p_i \frac{Df_i(\mathbf{p})}{f_i(\mathbf{p})} = \boldsymbol{\alpha}^\mathsf{T} D[\mathbf{p}]D\mathbf{f}(\mathbf{p}) = \lambda\boldsymbol{\alpha}^\mathsf{T}$ is normal to the carrying simplex Σ at $\mathbf{x} = \mathbf{p}$. Since $\nabla\varphi(\mathbf{p})$ is also a normal vector of $\mathcal{D}_0$ at $\mathbf{p}$, and both Σ and $\mathcal{D}_-$ are convex with $\mathcal{D}_0$ as part of the boundary of $\mathcal{D}_-$, the set $\Sigma \setminus \{\mathbf{p}\}$ is below the hyperplane $\nabla\varphi(\mathbf{p})^\mathsf{T}(\mathbf{x} - \mathbf{p}) = 0$ whereas $\mathcal{D}_-$ is above the plane. Thus, $\Sigma \subset \mathcal{D}_+ \cup \{\mathbf{p}\}$. Then the conclusion follows from corollary 1.

Example 2 Planar Leslie-Gower model

Consider the planar Leslie-Gower model

$$\mathbf{T}(\mathbf{x})^{\mathsf{T}} = \left(\frac{\alpha x}{1+x+ay}, \frac{\beta y}{1+y+bx} \right). \tag{11}$$

Cushing et al. [6] showed that if (a) $\alpha, \beta < 1$ then $\mathbf{e}_0 = (0,0)^{\mathsf{T}}$ is globally asymptotically stable on $\mathbb{R}^2_+$, (b) $\alpha > 1, \beta < 1$ then $\mathbf{e}_1 = (\alpha - 1, 0)^{\mathsf{T}}$ is globally asymptotically stable on $\mathrm{int}\mathbb{R}^2_+$, (c) $\alpha < 1, \beta > 1$ then $\mathbf{e}_2 = (0, \beta - 1)^{\mathsf{T}}$ is globally asymptotically stable on $\mathrm{int}\mathbb{R}^2_+$. When $\alpha > 1, \beta > 1$, $\mathbf{e}_0$ is a repeller and there are 4 distinct cases: When (a) $b(\alpha - 1) > \beta - 1, \alpha - 1 > a(\beta - 1)$ then $\mathbf{e}_1$ is asymptotically stable on $\mathrm{int}\mathbb{R}^2_+$ and $\mathbf{e}_2$ is a saddle, (b) $b(\alpha - 1) < \beta - 1, \alpha - 1 < a(\beta - 1)$ then $\mathbf{e}_2$ is asymptotically stable on $\mathrm{int}\mathbb{R}^2_+$ and $\mathbf{e}_1$ is a saddle, (c) when $b(\alpha - 1) < \beta - 1, \alpha - 1 > a(\beta - 1)$ then the interior fixed point $\mathbf{p}$ is globally asymptotically stable on $\mathrm{int}\mathbb{R}^2_+$ and (d) when $b(\alpha - 1) > \beta - 1, \alpha - 1 < a(\beta - 1)$ then the interior fixed point $\mathbf{p}$ is a saddle. Here we are concerned with the case $\alpha, \beta > 1$. An interior fixed point has coordinates $\mathbf{p}^{\mathsf{T}} = (\frac{a(1-\beta)+\alpha-1}{1-ab}, \frac{\beta-1+b(1-\alpha)}{1-ab})$ and so is feasible, since we are assuming $\alpha > 1, \beta > 1$ when either (a) $a < \frac{\alpha-1}{\beta-1} < \frac{1}{b}$ or (b) $\frac{1}{b} < \frac{\alpha-1}{\beta-1} < a$. As we will show, in the case (a) $\mathbf{p}$ is globally asymptotically stable in the interior of $\mathbb{R}^2_+$.

The sets $\mathcal{D}_+$, $\mathcal{D}_0$ and $\mathcal{D}_-$ are defined by

$$\varphi(\mathbf{x}) = \alpha_1 p_1 \ln\left(\alpha(1+x+ay)^{-1}\right) + \alpha_2 p_2 \ln\left(\beta(1+y+bx)^{-1}\right) > 0,$$

$\varphi = 0$ and $\varphi < 0$ respectively. The equation $\varphi(\mathbf{x}) = 0$ in $\mathbb{R}^2_+$ for $\mathcal{D}_0$ determines that y is a function of x. From $\varphi = 0$ we have $\varphi_x + \varphi_y \frac{dy}{dx} = 0$ so

$$\frac{dy}{dx} = -\frac{\varphi_x}{\varphi_y} = -\frac{\alpha_1 p_1(1+y+bx) + b\alpha_2 p_2(1+x+ay)}{a\alpha_1 p_1(1+y+bx) + \alpha_2 p_2(1+x+ay)} < 0.$$

Further,

$$\frac{d^2y}{dx^2} = \frac{(1-ab)^2 \alpha_1 p_1 \alpha_2 p_2 (\alpha_1 p_1 + \alpha_2 p_2)(1+y+bx)(1+x+ay)}{[a\alpha_1 p_1(1+y+bx) + \alpha_2 p_2(1+x+ay)]^3} > 0.$$

This shows that the function $y(x)$ determined by $\varphi = 0$ is strictly convex, so $\mathcal{D}_-$ is convex.

The geometry of the carrying simplex Σ for this model has recently been investigated [2]. Define $\delta = (1 + a(\beta - 1))(1 + b(\alpha - 1)) - \alpha\beta$. Then in [2] it was shown that Σ is convex when $\delta > 0$, concave when $\delta < 0$ and a straight line when $\delta = 0$. In the case (a), $1 + b(\alpha - 1) < \beta$ and $1 + a(\beta - 1) < \alpha$ and hence $\delta = (1 + b(\alpha - 1))(1 + a(\beta - 1)) - \alpha\beta < 0$, so that in case (a) the carrying simplex is convex. Hence, from corollary 2 we conclude that in case (a) the interior fixed point $\mathbf{p}$ is globally attracting.

For global asymptotic stability, we need only check that the eigenvalues of $D\mathbf{T}(\mathbf{p})$ lie in $(-1,1)$. A straightforward computation gives $D\mathbf{T}(\mathbf{p}) = I - \Omega$ where

$$\Omega = \begin{pmatrix} \frac{p_1}{\alpha} & \frac{ap_1}{\alpha} \\ \frac{bp_2}{\beta} & \frac{p_2}{\beta} \end{pmatrix}.$$

Then each eigenvalue of Ω satisfies $0 < \lambda < \mathrm{trace}\Omega = \frac{p_1}{\alpha} + \frac{p_2}{\beta}$. From $1 + b(\alpha - 1) < \beta$ and (a) we have $\beta - 1 - b(\alpha - 1) < (\beta - 1)(1 - ab)$ so $\frac{p_2}{\beta} < \frac{\beta-1}{\beta} < 1$. Similarly, from $1+a(\beta-1) < \alpha$ and (a) we have $\alpha-1-a(\beta-1) < (\alpha-1)(1-ab)$ so $\frac{p_1}{\alpha} < \frac{\alpha-1}{\alpha} < 1$. Thus, $\lambda \in (0,2)$ and each eigenvalue $1 - \lambda$ of $D\mathbf{T}(\mathbf{p})$ lies in $(-1,1)$.

Example 3 3-species May-Leonard Leslie-Gower models.

We take

$$T_i(\mathbf{x}) = \frac{bx_i}{1 + (\mathbf{A}\mathbf{x})_i}, i = 1,2,3, \mathbf{A} = \begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix}, \alpha, \beta > 0. \tag{12}$$

Note that for $b < 1$, the map $\mathbf{T}$ is a contraction with O as the unique fixed point. Thus we will assume $b > 1$ in what follows.

The map $\mathbf{T}$ has an unique interior fixed point at $\mathbf{p} = ((b-1)\sigma^{-1}, (b-1)\sigma^{-1}, (b-1)\sigma^{-1})$ where $\sigma = 1 + \alpha + \beta$. We will prove global asymptotic stability of $\mathbf{p}$ in $\mathring{\mathcal{C}}$ (theorem 1 given in section 1) via theorem 9.

From the definition of $\mathbf{T}$ we obtain

$$\begin{aligned} D\mathbf{T}(\mathbf{x}) = \mathrm{diag}[&\frac{b}{1 + (\mathbf{A}\mathbf{x})_1}, \frac{b}{1 + (\mathbf{A}\mathbf{x})_2}, \frac{b}{1 + (\mathbf{A}\mathbf{x})_3}] \\ &-\mathrm{diag}[\frac{bx_1}{(1 + (\mathbf{A}\mathbf{x})_1)^2}, \frac{bx_2}{(1 + (\mathbf{A}\mathbf{x})_2)^2}, \frac{bx_3}{(1 + (\mathbf{A}\mathbf{x})_3)^2}]\mathbf{A}. \end{aligned}$$

It was shown (for example, in [27]) that $\mathbf{T}$ is a competitive map, that $\mathbf{T}$ is injective on $\mathcal{C}$ and that (12) has a carrying simplex, but its geometry is not known. Now we determine parameter values for which $\mathbf{p}$ is asymptotically stable through showing that $D\mathbf{T}(\mathbf{p})$ has eigenvalues of modulus less than one. From the expression of $D\mathbf{T}(\mathbf{x})$ we see that $D\mathbf{T}(\mathbf{p}) = I - \frac{1}{b}D[\mathbf{p}]\mathbf{A}$, which has eigenvalues

$$\lambda_1 = \frac{1}{b},\ \lambda_{2,3} = \frac{2b(\alpha+\beta+1) + (b-1)(\alpha+\beta-2)}{2b(\alpha+\beta+1)} \pm \frac{\sqrt{3}(b-1)|\alpha-\beta|}{2b(\alpha+\beta+1)}i.$$

Then $|\lambda_{2,3}|^2 < 1$ if and only if $(1 - b^{-1})[(\alpha-\beta)^2 + (1-\alpha)(1-\beta)] < (\alpha+\beta+1)(2-\alpha-\beta)$. Under the conditions $b > 1$, $\alpha \le 1$, $\beta \le 1$ with $\alpha + \beta < 2$, we have

$$(\alpha-\beta)^2+(1-\alpha)(1-\beta)-(\alpha+\beta+1)(2-\alpha-\beta) = 2\alpha(\alpha-1)+2\beta(\beta-1)+\alpha\beta-1 < 0.$$

Thus, $\mathbf{p}$ is asymptotically stable when $b > 1$, $\alpha \leq 1$, $\beta \leq 1$ with $\alpha + \beta < 2$.

The rest is to show by theorem 9 that $\mathbf{p}$ attracts $\mathring{\mathcal{C}}$.

The matrix $D\mathbf{T}(\mathbf{p})$ has a left eigenvector $\boldsymbol{\alpha}^\mathsf{T} = (1, 1, 1)$ with associated eigenvalue $\mu_1 = 1/b$. The function $\varphi(\mathbf{x}) = \boldsymbol{\alpha}^\mathsf{T} D[\mathbf{p}] \ln \mathbf{f}(\mathbf{x})$ becomes

$$\varphi(\mathbf{x}) = \frac{(b-1)}{\alpha + \beta + 1}[3 \ln b - \ln(1 + (\mathbf{A}\mathbf{x})_1) - \ln(1 + (\mathbf{A}\mathbf{x})_2) - \ln(1 + (\mathbf{A}\mathbf{x})_3)].$$

For any distinct $\mathbf{x}, \mathbf{y} \in \mathcal{C}$, we can check that $\frac{d^2\varphi}{ds^2}(s\mathbf{x} + (1-s)\mathbf{y}) > 0$ for all $s \in [0, 1]$ so that $\varphi(\mathbf{x})$ is convex. For the function

$$\xi(\mathbf{x}) = \boldsymbol{\alpha}^\mathsf{T}(\mathbf{x} - \mathbf{p}) = \|\mathbf{x}\|_1 - \theta_0, \ \theta_0 = 3(b-1)/(\alpha + \beta + 1),$$

define $\mathcal{K} = \{\mathbf{x} \in \mathcal{C} : \xi(\mathbf{x}) \leq 0\}$. If we can prove that $\xi(\mathbf{T}(\mathbf{x})) < \xi(\mathbf{x})$ holds for all $\mathbf{x} \in \mathcal{C} \setminus \{\mathbf{p}\}$ with $\xi(\mathbf{x}) \geq 0$, then $\mathbf{p}$ attracts $\mathring{\mathcal{C}}$ by theorem 9. We are therefore working with a general $\theta \geq \theta_0$ so as to show that for each $\theta \geq \theta_0$ points on the plane $\|\mathbf{x}\|_1 = \theta$ move below this plane.

For this purpose, we define the function $\phi_\theta(\mathbf{x}) = \theta - \|\mathbf{x}\|_1$ for a fixed $\theta \geq \theta_0$. Then $\Pi_\theta = \phi_\theta^{-1}(0)$ defines a plane with normal $(1, 1, 1)^\mathsf{T}$ passing through the point $(\frac{\theta}{3}, \frac{\theta}{3}, \frac{\theta}{3})^\mathsf{T}$. We need only show that $\phi_\theta(\mathbf{T}(\mathbf{x})) > 0$ for all $\mathbf{x} \in \Pi_\theta \cap \mathcal{C} \setminus \{\mathbf{p}\}$ for all $\theta \geq \theta_0$. We thus find the extrema of

$$\phi_\theta(\mathbf{T}(\mathbf{x})) = \theta - \sum_{i=1}^{3} \frac{bx_i}{1 + (\mathbf{A}\mathbf{x})_i}$$

on $\mathbf{x} \in \Pi_\theta \cap \mathcal{C}$ which written in terms of extrema of the function

$$\Psi_\theta(\mathbf{u}) = \theta - \frac{b\theta u_1}{Cu_1 + Au_2 + Bu_3} - \frac{b\theta u_2}{Bu_1 + Cu_2 + Au_3} - \frac{b\theta u_3}{Au_1 + Bu_2 + Cu_3}$$

on $\mathbf{u} \in \Delta_3 := \{\mathbf{x} \in \mathcal{C} : \|\mathbf{x}\|_1 = 1\}$, where $C = \theta + 1, A = \theta\alpha + 1, B = \theta\beta + 1$. Thus, we need only show that $\Psi_\theta(\mathbf{u}) > 0$, except $u_1 = u_2 = u_3$ when $\theta = \theta_0$, under the conditions of theorem 1. But note that if for some $\theta_1 > 0$ and $\mathbf{u} \in \mathcal{C}$ we have $\Psi_{\theta_1}(\mathbf{u}) \geq 0$, then $\theta_2 > \theta_1$ implies $\Psi_{\theta_2}(\mathbf{u}) > \Psi_{\theta_1}(\mathbf{u}) \geq 0$ since each of A, B, C are increasing with θ. Hence we need only concern ourselves with the case $\theta = \theta_0$. From now on we drop the θ subscript on the understanding that $\theta = \theta_0$.

We now show that if $\phi(\mathbf{T}(\mathbf{x})) > 0$ for $\mathbf{x} \in \partial\Pi_\theta \cap \mathcal{C}$ then $\phi(\mathbf{T}(\mathbf{x})) \geq 0$ for all $\mathbf{x} \in \Pi_\theta \cap \mathcal{C}$ where the equality holds only for $\mathbf{x} = \mathbf{p}$. Indeed, the set $\Pi_\theta \cap \mathcal{C}$ consists of line segments passing through $\mathbf{p}$ with two ends in $\partial\Pi_\theta \cap \mathcal{C}$. Pick up any one such line segment with two points $\mathbf{x}_1, \mathbf{x}_2 \in \partial\Pi_\theta \cap \mathcal{C}$ such that the line segment is given by $\mathbf{x}(s) = s\mathbf{x}_1 + (1-s)\mathbf{x}_2$ for $s \in [0, 1]$ and $\mathbf{x}(s^*) = \mathbf{p}$ for some $s^* \in (0, 1)$. We need only show that $\phi(\mathbf{T}(\mathbf{x}(s))) > 0$

for $s \in [0,1]$ with $s \neq s^*$. To this end, we write $\phi(\mathbf{T}(\mathbf{x}(s))) = \frac{h(s)}{H(s)}$ where $H(s) = \prod_{i=1}^{3}(1 + (\mathbf{A}\mathbf{x}(s))_i) > 0$ and

$$\begin{aligned}h(s) = \theta H(s) &- b(\mathbf{x}(s))_1(1 + (\mathbf{A}\mathbf{x}(s))_2)(1 + (\mathbf{A}\mathbf{x}(s))_3)\\ &- b(\mathbf{x}(s))_2(1 + (\mathbf{A}\mathbf{x}(s))_1)(1 + (\mathbf{A}\mathbf{x}(s))_3)\\ &- b(\mathbf{x}(s))_3(1 + (\mathbf{A}\mathbf{x}(s))_1)(1 + (\mathbf{A}\mathbf{x}(s))_2).\end{aligned}$$

Then $h(s)$ is a polynomial of degree at most three. As $h(s^*) = \theta b^3 - b^3\|\mathbf{p}\|_1 = 0$,

$$\begin{aligned}h'(s^*) &= (\theta - 2p_1)b^2(1,1,1)\mathbf{A}(\mathbf{x}_1 - \mathbf{x}_2) - b^3(1,1,1)(\mathbf{x}_1 - \mathbf{x}_2)\\ &= [b^2 p_1(\alpha + \beta + 1) - b^3](\|\mathbf{x}_1\|_1 - \|\mathbf{x}_2\|_1)\\ &= [b^2(b-1) - b^3](\theta - \theta) = 0,\end{aligned}$$

and $h(0) > 0$ and $h(1) > 0$ by $\phi(\mathbf{T}(\mathbf{x})) > 0$ for $\mathbf{x} \in \partial\Pi_\theta \cap \mathcal{C}$, $s = s^*$ is a repeated root of h so $h(s) > 0$ for $s \in [0,1]$ with $s \neq s^*$.

The first step is to find conditions for which $\Psi(\mathbf{u}) > 0$ for $\mathbf{u} \in \partial\Delta_3$. For example, when $u_3 = 0$ we have

$$\Psi(u_1, u_2, 0) = \theta - \frac{b\theta u_1}{Cu_1 + Au_2} - \frac{b\theta u_2}{Bu_1 + Cu_2}.$$

At the vertex $\mathbf{u} = (1,0,0)^\mathsf{T}$, $\Psi(\mathbf{u}) = \theta - \frac{b\theta}{C} > 0$ if $b < C$. Similarly when $\mathbf{u} = (0,1,0)^\mathsf{T}$, $\Psi(\mathbf{u}) = \theta - \frac{b\theta}{C} > 0$ when $b < C$. Thus $b < C$ is a necessary condition for $\Psi(\mathbf{u}) > 0$ on $\partial\Delta_3$. On a boundary line $u_3 = 0$ when $u_2 > 0$, we may introduce $X = u_1/u_2$ and consider the function

$$p(X) = \theta - \frac{b\theta X}{CX + A} - \frac{b\theta}{BX + C}.$$

Lemma 2 *For $a_1, a_2, a_3, b_1, b_2, b_4, c_1 > 0$,*

$$c_1 - \frac{a_1 X}{a_2 X + a_3} - \frac{b_1}{b_2 X + b_3} > 0, \quad \forall X \geq 0, \tag{13}$$

when $a_1 \leq a_2 c_1$, $b_1 < b_3 c_1$ and either (i) or (ii) below holds:

(i) $(c_1 a_2 b_3 + c_1 a_3 b_2 - a_1 b_3 - b_1 a_2)^2 < 4a_3 b_2(c_1 a_2 - a_1)(c_1 b_3 - b_1)$,

(ii) $a_2 b_1 + a_1 b_3 - a_3 b_2 c_1 - a_2 b_3 c_1 \leq 0$.

Proof The expression on the left hand side of (13) can be written as

$$\frac{X^2(a_2 b_2 c_1 - a_1 b_2) + X(a_3 b_2 c_1 + a_2 b_3 c_1 - a_2 b_1 - a_1 b_3) + a_3 b_3 c_1 - a_3 b_1}{(a_2 X + a_3)(b_2 X + b_3)}.$$

This is positive when

$$X^2(a_2 b_2 c_1 - a_1 b_2) + X(a_3 b_2 c_1 + a_2 b_3 c_1 - a_2 b_1 - a_1 b_3) + a_3 b_3 c_1 - a_3 b_1 > 0.$$

From the cases $X = 0$ and $X > 0$ large we require $a_1 \leq a_2 c_1$ and $b_1 < b_3 c_1$. If (ii) holds then the coefficients of X and X^2 are nonnegative so the inequality holds for $X \geq 0$. Under (i) the polynomial has a positive minimum value.

Applying lemma 2 with $a_1 = b, a_2 = C, a_3 = A, b_1 = b, b_2 = B, b_3 = C, c_1 = 1$, we require $b < C$ and either $0 < 4AB(C-b)^2 - (C^2 + AB - 2bC)^2 = (C^2 - AB)(AB-(C-2b)^2) = (C^2-AB)(4b(C-b)-(C^2-AB))$ or $2bC-C^2-AB \leq 0$ for $\Psi > 0$ on the boundary line $u_3 = 0$ of Δ_3. The same conditions are needed on the other boundary lines. Note that $2bC-AB-C^2 < C^2-AB$ since $b < C$. Thus, $C^2 - AB \leq 0$ implies $2bC - AB - C^2 < 0$. In summary, we have

Lemma 3 *The function $\phi(\mathbf{T}(\mathbf{x})) > 0$ on the boundary of $\Pi_\theta \cap \mathcal{C}$ if and only if $C > b$ and at least one of the following inequalities holds:*

$$(C^2 - AB)(AB - (C-2b)^2) > 0, \tag{14}$$

$$2bC - C^2 - AB \leq 0. \tag{15}$$

First consider the condition $C > b$. This translates to $1+\theta_0 > b$. Thus $\frac{3(b-1)}{1+\alpha+\beta} > b-1$ which requires

$$\alpha + \beta < 2.$$

Now

$$\begin{aligned} C^2 - AB &= \theta_0 \left((2-\alpha-\beta) + (1-\alpha\beta)\theta_0\right), \\ AB - (C-2b)^2 &= (b-1)(\alpha+\beta+1)^{-2}[3\left(\alpha^2+\beta^2-\alpha-\beta-\alpha\beta+1\right) \\ &\quad -b\left(4\alpha^2+4\beta^2-4\alpha-4\beta-\alpha\beta+1\right)], \\ 2bC - C^2 - AB &= -(b-1)(\alpha+\beta+1)^{-2}[3b(1-2\alpha-2\beta+3\alpha\beta) \\ &\quad -5(1-\alpha-\beta)+\alpha^2+\beta^2-7\alpha\beta]. \end{aligned}$$

Thus when $\alpha+\beta < 2$ we have $\alpha\beta < 1$ and so $C^2 > AB$. Hence when $\alpha+\beta < 2$ and

$$b\left(4\alpha^2+4\beta^2-4\alpha-4\beta-\alpha\beta+1\right) < 3\left(\alpha^2+\beta^2-\alpha-\beta-\alpha\beta+1\right)$$

inequality (14) of lemma 3 is satisfied. Similarly when $\alpha+\beta < 2$ and

$$3b(1-2\alpha-2\beta+3\alpha\beta) \geq 5(1-\alpha-\beta)+7\alpha\beta-\alpha^2-\beta^2$$

inequality (15) of lemma 3 is satisfied.

This establishes theorem 1 given in section 1. Figure 4 illustrates the region in (b, α, β) space satisfying the conditions of theorem 1 where the interior fixed point of Leslie-Gower model (12) is globally stable.

Example 4 3-species May-Leonard May-Oster models

The Competitive May-Oster Model is an analogue of the continuous time May-Leonard system for the May-Oster model. The model has been studied by Hofbauer, Hutson and Jansen [20] particularly in the context of permanence,

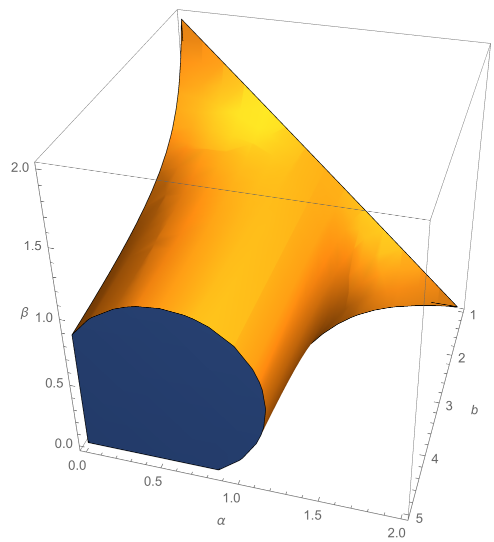

Fig. 4 Region in (b, α, β) space satisfying the conditions of theorem 1 where the interior fixed point of Leslie-Gower model (12) is globally stable

and also by Roeger in terms of local asymptotic stability, limit cycles and heteroclinic cycles [32]. The map is defined by

$$T_i(\mathbf{x}) = x_i \exp r(1 - (\mathbf{A}\mathbf{x})_i), \quad i \in I_3, \qquad \mathbf{A} = \begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix}. \tag{16}$$

There is a unique interior fixed point $\mathbf{p}$ that satisfies $\mathbf{A}\mathbf{p} = \mathbb{1} = (1, 1, 1)^\mathsf{T}$, i.e. $\mathbf{p} = \frac{1}{1+\alpha+\beta}\mathbb{1}$, if $(\alpha, \beta) \neq (1, 1)$. It is clear that all orbits are bounded.

We easily compute

$$D\mathbf{T}(\mathbf{x}) = \mathrm{diag}[e^{r-r(\mathbf{A}\mathbf{x})_1}, e^{r-r(\mathbf{A}\mathbf{x})_2}, e^{r-r(\mathbf{A}\mathbf{x})_3}](I - rD[\mathbf{x}]\mathbf{A}).$$

At $\mathbf{x} = \mathbf{p}$ we have

$$D\mathbf{T}(\mathbf{p}) = I - r\,\mathrm{diag}(\mathbf{p})\mathbf{A} = I - \frac{r}{1+\alpha+\beta}\mathbf{A}.$$

Let λ be an eigenvalue of $\mathbf{A}$ and $\theta_0 = 3(1 + \alpha + \beta)^{-1}$. It is easy to see that $\mathbf{A}$ has a positive eigenvector $\boldsymbol{\alpha}^\mathsf{T} = (1, 1, 1)$ and the corresponding eigenvalue is $\lambda = 1 + \alpha + \beta$. Hence $D\mathbf{T}(\mathbf{p})$ has a positive (left) eigenvector $\boldsymbol{\alpha}^\mathsf{T} = (1, 1, 1)$ associated with eigenvalue $\mu = 1 - r$.

Clearly, $\det D\mathbf{T}(\mathbf{x}) = 0$ if and only if $\det(I - D[r\mathbf{x}]\mathbf{A}) = 0$. If the matrix norm $\|D[r\mathbf{x}]\mathbf{A}\|_\infty < 1$ then $\det(I - D[r\mathbf{x}]\mathbf{A}) \neq 0$ and $D\mathbf{T}(\mathbf{x})^{-1} \gg 0$, so that $\mathbf{T}$ is strongly competitive. Indeed in $\|\mathbf{x}\|_1 < 1/r$ we have $\|D[r\mathbf{x}]\mathbf{A}\|_\infty < 1$

provided that $\alpha, \beta < 1$. This shows that $\mathbf{T}(\mathbf{x})$ is competitive and injective on $\{\mathbf{x} \in \mathcal{C} : 0 \le \|\mathbf{x}\|_1 < 1/r\}$ when $\alpha, \beta < 1$.

The function $\varphi(\mathbf{x}) = \boldsymbol{\alpha}^\mathsf{T} D[\mathbf{p}] \ln \mathbf{f}(\mathbf{x})$ becomes $\varphi(\mathbf{x}) = \frac{r}{\alpha+\beta+1} \sum_{j=1}^{3} (1-(\mathbf{A}\mathbf{x})_j) = \frac{r\boldsymbol{\alpha}^\mathsf{T}\mathbf{A}(\mathbf{p}-\mathbf{x})}{\alpha+\beta+1} = r(\theta_0 - \|\mathbf{x}\|_1)$. For simplicity, we drop the factor r from the expression of φ without loss of generality. Then the sets $\mathcal{D}_+$, $\mathcal{D}_0$, $\mathcal{D}_-$ are defined by $\varphi > 0$, $\varphi = 0$, $\varphi < 0$ respectively.

If we can find appropriate conditions such that $\varphi(\mathbf{T}(\mathbf{x})) > 0$ for all $\mathbf{x} \in \mathcal{D}_0 \setminus \{\mathbf{p}\}$ and $\mathbf{T}$ has no invariant set in $\partial\mathcal{C} \cap \overline{\mathcal{D}}_-$, then theorem 7 takes effect so $\mathbf{p}$ is globally attracting. The global asymptotic stability of $\mathbf{p}$ then follows from a simple check that the eigenvalues of $D\mathbf{T}(\mathbf{p})$ satisfy $|\mu| < 1$.

That $\mathbf{T}$ has no invariant set in $\partial\mathcal{C} \cap \overline{\mathcal{D}}_-$ follows from the analysis of two-dimensional May-Oster model in example 1 in section 6.

The three eigenvalues of $D\mathbf{T}(\mathbf{p})$ are

$$\mu_1 = 1 - r,\ \mu_{2,3} = \frac{2(\alpha+\beta+1) - r(2-\alpha\beta)}{2(\alpha+\beta+1)} \pm i \frac{\sqrt{3} r |\alpha - \beta|}{2(\alpha+\beta+1)}.$$

Then $0 < \mu_1 < 1$ since $r \in (0, 1)$. Clearly, $|\mu_{2,3}|^2 < 1$ if and only if

$$r < \frac{4(\alpha+\beta+1)(2-\alpha-\beta)}{(2-\alpha-\beta)^2 + 3(\alpha-\beta)^2}.$$

But the numerator minus denominator gives $8\alpha(1-\alpha)+8\beta(1-\beta)+4(1-\alpha\beta) > 0$, so we require

$$r < 1 < \frac{4(\alpha+\beta+1)(2-\alpha-\beta)}{(2-\alpha-\beta)^2 + 3(\alpha-\beta)^2}$$

for asymptotic stability of $\mathbf{p}$.

Our task is now to derive conditions for $\varphi(\mathbf{T}(\mathbf{x})) > 0$ for all $\mathbf{x} \in \mathcal{D}_0 \setminus \{\mathbf{p}\}$. From $\varphi(\mathbf{x}) = \theta_0 - x_1 - x_2 - x_3$ we have

$$\begin{aligned}
\varphi(\mathbf{T}(\mathbf{x})) &= \theta_0 - x_1 e^{r - r(\mathbf{A}\mathbf{x})_1} - x_2 e^{r - r(\mathbf{A}\mathbf{x})_2} - x_3 e^{r - r(\mathbf{A}\mathbf{x})_3} \\
&= \theta_0 - \frac{x_1}{e^{-r + r(\mathbf{A}\mathbf{x})_1}} - \frac{x_2}{e^{-r + r(\mathbf{A}\mathbf{x})_2}} - \frac{x_3}{e^{-r + r(\mathbf{A}\mathbf{x})_3}} \\
&\ge \theta_0 - \frac{x_1}{1 - r + r(\mathbf{A}\mathbf{x})_1} - \frac{x_2}{1 - r + r(\mathbf{A}\mathbf{x})_2} - \frac{x_3}{1 - r + r(\mathbf{A}\mathbf{x})_3}.
\end{aligned}$$

Set $\varrho(\mathbf{x}) = \theta_0 - \sum_{i=1}^{n} \frac{x_i}{1 - r + r(\mathbf{A}\mathbf{x})_i}$. Then $\varphi(\mathbf{T}(\mathbf{x})) > 0$ if we can show that $\varrho(\mathbf{x}) > 0$ for $\mathbf{x} \in \mathcal{D}_0 \setminus \{\mathbf{p}\}$. Note that by introducing $b = 1, C = r\theta_0 + 1 - r$, $A = \alpha r\theta_0 + 1 - r$ and $B = \beta r\theta_0 + 1 - r$, we may reduce ϱ in $\mathbf{u}$ coordinates to the form of Ψ in the previous example.

To apply lemma 3 to ϱ, we need to translate the conditions of inequalities (14) and (15) in terms of r, α, β. The inequality $C > b$ translates to $r\theta_0 + 1 - r > 1$ which simplifies to $\alpha + \beta < 2$ as in the previous example. Similarly we find that it is always the case that $C^2 > AB$ and so that in addition to

$\alpha + \beta < 2$ we need either $AB - (C-2)^2 > 0$ or $AB - 2C + C^2 \geq 0$. But $AB - (C-2)^2 = \frac{r\left(2-(\alpha+\beta)^2+\alpha+\beta-3r\left(\alpha^2-\alpha(\beta+1)+(\beta-1)\beta+1\right)\right)}{(\alpha+\beta+1)^2}$ and $AB - 2C + C^2 = \frac{r\left(r\left(-\alpha^2-\alpha(5-7\beta)-\beta(\beta+5)+5\right)-(\alpha+\beta+1)(2-\alpha-\beta)\right)}{(\alpha+\beta+1)^2}$. Hence we conclude that the May-Oster model has a globally attracting interior fixed point when either

$$3r(1+\alpha^2+\beta^2-\alpha-\beta-\alpha\beta) < (2-\alpha-\beta)(1+\alpha+\beta)$$

or

$$r(5-\alpha^2-\beta^2-5(\alpha+\beta)+7\alpha\beta) \geq (2-\alpha-\beta)(1+\alpha+\beta).$$

Figure 5 shows the regions in $(r, \alpha, \beta)-$space where global stability for the May-Oster model is obtained.

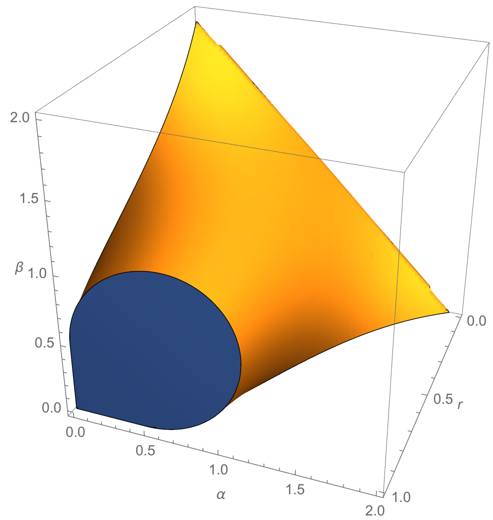

Fig. 5 Region in (r, α, β) space (a) satisfying the conditions of theorem 2 where the May-Oster model (16) is globally stable.

8 Conclusions and discussion

Here we have introduced a method for identifying global stability of interior fixed points of competitive, discrete-time, population models. In its current form, our method is restricted to models under parameter ranges where there are no periodic orbits, but is evidently applicable to a wide range of standard population models. We have attempted to elucidate our method in terms of ecological concepts, and in particular have introduced the idea of a principal reproductive mode, which is similar to Fisher's reproductive value, but not bound to age-structured models. We have also introduced the notion of the principal component of reproductive rate which measures the net reproductive growth using the principal reproductive mode. The eventual positiveness of the principal component of reproductive rate is diagnostic of global convergence to a steady coexistence state. We have also discussed our method in relation to standard approaches to system permanence.

We have provided basic theorems for testing global attraction and stability of an interior fixed point in the first orthant, which is a generalisation of the split Lyapunov method from continuous dynamical systems to discrete systems. These results have then been refined to incorporate the use of a carrying simplex, an attracting invariant manifold of codimension one which is a common feature of competitive population models. We have linked the principal reproductive mode to the normal direction of the carrying simplex at the interior fixed point.

The ideas developed in the paper have been demonstrated to work with some well-known two and three dimensional models. For planar models, the well-known competitive systems approach is simpler than our method, but for 3 species systems or richer, our method performs well. In particular, we have extended results on local stability of some May-Leonard models to global results.

However, there are some issues that we are unable to deal with in this paper so they need further investigation.

Problem 1 Theorem 10 for global stability requires conditions in addition to those for global attraction. Are these extra conditions for stability really necessary? Is stability also guaranteed by the conditions for global attraction in theorems 7, 8 or 9?

Problem 2 Theorem 5 provides an alternative rule for positive invariance to Sacker's rule (theorem 4). Based on this criteria for global attraction and stability are proved (theorems 8 and 10). Applications of these criteria to concrete models need to be fulfilled.

Problem 3 For continuous systems possessing a carrying simplex, split Lyapunov method is also applicable to global repulsion of a fixed point on the carrying simplex. Is the generalisation of the method from continuous system to discrete system also possible for global repulsion on the carrying simplex?

Problem 4 Further development of the method for a boundary fixed point of discrete systems is needed.

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