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# Global stability in a multi-species periodic Leslie-Gower model

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# Global stability in a multi-species periodic Leslie–Gower model

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We consider a population model consisting of $d$ species interacting in a $p$-periodic environment and modelled by a $d$-dimensional system of Leslie–Gower-type difference equations (coupled Beverton–Holt equations). It is shown that if the interspecific competition (coupling) is sufficiently small and the inherent growth rate of each species is such that in the absence of competition each species will grow to its (positive) individual carrying capacity, then there is a positive asymptotically stable $p$-periodic state that globally attracts all positive initial states. Three examples are studied numerically in which the competition is large and the principle of competitive exclusion is observed. The rate of decay to extinction is observed to be sensitive to the inherent growth rate of the dying species. The individual carrying capacities are seen to play a determining role in the case of equal and large competition and equal inherent growth rates.

**Keywords:** periodic difference equation; global stability; Leslie–Gower model

*AMS Subject Classification*: 39A11; 92; 92D; 92D25

## 1. Introduction

The study of competition models inevitably leads one to consider either the Lotka–Volterra model in the continuous case or the Leslie–Gower model [10] in the discrete case. The typical Leslie–Gower model consists of two Beverton–Holt equations with added coupling (interspecific competition). When the interspecific competition is strong, one species will be driven to extinction; the principle of competitive exclusion that is one of the important tenets in ecology (see [2,3,7] for results and many references to this phenomenon). In [11], global stability in a *two*-species model is considered using techniques of monotone systems [9]. In [4], multi-species models are considered, taking into account harvesting and stocking.

See [6] for further results on stage-structured models for larvae, pupae and adults, the well-known 'LPA' model that is essentially a delay equation for the larvae and adults. In [5], non-equilibrium competitive coexistence for a two-species LPA model was explored and a boundary 2-cycle was established. See also [1] in which a two-species juvenile–adult model is studied with the assumption that there is no competition between juveniles and adults.

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For the Beverton–Holt (scalar) equation, the issue of global asymptotic stability, even in the periodic case, has been settled in [8]. Since the functions defining these equations, being fractional linear, form a semi-group $\mathcal{B}$ under composition, the existence and global asymptotic stability of a periodic equation reduces to establishing a fixed point with the same property for a single (autonomous) equation. In fact, in [8], it was shown that $\mathcal{B}$ is a sub-semi-group of the larger semi-group $\mathcal{K}$ of continuous functions $f : \mathbb{R}_+ \to \mathbb{R}_+$ that are concave, increasing and cross the diagonal in $\mathbb{R}_+ \times \mathbb{R}_+$. In [12], the result was extended to $C^3$ functions that are either concave increasing or convex decreasing and have non-negative Schwarzian. These conditions are satisfied by certain rational functions with the roots of the numerator *interlaced* with the roots of the denominator.

In this paper, we consider $d$ species interacting in a periodic environment modeled by a $d$-dimensional system of Leslie–Gower-type equations, or equivalently coupled Beverton–Holt equations. It is assumed that the inherent growth rate of each species is such that in the absence of competition each species will grow to its (positive) individual carrying capacity. It is shown that if the interspecific competition (coupling) is sufficiently small, then there is a positive asymptotically stable periodic state that globally attracts all positive initial states.

We then study numerically, in three four-dimensional examples, some cases in which the interspecific competition is large. In the first example, we see that large competition against just species number one, not surprisingly, drives that species to extinction. In the second example, we see that an increase in the inherent growth rate for species one by a factor of 1.77 must be countered by a 4.3-fold increase in the competition by all three competing species in order to achieve the same rate of decay to extinction. In the third example, we make all the competition large and equal and all the inherent growth rates equal and observe that the species with the smallest individual carrying capacity is driven to extinction.

## 2. Autonomous two-dimensional case

We begin with a discussion of this case in order to develop some notation that will make the $d$-dimensional case easier to formulate and discuss.

The two-species Leslie–Gower model is usually written in the following form:

$$\begin{aligned} x_1(n+1) &= \frac{b_1 x_1(n)}{1 + c_{11}x_1(n) + c_{12}x_2(n)} \\ x_2(n+1) &= \frac{b_2 x_2(n)}{1 + c_{21}x_1(n) + c_{22}x_2(n)}. \end{aligned} \tag{1}$$

We propose the following equivalent form of Equation (1) that is a pair of coupled Beverton–Holt equations. In addition, we view a difference equation as a mapping $x(n+1) = f(x(n))$ and thus focus our attention on the right-hand side $f$:

$$\begin{aligned} f_1(x_1, x_2) &= \frac{\mu_1 K_1 x_1}{K_1 + (\mu_1 - 1)x_1 + c_{12}x_2} \\ f_2(x_1, x_2) &= \frac{\mu_2 K_2 x_2}{K_2 + c_{21}x_1 + (\mu_2 - 1)x_2}. \end{aligned} \tag{2}$$

Here the coupling parameters $c_{ij}$ are the coefficients of *interspecific competition*. If both $c_{ij} = 0$ and $\mu_i > 1$, the system is decoupled and each $x_i(n)$ with $x_i(0) > 0$ asymptotically approaches its *carrying capacity* (fixed point), $K_i$ as $n \to \infty$.

Our next goal will be to develop a notation and some operations that will make it straightforward to consider higher-dimensional maps. For those familiar with Matlab programming, these operations will not seem so strange.

Let $a$ be a scalar and $u$ and $v$ be column vectors in $\mathbb{R}^d$ and $C$ an $d \times d$ matrix. Define, in addition to the usual inner product and linearity rules,

$$
\begin{aligned}
uv &= \mathrm{col}\,(u_1v_1, u_2v_2, \ldots, u_dv_d),\\
\frac{u}{v} &= \mathrm{col}\left(\frac{u_1}{v_1}, \frac{u_2}{v_2}, \ldots, \frac{u_d}{v_d}\right), \quad \text{if} \quad v_1v_2\cdots v_d \neq 0,\\
\mathrm{diag}\, u &= \text{the diagonal matrix with } u \text{ on the diagonal},\\
\mathrm{diag}\, C &= \mathrm{col}\,(c_{11}, c_{22}, \ldots, c_{dd}),\\
C^0 &= C - \mathrm{diag}\,\mathrm{diag}\, C, \quad C \text{ with its diagonal entries set to zero},\\
u \geq 0 &\iff u_i \geq 0\ \forall i \quad \text{and} \quad u > 0 \iff u_i > 0\ \forall i.
\end{aligned}
$$

We may now now rewrite Equation (2) as

$$
f(x) = \frac{(\mu_1, \mu_2)'(K_1, K_2)'(x_1, x_2)'}{(K_1, K_2)' + [\mathrm{diag}(\mu_1, \mu_2) - I + C^0](x_1, x_2)'}, \tag{3}
$$

where the product in the denominator is the usual matrix–vector multiplication and '′' means transpose.

To further simplify this and eliminate cumbersome notation, we define the parameters

$$
\mu = \mathrm{diag}\,\mathrm{col}\,(\mu_1, \mu_2), \quad \text{growth parameter}, \tag{4}
$$

$$
K = \mathrm{col}\,(K_1, K_2), \quad \text{individual carrying capacity}, \tag{5}
$$

$$
C^0 = \begin{pmatrix} 0 & c_{12} \\ c_{21} & 0 \end{pmatrix}, \quad \text{non-negative coupling parameters}. \tag{6}
$$

With these, Equation (2) takes the form

$$
f(x) = \frac{\mu K x}{K + (\mu - I + C^0)x}. \tag{7}
$$

This form is not specific to $\mathbb{R}^2$, but can be interpreted in $\mathbb{R}^d$ as well. With $C^0 = 0$, Equation (7) represents $d$ independent Beverton–Holt equations.

## 3. Interior fixed point, autonomous case: $p = 1$

We consider the positive cone

$$
\mathcal{C}^0 = \{x \in \mathbb{R}^d | x_i > 0\ \forall i\}. \tag{8}
$$

The condition for a fixed point of Equation (7) in $\mathcal{C}^0$ is just $f(x) = x$, which yields

$$
(\mu - I)K = (\mu - I + C^0)x, \tag{9}
$$

or in two dimensions is just

$$
\begin{aligned}
(\mu_1 - 1)K_1 &= (\mu_1 - 1)x_1 + c_{12}x_2\\
(\mu_2 - 1)K_2 &= c_{21}x_1 + (\mu_2 - 1)x_2.
\end{aligned} \tag{10}
$$

Equation (9) is a simple linear system and we have the following theorem.

THEOREM 3.1 *Assume $\mu_i > 1$ for all $i = 1, 2, \ldots, d$ and the coupling terms $C^0$ are sufficiently small. Then there exists a unique fixed point $\tilde{x} \in \mathcal{C}^0$ that reduces to $K = col\,(K_1, K_2, \ldots, K_d)$ when $C^0 = 0$.*

The theorem applies equally well to any of the invariant coordinate 'faces'

$$\mathcal{F} = \{(x_1, x_2, \ldots, x_d) \mid x_j = 0, \text{ for } k \text{ of the indices }, 1 \le k < d\}.$$

In order to study stability, we note the following lemma.

LEMMA 3.2 *The function $f$ is bounded in $\mathbb{R}^d_+$. More precisely, each component function*

$$0 \le f_j(x) \le B_j \doteq \frac{\mu_j K_j}{\mu_j - 1}. \tag{11}$$

*Therefore,*

$$f : \mathbb{R}^d_+ \longrightarrow \mathcal{B}_0 \doteq [0, B_1] \times [0, B_2] \times \cdots \times [0, B_d]. \tag{12}$$

We next define $K_{\min}$ and $K_{\max}$ to be the minimum and maximum of the $K_i$ and $b = K_{\min}/2$. We then have the following lemma.

LEMMA 3.3 *Assume each row $c_i$ of the matrix $C^0$ in Equation (7) satisfies*

$$\|c_i\| \le \frac{(\mu - 1)K_{\min}}{2\sqrt{d}K_{\max}} = \frac{(\mu - 1)}{\sqrt{d}K_{\max}} b, \tag{13}$$

*where $\|\cdot\|$ is the euclidean norm. Then the compact set*

$$\mathcal{B} \doteq [b, B_1] \times [b, B_2] \times \cdots \times [b, B_d] \tag{14}$$

*is invariant under the action of $f$, i.e.*

$$f : \mathcal{B} \longrightarrow \mathcal{B}. \tag{15}$$

The proof will follow by setting $v = x$ in the next more general lemma needed later.

LEMMA 3.4 *Define $\hat{f}(x) : \mathcal{B} \to \mathbb{R}^d$ as follows. Let $v \in \mathcal{B}$ be arbitrary and define (cf. Equation (7))*

$$\hat{f}(x) = \frac{\mu K x}{K + (\mu - I)x + C^0 v}.$$

*Assume the rows $c_i$ of the matrix $C^0$ satisfy Equation (13). Then*

$$\hat{f} : \mathcal{B} \longrightarrow \mathcal{B}. \tag{16}$$

*Proof* Let $\langle p, q\rangle$ denote the inner product of vectors $p$ and $q$. For $x_i \ge b = K_{\min}/2$, the $i$th component of $\hat{f}$ satisfies

$$\begin{aligned}\hat{f}_i(x) &= \frac{\mu_i K_i x_i}{K_i + (\mu_i - 1)x_i + \langle c_i, v\rangle} \ge \frac{\mu_i K_i b}{K_i + (\mu_i - 1)b + \langle c_i, v\rangle}\\ &\ge \frac{\mu_i K_i b}{K_i + (\mu_i - 1)b + \|c_i\|\|v\|} \ge \frac{\mu_i K_i b}{K_i + (\mu_i - 1)b + \|c_i\|\sqrt{d}K_{\max}}\\ &\ge \frac{\mu_i K_i b}{K_i + 2(\mu_i - 1)b} = \frac{\mu_i K_i b}{K_i + (\mu_i - 1)K_{\min}} \ge \frac{\mu_i K_i b}{K_i + (\mu_i - 1)K_i} = b.\end{aligned}$$

This together with Equation (12) completes the proof. ■

### 3.1. *Dynamic reduction*

In the technique of *dynamic reduction* introduced in [14], one defines a class of $p$-periodic sequences of column vectors $v_n$:

$$\mathcal{P}_p = \{v = (v_1, v_2, \ldots)|v_{n+p} = v_n \in \mathcal{B},\ \forall n\}. \tag{17}$$

For $p = 1$, the case we are currently considering, the 'sequences' are independent of $n$, i.e. constant sequences. For each $v \in \mathcal{P}_p$, one then looks at the 'reduced' version of difference equation with the right-hand side (7):

$$x(n+1) = \hat{f}(x(n)) = \frac{\mu K x(n)}{K + (\mu - I)x(n) + C^0 v}, \tag{18}$$

which is just a system of $d$ *uncoupled* difference equations. Next define $B = \text{col}\ (B_1, B_2, \ldots, B_d)$. We then have

THEOREM 3.5 *In addition to Equation* (13), *assume that the rows of $C^0$ satisfy*

$$\frac{\mu K}{K + C^0 B} > 1 \quad \textit{element-wise}. \tag{19}$$

*Then Equation* (18) *has a fixed point $w \in \mathcal{B}$, thus establishing a mapping*

$$\mathcal{T} : \mathcal{P}_1 \to \mathcal{P}_1, \quad w = \mathcal{T}(v). \tag{20}$$

*For $C^0$ sufficiently small, $\mathcal{T}$ is a contraction yielding a unique fixed point $v^*$. In addition, $v^*$ is an exponentially asymptotically stable fixed point of Equation* (7) *that is globally attracting with respect to the cone $\mathcal{C}^0$* (*Equation* (8)).

*Proof* Each component function $\hat{f}_i$ in Equation (18) is fractional linear, concave increasing and from Equation (19) has a slope at the origin that is greater than one. Thus, either by [8] or [12], one obtains an exponentially asymptotically stable solution (fixed point) $w_i$ and from Lemma 3.4, $w = \text{col}\ (w_1, \ldots, w_d) \in \mathcal{B}$. This establishes Equation (20).

Note that since $w$ satisfies Equation (18),

$$w = \frac{\mu K w}{K + (\mu - I)w + C^0 v},$$

and thus

$$\mathcal{T}'(v) = \frac{\mathrm{d}w}{\mathrm{d}v} = -(\mu - I)^{-1} C^0,$$

from which it follows that $\mathcal{T}$ is a contraction for $C^0$ sufficiently small. For the remaining details of the proof, see [14]. ■

## 4. Periodic case: $p > 1$

The periodic version of Equation (7) is $x(n+1) = f_n(x(n))$, where

$$f_n(x) = \frac{\mu_n K_n x}{K_n + (\mu_n - I + C_n^0)x}. \tag{21}$$

For the sake of simplicity of presentation, we shall work with the case where the dimension $d = 2$, the period $p = 3$ and only the individual carrying capacities $K_i$ are periodic:

$$x(n+1) = f_n(x(n)) = \begin{pmatrix} f_{1,n} \\ f_{2,n} \end{pmatrix}, \quad \text{where } f_n \equiv f_{(n \bmod 3)},$$

and

$$\begin{aligned} f_{1,n}(x_1, x_2) &= \frac{\mu_1 K_{1,n} x_1}{K_{1,n} + (\mu_1 - 1)x_1 + c_{12}x_2} \\ f_{2,n}(x_1, x_2) &= \frac{\mu_2 K_{2,n} x_2}{K_{2,n} + (\mu_2 - 1)x_2 + c_{21}x_1}. \end{aligned} \tag{22}$$

The evolution of the maps $f_n$ along with the state variable $x(n)$ is illustrated in the skew-product [13] setting (Figure 1).

Before proceeding, however, let us prove the *periodic* version of Lemmas 3.2 and 3.4 in the general case.

LEMMA 4.1 *The functions $f_n$ are bounded in $\mathbb{R}_+^d$. More precisely, each component function satisfies*

$$0 \le f_{j,n}(x) \le B_{j,n} \doteq \frac{\mu_{j,n} K_{j,n}}{\mu_{j,n} - 1}. \tag{23}$$

*Therefore*,

$$f : \mathbb{R}_+^d \longrightarrow \mathcal{B}_{0,n+1} \doteq [0, B_{1,n}] \times [0, B_{2,n}] \times \cdots \times [0, B_{d,n}]. \tag{24}$$

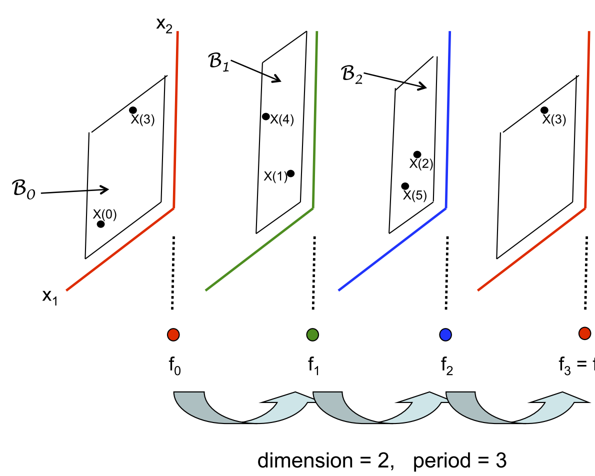


Figure 1. Orbit in skew-product flow.

LEMMA 4.2 *For $v(n) \in \mathcal{B}_{0,n}$ define $\hat{f}_n = \mathrm{col}(\hat{f}_{1,n}, \dots, \hat{f}_{d,n})$ with*

$$\hat{f}_{i,n}(x) = \frac{\mu_{i,n} K_{i,n} x_i}{K_{i,n} + (\mu_{i,n} - I)x_i + [C_n^0 v(n)]_i}. \tag{25}$$

*and set*

$$K_{\min / \max} = \min / \max K_{i,j} \quad i = 1, \dots, d, \quad j = 1, \dots, p,$$

*and $b = K_{\min}/2$. Assume each row $c_{i,n}$ of the matrices $C_n^0$ in Equation (25) satisfies*

$$\|c_{i,n}\| \le \frac{(\mu_{i,n} - 1)K_{\min}}{2\sqrt{d}K_{\max}} = \frac{(\mu_{i,n} - 1)}{\sqrt{d}K_{\max}} b,$$

*where $\| \cdot \|$ is the euclidean norm. Then the compact set*

$$\mathcal{K} \doteq \bigcup_{j=0,\dots,p-1} \mathcal{B}_j \times f_j \subset \mathbb{R}_+^d \times \{f_0, f_1, \dots, f_{p-1}\},$$

*where*

$$\mathcal{B}_{n+1} \doteq [b, B_{1,n}] \times [b, B_{2,n}] \times \cdots \times [b, B_{d,n}] \tag{26}$$

*is invariant in the skew-product dynamical system, i.e.*

$$f_j : \mathcal{B}_j \to \mathcal{B}_{j+1}.$$

*Note:* The set on the right is labelled with '$j + 1$' since it lies in the domain of $f_{j+1}$ with subscripts taken mod $p$ (Figure 1).

*Proof* Let $\langle p, q \rangle$ denote the inner product of vectors $p$ and $q$. For $x \ge b = K_{\min}/2$, the $i$th component of $\hat{f}$ satisfies

$$\begin{aligned}
\hat{f}_i(x) &= \frac{\mu_{i,n} K_{i,n} x_i}{K_{i,n} + (\mu_{i,n} - 1)x_i + \langle c_{i,n}, v \rangle} \ge \frac{\mu_{i,n} K_{i,n} b}{K_{i,n} + (\mu_{i,n} - 1)b + \langle c_{i,n}, v \rangle} \\
&\ge \frac{\mu_{i,n} K_{i,n} b}{K_{i,n} + (\mu_{i,n} - 1)b + \|c_{i,n}\| \|v\|} \ge \frac{\mu_{i,n} K_{i,n} b}{K_{i,n} + (\mu_{i,n} - 1)b + \|c_{i,n}\| \sqrt{d} K_{\max}} \\
&\ge \frac{\mu_{i,n} K_{i,n} b}{K_{i,n} + 2(\mu_{i,n} - 1)b} = \frac{\mu_{i,n} K_{i,n} b}{K_{i,n} + (\mu_{i,n} - 1)K_{\min}} \ge \frac{\mu_{i,n} K_{i,n} b}{K_{i,n} + (\mu_{i,n} - 1)K_{i,n}} = b.
\end{aligned}$$

This together with Equation (24) completes the proof. ∎

### 4.1. *Dynamic reduction: periodic case*

To apply dynamic reduction, we first separate out the coupling terms in Equation (21) to obtain

$$f_{1,n}(x) = \frac{\mu_1 K_{1,n} x_1}{K_{1,n} + (\mu_1 - 1)x_1 + g_1(x)}, \quad g_1(x) = c_{12} x_2,$$

$$f_{2,n}(x) = \frac{\mu_2 K_{2,n} x_2}{K_{2,n} + (\mu_2 - 1)x_2 + g_2(x)}, \quad g_2(x) = c_{21} x_1,$$

or simply

$$x(n + 1) = F_n(x(n), g(x(n))). \tag{27}$$

We next define the class of three periodic sequences

$$\mathcal{P}_3 = \{v = (v^0, v^1, v^2) | v^j \in \mathcal{B}_j\},$$

where all subscripts are taken mod 3. For $v \in \mathcal{P}_3$, we get the reduced equation

$$(n+1) = F_n(x(n), g(v(n))), \quad \text{where} \quad v(j) = v^{(j \mod 3)}, \tag{28}$$

and

$$F_{1,n}(x(n), g(v(n))) = \frac{\mu_1 K_{1,n} x_1(n)}{K_{1,n} + (\mu_1 - 1)x_1(n) + c_{12} v_2(n)}$$
$$F_{2,n}(x(n), g(v(n))) = \frac{\mu_2 K_{2,n} x_2(n)}{K_{2,n} + (\mu_2 - 1)x_2(n) + c_{21} v_1(n)}, \tag{29}$$

where again, for the sake of clarity, we have suppressed the periodic dependence in the $\mu_i$ and $c_{ij}$.

The difference equations on the right-hand sides of Equation (29) are uncoupled and each such equation is a three periodic concave increasing function mapping $\mathbb{R}^+ \to \mathbb{R}^+$. By [8,12], we obtain an exponentially asymptotically stable periodic solution,

$$w = (w^0, w^1, w^2), \quad w^j \in \mathcal{B}_j \subset \mathbb{R}^2, \tag{30}$$

that globally attracts all initial states in the positive cone $\mathcal{C}^0$. Thus, we have the mapping $\mathcal{T}$ : $\mathcal{P}_3 \to \mathcal{P}_3$, $w = \mathcal{T}(v)$ (Figure 2).

We next introduce the following notation: For $\mathcal{U} \subset \mathbb{R}^d_+$ and a periodic vector valued sequence of functions $V = \{V_1, V_2, \ldots, V_{p-1}, V_p = V_0\}$ with $V_n : \mathcal{U} \to \mathbb{R}^d_+$ we define $|V|_0 \doteq \max_{n=1,\ldots,p} \sup_{u \in \mathcal{U}} |V_n(u)|$. For a fixed $g = \{g_1, g_2, \ldots, g_{p-1}\}$ with $g_n : \mathcal{U} \to \mathbb{R}^s_+$, and $F = \{F_0, \ldots, F_{p-1}\}$ with $F_n = F_n(\xi, g_n(\eta))$ define $|F|_0 \doteq \max_{n=1,\ldots,p} \sup_{\xi,\eta \in \mathcal{U}} |F_n(\xi, g_n(\eta))|$. For $F = F(x, g)$, we will use $\partial_1 F$ and $\partial_2 F$ to mean differentiation with respect to the first and second arguments.

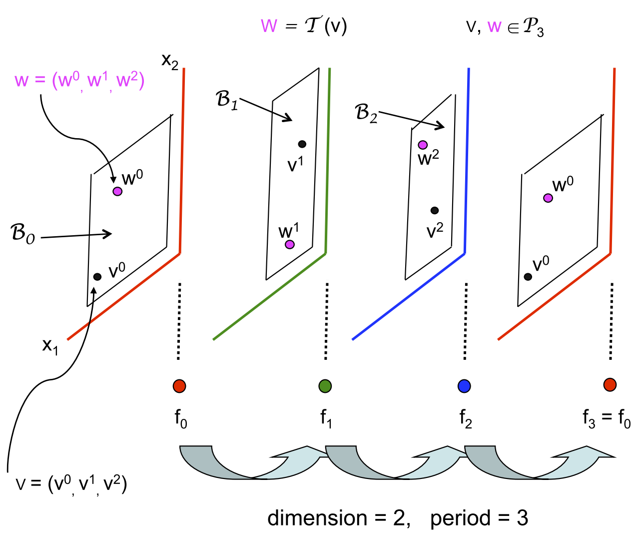


Figure 2. Mapping $\mathcal{T}$.

Referring to Equation (28), let us temporarily suppress the dependency of the $F_j$ on $g$ and define

$$H_j(x(n)) \doteq F_j(x(n), g(v(n))),$$

so that the periodic solution (30) satisfies $w^{n+1} = H_n(w^n)$, where $n$ is understood 'mod 3'. Then we see that the first element $w^0$ of the periodic solution (30) is a fixed point of the composite map,

$$w^0 = H_2 \circ H_1 \circ H_0(w^0). \tag{31}$$

In computing the derivative with respect to $v$, we need the following estimates:

$$\begin{aligned} D_v w^{n+1}(v) &= D_v H_n(w^n(v)) = D_v F_n(w^n(v), g(v)) \\ &= \partial_1 F_n(w^n(v), g(v)) D_v w^n(v) + \partial_2 F_n(\cdots) D_v g(v) \\ &= \Delta_n D_v w^n(v) + h_n, \end{aligned}$$

where

$$|h_n| \leq \sup_v |\partial_2 F_n(w^n(v), g(v)) g'(v)| = \mathcal{O}(|\partial_2 F g'|_0),$$

and

$$\Delta_n \doteq \partial_1 F_n(w^n(v), g(v)).$$

Thus, from Equation (31), and recalling that we are taking the period $p = 3$ for simplicity of presentation,

$$\begin{aligned} D_v w^0(v) &= \Delta_2 \Delta_1 \Delta_0 D_v w^0(v) + \mathcal{O}(|\partial_2 F\ g'|_0) \\ &= \Delta^* D_v w^0(v) + \mathcal{O}(|\partial_2 F\ g'|_0), \end{aligned} \tag{32}$$

where

$$\Delta^* \doteq \Delta_2 \Delta_1 \Delta_0.$$

From the *exponential* asymptotic stability of $w^0(v)$ as a periodic solution of the difference equation (28), one has

$$\sigma(\Delta^*) \subset \{z \in \mathbb{C} : |z| \leq \alpha < 1\}.$$

Thus $(I - \Delta^*)$ has a bounded inverse and from Equation (32),

$$D_v w^0(v) = (I - \Delta^*)^{-1} \mathcal{O}(|\partial_2 F\ g'|_0). \tag{33}$$

Next we define a norm in $\mathcal{P}_3$ to be

$$\|v\| \doteq \max\,(|v^0|, |v^1|, |v^2|).$$

Then it follows from Equation (33) that for $\delta \in (0, 1)$ and $|\partial_2 F\ g'|_0$ sufficiently small,

$$|D_v w^0(v)| \leq \delta,$$

and from the mean-value estimate,

$$|w^0(\xi) - w^0(\eta)| \leq \sup_{t \in [0,1]} |D_v w^0(v_t)| \|\xi - \eta\| \leq \delta \|\xi - \eta\|, \quad v_t = t\eta + (1-t)\xi,$$

for any pair $\xi, \eta \in \mathcal{P}_3$ and $t \in [0, 1]$. Therefore,

$$\|w(\xi) - w(\eta)\| \leq \delta \|\xi - \eta\|, \quad \text{i.e.} \quad \|\mathcal{T}(\xi) - \mathcal{T}(\eta)\| \leq \delta \|\xi - \eta\|,$$

and $\mathcal{T}$ is a contraction. Thus, $\mathcal{T}$ has a unique fixed point in $v^* \in \mathcal{P}_3$. Being fixed under the action of $\mathcal{T}$ means that when $v^*$ is inserted into Equation (28) in place of $v$, this equation has $v^*$ as its asymptotically stable three periodic solution, i.e. $v^*$ is the asymptotically stable three periodic solution of Equation (27).

The global asymptotic stability follows by the argument given in [14]. Thus, we have established the following theorem.

THEOREM 4.3 *Consider the p-periodic, d-dimensional system* (21) *which we repeat:* $x(n+1) = f_n(x(n))$ *where*

$$f_n(x) = \frac{\mu_n K_n x}{K_n + (\mu_n - I + C_n^0)x}, \quad x \in \mathbb{R}_+^d \tag{34}$$

*and assume* $\mu_{i,n} > 1, i = 1, 2, \ldots, d$ *and all the 'n' subscripts are understood* 'mod $p$'*. Then if the coupling is sufficiently weak,* $\|C_n^0\| \ll 1$, *Equation* (34) *has a strictly positive, asymptotically stable p-periodic solution*

$$v^* = \{\hat{x}(0), \hat{x}(1), \ldots\}, \quad \hat{x}(n+p) = \hat{x}(n).$$

*Further,* $v^*$ *is globally attracting with respect to initial conditions* $x(0) > 0$.

## 5. Large inter-specific competition: numerical examples

In the previous sections, we considered the result of small inter-specific competition, i.e. small coupling $C^0$ in Equation (7) or Equation (34) in the periodic case. No species was driven to extinction and a coexistence state was established that attracted all initial states starting in the positive cone $\mathcal{C}^0$ defined in Equation (8).

We now consider, in dimension 4, the effect of strong competition against species number one, $x_1$, with inherent growth rates approximately equal in Section 5.1. Then, in Section 5.2, we increase the inherent growth rate for $x_1$ and note the rather large increase in competition against $x_1$ needed to achieve the same decay rate to extinction as in case 1. In Section 5.3, we consider the case of equal competition and equal inherent growth rates and see that the individual carrying capacities determine the species that goes extinct.

As a point of reference, let us consider an example of *small competition* with

$$C^0 = \frac{1}{100}\begin{bmatrix} 0 & 1 & 3 & 1 \\ 4 & 0 & 1 & 1 \\ 3 & 2 & 0 & 3 \\ 2 & 1 & 3 & 0 \end{bmatrix}, \tag{35}$$

$$K = \begin{bmatrix} 2 & 2.5 & 3 & 3.5 \end{bmatrix} \quad \text{and} \quad \mu = \begin{bmatrix} 1.3 & 1.4 & 1.5 & 1.6 \end{bmatrix}. \tag{36}$$

Numerically, we find the attractive fixed point to be (Figure 3),

$$x_{\text{fix}} \approx [1.56 \;\; 2.20 \;\; 2.62 \;\; 3.28].$$

### 5.1. *Inherent growth rates approximately equal*

We now consider the example in Equations (35) and (36) in which the inherent growth rates of all species are approximately equal and increase the competition against species one to $C(\text{row}1) = 4.45\, C^0(\text{row}1)$. The attractive fixed point is now (Figure 4),

$$x_{\text{fix}} \approx [0 \;\; 2.35 \;\; 2.71 \;\; 3.33].$$

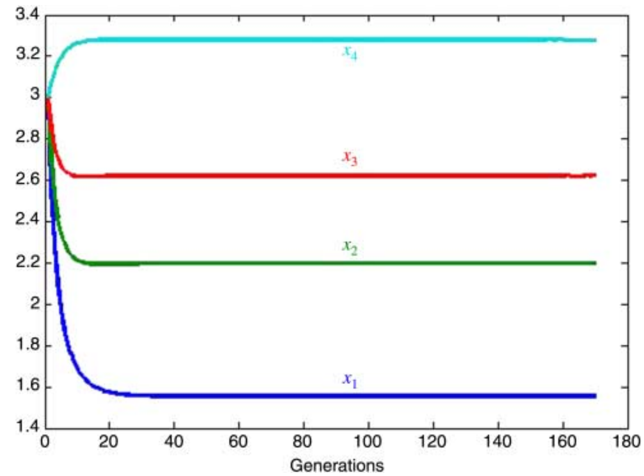


Figure 3. Coexistence.

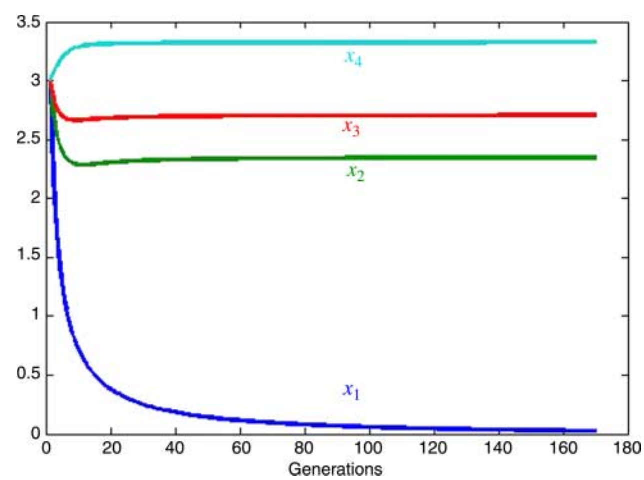


Figure 4. Large competition against species 1.



Specifically,

$$x_1 < 2.4 \times 10^{-4} \quad \text{after 1000 generations ,}$$
$$x_1 < 2.8 \times 10^{-8} \quad \text{after 2700 generations ,}$$
$$x_1 < 2.6 \times 10^{-12} \quad \text{after 4450 generations .}$$

By increasing the competition against species 1 just 1.1% to $C(\text{row } 1) = 5\,C^0(\text{row } 1)$, the attractive fixed point remains unchanged to the accuracy shown, but species $x_1$ approaches extinction much faster, *viz.*

$$x_1 < 2.9 \times 10^{-14} \quad \text{after just 883 generations.}$$

### 5.2. *One dominant inherent growth rate*

We now consider the example in Equations (35) and (36) except that now we take the inherent growth rate of species 1 to be 1.77 times that given in Equation (36). Thus, let

$$\mu = [2.3 \ \ 1.4 \ \ 1.5 \ \ 1.6],$$

the attractive fixed point then becomes

$$x_{\text{fix}} \approx [1.90 \ \ 2.16 \ \ 2.60 \ \ 3.27].$$

For $C(\text{row } 1) = 19\, C^0(\text{row } 1)$, the attractive fixed point is

$$\begin{aligned} x_{\text{fix}} &\approx [0 \ \ 2.35 \ \ 2.71 \ \ 3.33] \\ x_1 &< 1.9 \times 10^{-4} \quad \text{after 1000 generations,} \\ x_1 &< 2.1 \times 10^{-8} \quad \text{after 3000 generations,} \\ x_1 &< 2.4 \times 10^{-12} \quad \text{after 5000 generations.} \end{aligned}$$

Thus, by increasing the inherent growth rate of species one from 1.3 to 2.3, a factor of 1.77, the competition against species one must be increased by a factor of 4.3 *for all three competing species* in order to achieve the same asymptotic rate to extinction.

By increasing the competition against species one by approximately 5.3% to $C(\text{row } 1) = 20\, C^0(\text{row } 1)$, the attractive fixed point remains unchanged to the accuracy shown, but species $x_1$ approaches extinction much faster, *viz.*

$$x_1 < 2.9 \times 10^{-14} \quad \text{after just 857 generations.}$$

Thus, increasing the competition by a factor only 5.3%, we see a much larger decay to extinction by species one.

### 5.3. *Equal but large competition*

Here we consider the case in which all the competition is equal and the inherent growth rates are equal. As a point of reference, consider the small competition case where in Equation (3),

$$C^0 = \frac{1}{100}\begin{bmatrix} 0 & 1 & 1 & 1 \\ 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 1 \\ 1 & 1 & 1 & 0 \end{bmatrix},$$

$$K = [2\ 2.5\ 3\ 3.5] \quad \text{and} \quad \mu = [1.6\ 1.6\ 1.6\ 1.6].$$

The attractive fixed point is

$$x_{\text{fix}} \approx [1.82\ 2.33\ 2.84\ 5.38].$$

Replacing $C^0$ by $C = 20C^0$, it is no surprise that the individual carrying capacities $K$, the only parameters left that are not at parity with one another, determine the ordering of the coordinates of the fixed point

$$x_{\text{fix}} \approx [0\ 0.45\ 1.20\ 4.95],$$

see Figure 5.

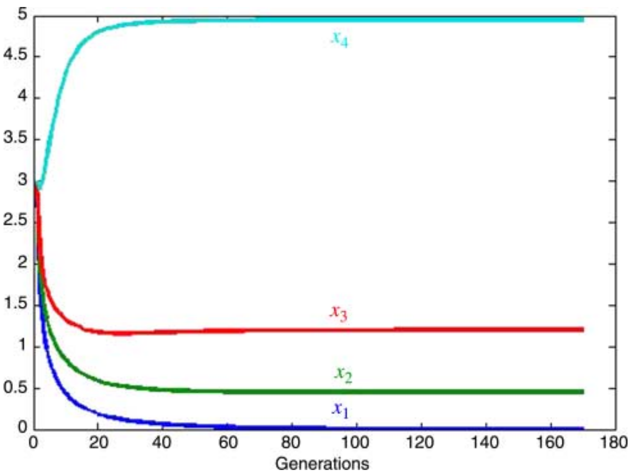


Figure 5. Extinction determined by carrying capacities.

## 6. Conclusions

We have studied $d$ species interacting in a $p$-periodic environment and modeled by a $d$-dimensional system of Leslie–Gower-type equations (coupled Beverton–Holt equations). It is shown that if the interspecific competition (coupling) is sufficiently small and the inherent growth rate of each species is such that in the absence of competition each species will grow to its (positive) individual carrying capacity, then there is a positive asymptotically stable $p$-periodic state that globally attracts all positive initial states, i.e. coexistence.

We also study three cases of large competition, all of which lead to competitive exclusion with species one, $x_1$ going extinct. In the first, we let the competition be unbalanced and discriminating against $x_1$ with inherent growth rates approximately equal. In case 2, we increase the inherent growth rate for $x_1$ by a factor of 1.77 and see that the competition against $x_1$ must be increased by a factor of 4.3 in order to obtain the same rate of decay to extinction as in case 1. In case 3, we set all the competition equal and large and all the inherent growth rates equal and see that the ordering of the size of the species at equilibrium is the same as that of the individual carrying capacities, with the species having the least carrying capacity, $x_1$, going extinct.

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