RESEARCH ARTICLE

Coexistence and extinction in a competitive exclusion Leslie/Gower model with harvesting and stocking

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Dedicated to Professor Saber Elaydi on the occasion of his 65th Birthday.

The principle of competitive exclusion states that when the competition between species is sufficiently strong, only the dominant species survives. In this paper, we examine the strategies of using stocking and harvesting to prevent the extinction of the weak species in a competitive exclusion environment. We find that in a system governed by the Leslie/Gower model careful stocking will ensure the coexistence between all species. We also find that constant harvesting of the dominant species may guarantee the survival of the weaker species when the parameters of the model are in a certain range. Mixed strategies and conditional harvesting strategies are also discussed.

Keywords: Competitive exclusion; Leslie/Gower model; Stocking; Harvesting; Coexistence; Extinction

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1. Introduction

When several species compete for the same limited resource, it is likely that some or all of the species can be driven to extinction due to direct confrontation and resource exploitation. The principle of competitive exclusion (PCE) asserts that when there is strong competition between the species, at most one species can survive. In particular, when one species in some way dominates the others, coexistence is not possible. Competitive exclusion is well supported both experimentally and theoretically. In fact, laboratory experiments on yeast and protozoa [19], flour beetles [28–30] and actual observations on the populations of tropical stream fishes [39] are all in total accord with the PCE. On the other hand, both continuous-time Lotka-Volterra models [2] and discrete-time models [1, 17], as well as chemostat models [35] have validated PCE under reasonable assumptions about model parameters.

Exterior intervention (human or other) can actually change the fate of the “doomed to be extinct” species in two possible ways. The first is the constant re-introduction of the weaker species to guarantee their survival, and the second is the weakening of the fittest population through harvesting in order to increase the chances of survival of the weak species. In fact, stocking and harvesting have long

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been recognized as means of exploiting and managing natural resources, and have been used to prevent the extinction of species and enhance their survival. A recent example is the restoration of lake trout *Salvelinus namaycush* in Parry Sound of Lake Huron by controlling sea lampreys *Petromyzon marinus* and stocking yearling lake trout [32]. Harvesting is usually viewed as a conventional way of population management with acceptable costs. However, stocking (also referred to as feeding and planting) is considered as a management tool only in situations when species are threatened. While stocking is not a panacea for problems of species extinction, it can be viewed as a positive step in the sense that it is one of the ways man can give back to nature. Cost and efficiency aside, one would argue that putting a certain amount of effort into stocking fish into a river is more acceptable than putting the same amount of effort into controlling fisheries. When compared with other conventional methods, stocking is definitely one of the most expensive management tools. However, it is a necessary step to take when other methods fail, or when the fruits of other strategies are in process. Stocking lobsters for example has been shown to be an effective strategy in the U.K. [14] where released juveniles have been shown to reach market size and estimates of their survival are high. We should also add that stocking is not necessarily a human intervention. In fact, the spreading of plant seeds by migrating birds could be viewed as nature's way of stocking plant species.

Harvesting strategies and optimal harvesting in population models have been the focus of several papers [3, 5, 7, 8, 21, 22, 27, 36, 37]. The effect of harvesting and stocking has also been studied by many authors. For example, in a series of papers, Brauer and Soudack have studied the effect of harvesting and stocking of either species in predator-prey models [9–13]. Yakubu [38] studied the effect of stocking (planting) and harvesting in a two dimensional competitive exclusion system of the form

$$x_1(n+1) = x_1(n)g_1(x_1(n) + x_2(n)) , \quad x_2(n+1) = x_2(n)g_2(x_1(n) + x_2(n)) \quad (1.1)$$

with decreasing smooth density dependent growth functions g_i . He found that a stable coexistence between the two competing species is possible as long as the constant stocking rate is not high. If the stocking rate is too high, then not only will the endangered species recover but it will ultimately exclude the previously dominant species. A similar reversal of exclusion occurs if the dominant species is harvested too aggressively [38]. Selgrade and Roberds [34] studied the destabilization of period-doubling bifurcations using constant stocking or harvesting. Periodic harvesting has also been shown to have a destabilizing effect in the Ricker model [15].

The main objective of this paper is to study the effect of harvesting and/or stocking in a competitive exclusion environment made of n species. Specifically, we will study a modified version of the Leslie/Gower of the form

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + \sum_{j=1}^n c_{ij} x_j(t)} + h_i, \quad i = 1, \dots, n \quad t = 0, 1, 2, \dots \quad (1.2)$$

where x_i is the population of the i^{th} species, b_i, c_{ij} are positive constant coefficients and h_i are constant real numbers representing the outside intervention in the system.

When $\sum_{j=1}^n |h_i| = \sum_{i=1}^n \sum_{j \neq i} |c_{ij}| = 0$, the system of equations (1.2) reduces to

a system of uncoupled Beverton-Holt equations [6], namely

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + c_{ii} x_i(t)}, \quad i = 1, \dots, n. \quad (1.3)$$

If $\sum_{i=1}^n \sum_{j \neq i} |c_{ij}| = 0$, then no coupling is present in the system, and (1.2) reduces to a system of uncoupled Riccati equations of the form

$$x_i(t+1) = \frac{\alpha_i + \beta_i x_i(t)}{1 + \gamma_i x_i(t)}, \quad i = 1, \dots, n \quad (1.4)$$

where $\alpha_i = h_i$, $\beta_i = b_i + h_i c_{ii}$ and $\gamma_i = c_{ii}$. The Leslie/Gower model [26]

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + \sum_{j=1}^n c_{ij} x_j(t)}, \quad i = 1, \dots, n \quad (1.5)$$

appears when $\sum_{j=1}^n |h_j| = 0$. The dynamics of system (1.5) when $n = 2$ was studied in [17, 18] where it was shown that under some assumptions on the parameters c_{ij} , the model supports competitive exclusion, i.e., only the dominant species survives. Ackleh et al. [1] also studied a special case of system (1.5) where the PCE was also well supported.

The rest of this paper is organized as follows: In Section 2, we present results about a special system of rational difference equations that all share the same denominator. This system which serves as a simplified Leslie/Gower model does support PCE and is studied in detail in Section 3 under constant stocking and harvesting. In Section 4, we first show that a general Leslie/Gower model can have very rich dynamics and prove that in the case of competitive exclusion, careful stocking is a viable strategy to guarantee coexistence between all species. The effect of harvesting on a 2-specie model is studied in Section 5. Finally, a discussion and some closing remarks are given in Section 6.

2. A system of linear rational difference equations

Rational difference equations have been the focus of many studies in the last few years due to their rich and complex dynamics. The monographs [23, 24] and [25] offer an excellent reference on results, open problems and conjectures about the global behavior of rational difference equations. Systems of rational difference equations have also received some attention, see for instance [1, 16–18, 20].

In this section, we consider the system of linear rational difference equations of the form

$$y_i(t+1) = \frac{\alpha_i + \sum_{j=1}^n \beta_{ij} y_j(t)}{\gamma + \sum_{j=1}^n \delta_j y_j(t)}, \quad i = 1, 2, \dots, n. \quad (2.1)$$

System (2.1) has been studied by Bajo and Liz [4] who focused on the global periodicity of such rational maps in both $\mathbb{R}^n$ and $\mathbb{C}^n$. System (2.1) can be written in matrix form as

$$\lambda(t)Y(t+1) = AY(t), \quad (2.2)$$

where $Y(t) = [1, y_1(t), \dots, y_n(t)]^T$ and

$$A = \begin{bmatrix} \gamma & \delta_1 & \delta_2 & \dots & \delta_n \\ \alpha_1 & \beta_{11} & \beta_{12} & \dots & \beta_{1n} \\ \alpha_2 & \beta_{21} & & & \beta_{2n} \\ \vdots & & & & \vdots \\ \alpha_n & \beta_{n1} & \dots & \dots & \beta_{nn} \end{bmatrix}. \quad (2.3)$$

Obviously,

$$\lambda(t) = \gamma + \sum_{j=1}^n \delta_j y_j(t).$$

A simple induction argument shows that

$$Y(t) = \frac{1}{\lambda(t)\lambda(t-1)\dots\lambda(1)} A^t Y(0), \quad \text{for all } t \geq 1, \quad (2.4)$$

provided the product $\lambda(t)\lambda(t-1)\dots\lambda(1) \neq 0$. But interestingly, one need not know the values of $\lambda(s)$, for all $1 \leq s \leq t$ in order to compute the vector $Y(t)$. In fact, it suffices to compute the vector $A^t Y(0)$ and then norm it so that its first component equals 1. In the sequel of this section, we will refer to $y(t)$ as a solution of System (2.1) if $y(t)$ is defined for all $t \geq 0$.

PROPOSITION 2.1.

- (1) $(y_1^*, y_2^*, \dots, y_n^*)$ is a fixed point of (2.1) if and only if the vector $(1, y_1^*, y_2^*, \dots, y_n^*)$ is an eigenvector of the matrix A with a nonzero corresponding eigenvalue.
- (2) System (2.1) has a periodic solution $(y_1^*, y_2^*, \dots, y_n^*)$ of prime period p if and only if the vector $(1, y_1^*, y_2^*, \dots, y_n^*)^T$ is an eigenvector of the matrix A^p and is not an eigenvector of any matrix A^m for any $1 \leq m \leq p-1$.
- (3) All solutions of (2.1) are periodic if and only if there exists a constant k and an integer m such that $A^m = kI_{n+1}$, where I_{n+1} is the identity matrix on $\mathbb{R}^{n+1}$.
- (4) If A is diagonalizable with eigenvalues $|\mu_1| > |\mu_2| \geq |\mu_3| \geq \dots \geq |\mu_n|$, and corresponding eigenvectors $V_1 = (1, y_1^*, y_2^*, \dots, y_n^*)$, $V_2, \dots, V_n$ and if $(1, y_1(0), y_2(0), \dots, y_n(0)) \cdot V_1 \neq 0$, then

$$\lim_{t \rightarrow \infty} (y_1(t), y_2(t), \dots, y_n(t)) = (y_1^*, y_2^*, \dots, y_n^*).$$

Proof. To prove parts (1), (2) and (3) notice that if

$$A^p [1, y_1(t), \dots, y_n(t)]^T = \lambda [1, y_1(t), \dots, y_n(t)]^T \quad \text{and } \lambda \neq 0,$$

then

$$[y_1(t+p), \dots, y_n(t+p)]^T = [y_1(t), \dots, y_n(t)]^T.$$

To prove (4), it suffices to notice that if

$$Y(0) = [1, y_1(0), y_2(0), \dots, y_n(0)]^T = \sum_{i=1}^n a_i V_i$$

and $a_i \neq 0$, then $A^t Y(0) = a_1 \mu_1^t V_1 + a_2 \mu_2^t V_2 + \dots + a_n \mu_n^t V_n$. Since $|\mu_1| > |\mu_2|$, then

$$\lim_{t \rightarrow \infty} \frac{Y(t)}{\|Y(t)\|_2} = V_1.$$

□

3. A simplified Leslie/Gower model

The system we study in this section is a simple Leslie/Gower model that does not allow co-existence between different species, and forces all but one of the species to be extinct. Consider the system

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + \sum_{j=1}^n c_j x_j(t)}, \quad i = 1, \dots, n \quad (3.1)$$

where $b_1 > b_2 > b_3 > \dots > b_n > 0$ and $c_i > 0$. Notice that all equations in (3.1) share the same denominator. While this restriction might seem strong, it can be justified by the assumption that the maximum growth coefficients b_i of each population are equally affected (inversionally proportional) by a weighted sum of the individual populations. The rationale behind weighting each populations differently is that the carrying capacity of an environment varies with the species that it is hosting. System (3.1) has exactly $n+1$ fixed points, namely:

$$\begin{aligned} E_0 : x_i &= 0 \quad \text{for all } i = 1, \dots, n, \\ E_i : x_i &= \frac{b_i - 1}{c_i}, x_j = 0 \text{ for all } j \neq i. \end{aligned}$$

PROPOSITION 3.1. Assume that $x_i(0) > 0$ for all $i = 1, \dots, n$.

- (i) If $b_1 < 1$, then $\lim_{t \rightarrow \infty} x_i(t) = 0$ for all $i = 1, \dots, n$.
- (ii) If $b_1 > 1$, then $\lim_{t \rightarrow \infty} x_i(t) = 0$ for all $i = 2, \dots, n$, and $\lim_{t \rightarrow \infty} x_1(t) = \frac{b_1 - 1}{c_1}$.

Proof. System (3.1) is a special case of (2.1) with the corresponding matrix

$$A = \begin{bmatrix} 1 & c_1 & c_2 & \dots & c_n \\ 0 & b_1 & 0 & \dots & 0 \\ 0 & 0 & b_2 & \dots & 0 \\ \vdots & & \ddots & & \\ 0 & 0 & \dots & 0 & b_n \end{bmatrix}.$$

Part (i) of the proposition becomes trivial, and part (ii) follows from the fact that b_1 is the largest eigenvalue of the matrix A with the corresponding eigenvector

$$\left(1, \frac{b_1 - 1}{c_1}, 0, \dots, 0\right).$$

□

Cushing et al. [17] studied the two-population Leslie/Gower system

$$x_{t+1} = \frac{b_1 x_t}{1 + x_t + c_1 y_t} \quad y_{t+1} = \frac{b_2 y_t}{1 + c_2 x_t + y_t}, \quad (3.2)$$

and proved that if the lines $L_1 : x + c_1y = b_1 - 1$ and $L_2 : c_2x + y = b_2 - 1$ do not intersect in the first quadrant and L_1 lies above L_2 in the first quadrant, then E_1 is globally asymptotically stable in $\mathbb{R}_+^2$. For the two dimensional version of system (3.1) with $b_1 > b_2 > 1$, the two lines are actually parallel. Ackleh et al., [1] also considered the Beverton-Holt competition model described by the system of equations

$$x_i(t+1) = \frac{a_i x_i}{1 + b_i \sum_{j=1}^n x_j}, \quad i = 1, \dots, n \quad (3.3)$$

where $a_i \geq 1$ for all $i = 1, \dots, n$. System (3.3) is similar to (3.1) in the sense that it does not allow for the coexistence between species. In fact, the only fixed points of (3.3) are the equilibria $E_0 = (0, 0, \dots, 0)$, $E_1 = (\frac{a_1-1}{b_1}, 0, \dots, 0)$, $E_2 = (0, \frac{a_2-1}{b_2}, 0, \dots, 0)$, $\dots$ and $E_n = (0, \dots, 0, \frac{a_n-1}{b_n})$. If one also assumes that

$$\frac{a_1 - 1}{b_1} = \max_{i=1, \dots, n} \frac{a_i - 1}{b_i},$$

then E_1 (conjectured to be globally asymptotically stable) is the only asymptotically stable fixed point [1].

Since system (3.1) does not allow co-existence between species, we introduce an outside intervention in an attempt to yield the survival of all species. As we mention in the introduction, the outside intervention can be achieved either by replenishing the population of the weaker species or by harvesting or weeding out the stronger species. Let h_i be the outside intervention on the i^{th} species, the new system of equations becomes

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + \sum_{j=1}^n c_j x_j(t)} + h_i, \quad i = 1, \dots, n. \quad (3.4)$$

Notice that h_i can be either positive or negative depending on the outside intervention. Let λ be the dominant eigenvalue of the matrix

$$A = \begin{bmatrix} 1 & c_1 & c_2 & \dots & c_n \\ h_1 & b_1 + h_1 c_1 & h_1 c_2 & \dots & h_1 c_n \\ h_2 & h_2 c_1 & b_2 + h_2 c_2 & \dots & h_2 c_n \\ \vdots & & \ddots & & \\ h_n & h_n c_1 & h_n c_2 & \dots & b_n + h_n c_n \end{bmatrix}$$

and $(1, X^*)^T = (1, x_1^*, x_2^*, \dots, x_n^*)^T$ be its corresponding eigenvector. The strong ergodicity theorem asserts that generically, all initial conditions (except for a set of measure zero) will converge to $(1, X^*)^T$. In particular, we are led to the system of equations

$$\begin{cases} 1 + \sum_{i=1}^n c_i x_i^* = \lambda \\ b_i x_i^* + \lambda h_i = \lambda x_i^* \quad i = 1, \dots, n. \end{cases} \quad (3.5)$$

For the remaining of this paper we will assume that $b_i > 1$ for all $i = 1, 2, \dots, n$) indicating that in absence of competition all species can survive on their own.

3.1 The effect of stocking

When $h_i \geq 0$ for all $i = 1 \dots n$, the matrix A is non-negative. The Perron-Frobenius theorem and the strong ergodicity theorem assert that the leading eigenvalue of the matrix A must be non-negative and that almost all solutions (except for a set of measure zero) converge to the leading non-negative eigenvector.

THEOREM 3.2. *Assume that $h_i > 0$ for all $i = 2 \dots n$.*

- (1) *If $h_1 > 0$, then all species survive. In particular, there exists a value $\lambda > b_1$ and a globally asymptotically stable equilibrium point (in $\mathbb{R}_+^n$) $E_{all} = (x_1^*, x_2^*, \dots, x_n^*)$ satisfying*

$$\sum_{i=1}^n \frac{c_i h_i}{\lambda - b_i} = \frac{\lambda - 1}{\lambda}, \quad x_i^* = \frac{\lambda h_i}{\lambda - b_i} \quad i = 1, \dots, n. \quad (3.6)$$

- (2) *If $h_1 = 0$ and $\sum_{i=2}^n \frac{c_i h_i}{b_1 - b_i} < \frac{b_1 - 1}{b_1}$, then all species survive. In particular, the equilibrium point $E_{all} = (x_1^*, x_2^*, \dots, x_n^*)$ defined by*

$$\begin{cases} x_1^* = \frac{b_1 - 1}{c_1} - \frac{b_1}{c_1} \sum_{i=2}^n \frac{c_i h_i}{b_1 - b_i} \\ x_i^* = \frac{b_1 h_i}{b_1 - b_i} \end{cases} \quad i = 2, \dots, n \quad (3.7)$$

is globally asymptotically stable.

- (3) *If $h_1 = 0$ and $\sum_{i=2}^n \frac{c_i h_i}{b_1 - b_i} > \frac{b_1 - 1}{b_1}$, then there exists a value $\lambda > b_1$ such that the equilibrium point $E = (0, x_2^*, \dots, x_n^*)$ defined by*

$$x_i^* = \frac{\lambda h_i}{\lambda - b_i} \quad i = 2, \dots, n \quad (3.8)$$

is globally asymptotically stable.

Proof. If $h_1 > 0$, then using (3.5) we obtain condition (3.6). Now let f and g be the functions defined by

$$f(x) = \sum_{i=1}^n \frac{c_i h_i}{x - b_i} \quad g(x) = \frac{x - 1}{x}.$$

It is easy to check that on the interval $(b_1, +\infty)$, the function f is decreasing while the function g is increasing. Since $\lim_{x \rightarrow b_1^+} f(x) = +\infty$, $\lim_{x \rightarrow \infty} f(x) = 0$ and $\lim_{x \rightarrow \infty} g(x) = 1$, there exists a unique value λ that satisfies the conditions in (3.6). If $h_1 = 0$, then b_1 is an eigenvalue of the matrix A . Thus, either there exists a value $\lambda > b_1$ such that λ is the dominant eigenvalue or b_1 is the dominant eigenvalue. Either case is dictated by the equations in system (3.6). In fact, if b_1 is not the dominant eigenvalue, then x_1^* must be zero and we have

$$\sum_{i=2}^n \frac{c_i h_i}{\lambda - b_i} = \frac{\lambda - 1}{\lambda} > \frac{b_1 - 1}{b_1}.$$

When b_1 is the dominant eigenvalue, we obtain

$$c_1 x_1^* + b_1 \sum_{i=2}^n \frac{c_i h_i}{b_1 - b_i} = b_1 - 1,$$

which can only happen if $\sum_{i=2}^n \frac{c_i h_i}{b_1 - b_i} < \frac{b_1 - 1}{b_1}$. Finally, global stability follows from the strong ergodicity theorem. $\square$

In order to prevent the extinction of some of the species, a possible strategy is to constantly input an amount h_i for each of the species including the dominant one. Part 1 of Theorem 3.2 does predict that all species will indeed survive. In fact, in addition to the h_i members introduced at every stage, an extra population of

$$x_i^{\text{extra}} = \frac{b_i h_i}{\lambda - b_i}$$

will survive. This extra population grows with b_i and is proportional to h_i , which is totally in line with Yakubu's finding in the case of two populations where the extra-population after stocking a quantity h for the first species in system (1.1) is given by $hg_1(x_1 + x_2)/(1 - g_1(x_1 + x_2))$ [38].

A second possible strategy, is to stock only the weaker species since in principle the dominant species would need no help. Part 2 of Theorem 3.2 shows that this is an acceptable strategy as long as the sum of the weighted inputs does not exceed a certain threshold. Above this threshold, the previously dominant population will be driven to extinction.

We end this section by noting that if $(x_1^*, x_2^*, \dots, x_n^*)$ is a desirable steady state to achieve, then it is obtainable if $\sum_{i=1}^n c_i x_i^* > b_1 - 1$. Indeed, $(x_1^*, x_2^*, \dots, x_n^*)$ is reachable by taking

$$h_i = \frac{x_i^*(1 - b_1 + \sum_{i=1}^n c_i x_i^*)}{1 + \sum_{i=1}^n c_i x_i^*} \quad i = 1, 2, \dots, n.$$

3.2 The effect of harvesting

One might think that a possible way to prevent the weaker species from going extinct is to constantly harvest the dominant species. The purpose of this subsection is to show that this is not a viable strategy for system (3.1).

When we introduce harvesting of the dominant species $h_1 < 0$, the matrix A ceases to be non-negative and the existence of a dominant positive eigenvalue with a corresponding positive eigenvector is not guaranteed any more. Moreover, one has to worry in considering such a strategy that the populations $x_i(t)$ do not become extinct and more care should be given to the initial conditions and the basin of attraction of possible attractive fixed points.

In the absence of competition, the maximum harvesting allowed on the first species without forcing it to extinction is $H_{\max} = \frac{(\sqrt{b_1} - 1)^2}{c_1}$ [3]. Accordingly, let $0 < h = -h_1 < H_{\max}$ be the amount of harvesting for the first species. The

dominant eigenvalue of the matrix

$$A = \begin{bmatrix} 1 & c_1 & c_2 & c_3 & \dots & c_n \\ -h & b_1 - c_1 h & -c_2 h & -c_3 h & \dots & -c_n h \\ 0 & 0 & b_2 & 0 & \dots & 0 \\ 0 & 0 & 0 & b_3 & \ddots & 0 \\ \vdots & & & & \ddots & \ddots \\ 0 & 0 & 0 & & \dots & b_n \end{bmatrix}$$

is the maximum of $\tilde{\lambda} = (b_1 + 1 - hc_1 + \sqrt{(b_1 + 1 - hc_1)^2 - 4b_1})/2$ and b_2 . In fact, when

$$h \leq h_{\max} = \frac{(b_1 - b_2)(b_2 - 1)}{b_2 c_1}, \quad (3.9)$$

the dominant eigenvalue is $\tilde{\lambda}$ and its corresponding eigenvector is

$$\left[1, \tilde{\lambda} - 1, 0, \dots, 0\right]^T.$$

On the other hand, when $h > h_{\max}$, b_2 is the dominant eigenvalue and the dominant eigenvector is

$$\left[1, \frac{hb_2}{b_1 - b_2}, \frac{c_1 b_2 (h_{\max} - h)}{c_2 (b_1 - b_2)}, 0, \dots, 0\right]^T$$

whose third component is clearly negative. Of course, converging to a negative population indicates that some population goes extinct in finite time. In fact, when all initial populations are positive the dominant species will go extinct and the second species will be the only surviving species. These results are summarized in the following theorem.

THEOREM 3.3. *Assume that $x_2(0) > 0$ and let $h_{\max}$ be as defined in (3.9).*

(i) *If $h \leq h_{\max}$, and the initial population $x_1(0)$ is sufficiently large, then*

$$\begin{aligned} \lim_{t \rightarrow \infty} x_1(t) &= \frac{b_1 - 1 - hc_1 + \sqrt{(b_1 + 1 - hc_1)^2 - 4b_1}}{2} \quad \text{and} \\ \lim_{t \rightarrow \infty} x_i(t) &= 0 \quad \text{for all } i = 2, \dots, n. \end{aligned} \quad (3.10)$$

(ii) *If $h > h_{\max}$, then*

$$\lim_{t \rightarrow \infty} x_2(t) = \frac{b_2 - 1}{c_2} \quad \text{and} \quad \lim_{t \rightarrow \infty} x_i(t) = 0 \quad \text{for all } i \neq 2. \quad (3.11)$$

In light of this section, one can see that the only way to guarantee the coexistence of all species is to constantly introduce all species into the system, or carefully introduce the weaker species without causing the dominating species to perish.

3.3 Harvesting and stocking

In this subsection, we study the possibility of imposing co-existence by harvesting the dominant species and constantly introducing a fixed amount of every other species to guarantee its survival. Since $h_1 = -h < 0$, and $h_i > 0$ for all $i = 2, \dots, n$, the system of equations (3.5) yields that

$$x_1^* = \frac{\lambda h}{b_1 - \lambda}, \quad x_i^* = \frac{\lambda h_i}{\lambda - b_i} \quad i = 2, \dots, n, \quad (3.12)$$

and

$$\frac{c_1 h}{b_1 - \lambda} + \sum_{i=2}^n \frac{c_i h_i}{\lambda - b_i} = \frac{\lambda - 1}{\lambda}. \quad (3.13)$$

Equations (3.12) indicate that to obtain co-existence, the dominant eigenvalue λ must be in the open interval (b_2, b_1) . However, the existence of such a value λ that satisfies (3.13) is not always possible. Let

$$f(\lambda) = \frac{c_1 h}{b_1 - \lambda} + \frac{c_2 h_2}{\lambda - b_2} + \frac{c_3 h_3}{\lambda - b_3} + \dots + \frac{c_n h_n}{\lambda - b_n},$$

$g(\lambda) = (\lambda - 1)/\lambda$, and consider the following facts about both functions in the interval (b_2, b_1) .

- a) f is positive in the interval (b_2, b_1) .
- b) $\lim_{\lambda \rightarrow b_2^+} f(\lambda) = \lim_{\lambda \rightarrow b_1^-} f(\lambda) = +\infty$.
- c) f has a minimum in the interval (b_2, b_1) .
- d) g is strictly increasing in the interval (b_2, b_1) and $g(\lambda) \in (\frac{b_2-1}{b_2}, \frac{b_1-1}{b_1})$.

Obviously, if

$$\min_{\lambda \in (b_2, b_1)} f(\lambda) < \frac{b_2 - 1}{b_2},$$

then there exists two values $\lambda_1 < \lambda_2$ in the interval (b_2, b_1) and both satisfying equation (3.13). In this case, λ_2 is the desired dominant eigenvalue. But if

$$\min_{\lambda \in (b_2, b_1)} f(\lambda) > \frac{b_1 - 1}{b_1},$$

then no value of $\lambda \in (b_2, b_1)$ will satisfy equation (3.13). Whether or not the graphs of f and g intersect in the interval (b_2, b_1) depends on the values of h , h_2 , ... and h_n . In fact, sufficiently small values of h and h_i allow f and g to intersect in the interval (b_2, b_1) . But large values of either of the h_i are prohibitive.

The next proposition gives a sufficient condition for achieving co-existence between the species by having $f(\frac{b_1 + b_2}{2}) < g(\frac{b_1 + b_2}{2})$.

PROPOSITION 3.4. *If $h_1 < 0$, $h_i > 0$ for all $i = 2, \dots, n$ and*

$$\sum_{i=1}^n \frac{c_i h_i}{b_1 + b_2 - 2b_i} < \frac{b_1 + b_2 - 2}{2(b_1 + b_2)}$$

then all species survive.

3.4 Conditional harvesting

In an exploited environment, mortality is essentially due to harvesting rather than natural death. A threshold harvesting strategy or conditional harvesting can therefore play a major role in controlling the variability and fluctuations of competing populations. This strategy consists of harvesting an amount h_i from the i^{th} population whenever this population exceeds a threshold value x_i^{th} . Specifically, we write

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + \sum_{j=1}^n c_j x_j(t)} - h_i H(x_i(t) - x_i^{\text{th}}), \quad i = 1, \dots, n, \quad (3.14)$$

where $H(x)$ is the heaviside function.

Let us first understand the dynamics of a single species governed by a conditionally harvested Beverton-Holt equation of the form

$$y(t+1) = \begin{cases} \frac{b_i y(t)}{1 + c_i y(t)} & \text{If } y(t) < y_i^{\text{th}}, \\ \frac{b_i y(t)}{1 + c_i y(t)} - h_i & \text{If } y(t) \geq y_i^{\text{th}}. \end{cases} \quad (3.15)$$

In [3] we found that the only way to change the global attractor of the non-harvested system with conditional harvesting is to choose

$$y_i^{\text{th}} < \frac{b_i - 1}{c_i}. \quad (3.16)$$

In addition, if one wants to introduce cyclic behavior in the system without wiping out the species then the amount of harvesting h_i must satisfy the inequality

$$\frac{y_i^{\text{th}}(b_i - 1 - c_i y_i^{\text{th}})}{1 + c_i y_i^{\text{th}}} \leq h_i < M_i := \frac{b_i y_i^{\text{th}}}{1 + c_i y_i^{\text{th}}}. \quad (3.17)$$

In fact, one can easily show that when conditions (3.16) and (3.17) are both satisfied, and when $y(0) > 0$, then there exists t_0 such that for all $t \geq t_0$ we have

$$M_i - h_i \leq y(t) \leq M_i. \quad (3.18)$$

Let us now assume that $0 < x_i(0) \leq x_i^{\text{th}}$, and that the values of x_i^{th} and h_i in system (3.14) satisfy conditions (3.16) and (3.17). Clearly, for all $t \geq 1$ we have

$$x_i(t) \leq M_i \quad \text{for all } i = 1, \dots, n.$$

Moreover, we also have that for all $i = 1, \dots, n$

$$x_i(t) \geq \min \left(\frac{b_i x_i}{1 + \sum_{j=1}^n c_j M_j}, M_i - h_i \right), \quad \text{for all } i = 1, \dots, n.$$

In particular, for all $t \geq 1$ and for all $i = 1, \dots, n$, we have

$$\min(x_i^{\text{cond}}, M_i - h_i) \leq x_i(t) \leq M_i, \quad (3.19)$$

where x_i^{cond} is the stable fixed point of the Beverton-Holt equation

$$z_{n+1} = \frac{b_i z_n}{\left(1 + \sum_{j \neq i} c_j M_j\right) + c_i z_n}. \quad (3.20)$$

Clearly, choosing $\sum_{j \neq i} c_j M_j < b_i - 1$ guarantees that $x_i^{\text{cond}} > 0$ and thus the survival of the i^{th} species.

Figure 1. In these graphs, we consider System (3.14) with three species, where $b_1 = 4, b_2 = 3.5, b_3 = 3$ and $c_1 = c_2 = c_3 = 1$. In (a), there is no harvesting. Only species x_1 survives. In (b), we conditionally harvest species x_1 with $h_1 = 1.1$ and $x_1^{th} = 1.5$. Only species x_1 and x_2 survive. In (c), we conditionally harvest species x_1 with $h_1 = 1.2, x_1^{th} = 1.5$, and species x_2 with $h_2 = 0.8, x_2^{th} = 1.2$. All three species survive. The graphs show the last 100 iterations of 800 iterations for several initial conditions.

Figure 2. In these graphs, we consider System (3.14) with two species, where $b_1 = 4, b_2 = 2.5$ and $c_1 = c_2 = 1$. We conditionally harvest species x_1 with $h_1 = 1.2$ and $x_1^{th} = 2$. The graphs show a period 4 attractor.

THEOREM 3.5. Assume that for all $i = 1, \dots, n$, x_i^{th} and h_i satisfy conditions (3.16) and (3.17) respectively. If

$$0 < x_i(0) \leq \frac{b_i x_i^{th}}{1 + c_i x_i^{th}} \quad \text{and} \quad \sum_{j \neq i} c_j M_j < b_i - 1, \quad (3.21)$$

then the conditional harvest strategy in (3.14) will guarantee the survival of all species.

We end this section by adding a few simple yet important remarks.

1. When $n > 2$ species are present in system 3.14, the conditional harvesting of the dominant species will only guarantee the survival of species x_2 if any. In fact, as shown in Fig. 1, in order to guarantee the survival of the n^{th} species all other $n - 1$ species should be conditionally harvested.
2. Conditional harvesting can result in periodic cycles of the different populations. Naturally, the period and the stability of the periodic solutions depend on the model parameters. For example, Fig. 2 and Fig. 3 show that for the same parameters b_1, b_2, c_1, c_2 , and x_1^{th} different values of h lead to different cycles of different periods. However, as shown by the bifurcation diagram in Fig. 4 chaotic behavior is the most likely outcome for sufficiently large values of h .

Figure 3. In these graphs, we consider System (3.14) with two species, where $b_1 = 4, b_2 = 2.5$ and $c_1 = c_2 = 1$. We conditionally harvest species x_1 with $h_1 = 1.1$ and $x_1^{\text{th}} = 2$. The graphs show a period 11 attractor.

Figure 4. This graph shows the bifurcation diagram for System (3.14) with two species, where $b_1 = 4, b_2 = 3.5, c_1 = c_2 = 1$, and we conditionally harvest x_1 with $x_1^{\text{th}} = 1.7$ and h_1 varies between 0 and 1.7.

4. The general Leslie/Gower Model

Consider the Lotka-Volterra system of differential equations

$$\frac{dx_i(t)}{dt} = x_i(t) \left(A_i - \sum_{j=1}^n \alpha_{ij} x_j(t) \right), \quad i = 1, \dots, n. \quad (4.1)$$

where A_i and α_{ij} are all positive constants. By substituting $\frac{x_i(t+\delta) - x_i(t)}{\delta}$ for $\frac{dx_i(t)}{dt}$ and using a mixed implicit-explicit approximation we can write

$$\frac{x_i(t+\delta) - x_i(t)}{\delta} = A_i x_i(t) - x_i(t+h) \sum_{j=1}^n \alpha_{ij} x_j(t)$$

to obtain the set of equations

$$x_i(t+\delta) = \frac{(1 + \delta A_i) x_i(t)}{1 + \delta \sum_{j=1}^n \alpha_{ij} x_j(t)}, \quad i = 1, \dots, n.$$

Letting $\delta = 1$, $b_i = 1 + \delta A_i$ and $c_{ij} = \alpha_{ij}$, we obtain the system of difference equations

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + \sum_{j=1}^n c_{ij} x_j(t)}, \quad i = 1, \dots, n. \quad (4.2)$$

Clearly the values of $b_i > 1$ indicating that each species is able to survive on its own in the absence of competition. We can also assume without loss of generality, that $c_{ii} = 1$. The system of difference equations (4.2) is a generalization of (3.1) and actually has richer dynamics. In fact, system (4.2) allows coexistence between the species and can have up to 2^n fixed points. For example, the system

$$\begin{aligned} x_1(t+1) &= \frac{4x_1(t)}{1 + x_1(t) + x_2(t) + x_3(t)} \\ x_2(t+1) &= \frac{5x_2(t)}{1 + x_1(t) + 2x_2(t) + x_3(t)} \\ x_3(t+1) &= \frac{6x_3(t)}{1 + x_1(t) + x_2(t) + 3x_3(t)} \end{aligned} \quad (4.3)$$

has 8 fixed points, namely

$$\begin{aligned} E_0 &= (0, 0, 0) & E_1 &= (3, 0, 0) & E_2 &= (0, 4, 0) & E_3 &= (0, 0, 5) \\ E_{1,2} &= (2, 1, 0) & E_{1,3} &= (2, 0, 1) & E_{2,3} &= (0, \frac{7}{5}, \frac{6}{5}) & E_{\text{all}} &= (1, 1, 1), \end{aligned}$$

and E_{all} is locally asymptotically stable. We should note that Roeger [33] refers to system (4.2) as a May-Leonard M-L model of fractional type. Of course, different discretization schemes of (4.1) lead to several discrete models, see for example [33] and the references therein.

In what follows we denote by $E_{i_1, i_2, \dots, i_m}$ the non-negative fixed point of (4.2) for which $x_{i_1} > 0$, $x_{i_2} > 0$, ... and $x_{i_m} > 0$ while $x_j = 0$ for all $j \notin \{i_1, i_2, \dots, i_m\}$

whenever such a fixed point exists.

We now are ready to give the following result about the stability of the fixed points E_i when only a single species survives.

THEOREM 4.1. *Let $b = \min_{i=1,\dots,n} b_i$, $B = \max_{i=1,\dots,n} b_i$, $c_{\min} = \min_{i \neq j} c_{ij}$, and $c_{\max} = \max_{i \neq j} c_{ij}$. The following statements are true*

1. E_0 is a source.
2. The fixed point E_i is locally asymptotically stable if and only if

$$c_{ji} > \frac{b_j - 1}{b_i - 1} \quad \text{for all } j \neq i,$$

and is a saddle otherwise.

3. If $c_{\max} < (b - 1)/(B - 1)$, then every E_i is a saddle.
4. If $c_{\min} > (B - 1)/(b - 1)$, then every E_i is locally asymptotically stable.
5. If $b_i > b_j$ for some $i \neq j$ and for all $k = 1, \dots, n$, $c_{ik} \leq c_{jk}$, then E_j is a saddle. Moreover, if $x_i(0) \neq 0$ then $\lim_{t \rightarrow \infty} x_j(t) = 0$.
6. If there exists an index $i \leq n$ such that for all $j \neq i$

$$b_i > b_j \quad \text{and} \quad c_{ik} \leq c_{jk} \quad \text{for all } k = 1, \dots, n,$$

then E_i is globally asymptotically stable in $\mathbb{R}_+^n$.

Proof. Part 1. of the theorem is straight forward. To prove parts 2-4, consider the linearization matrix $J_k = [J_{ij}]$ about the fixed point E_k where

$$J_{ij} = \begin{cases} 0 & \text{if } i \neq j \text{ and } i \neq k \\ \frac{1}{b_k} & \text{if } i = j = k \\ -\frac{(b_k - 1)c_{kj}}{b_k} & \text{if } i = k \neq j \\ \frac{b_i}{1 + c_{ik}(b_k - 1)} & \text{if } i = j \neq k. \end{cases} \quad (4.4)$$

whose eigenvalues are $\lambda_{k1} = \frac{1}{b_k}$ and $\lambda_{kj} = \frac{b_j}{1 + c_{jk}(b_k - 1)}$ for $j \neq k$. Since $b_k > 1$, then E_k is either a saddle or a sink, depending on the values of c_{jk} . For the fixed point E_k , the condition in part 3 guarantees that the values of c_{jk} are too small and thus all of the λ_{kj} 's are greater than 1. On the other hand, the condition in part 4 has the opposite effect and makes E_k locally asymptotically stable. To prove parts 5 and 6, assume that $b_i > b_j$ for some $i \neq j$ and for all $k = 1, \dots, n$, $c_{ik} \leq c_{jk}$, then it is easy to see that

$$\frac{x_j(t+1)}{x_i(t+1)} < \frac{b_j x_j(t)}{b_i x_i(t)},$$

and thus $x_j(t)$ must converge to zero whenever $x_i(0) \neq 0$. $\square$

Theorem 4.1 asserts that it is possible that all E_i are locally asymptotically stable (LAS), indicating that depending on the initial conditions only one species can survive. Similarly, it is also possible that none of the E_i 's are LAS which

leaves co-existence between the species as the only possible outcome. This co-existence however, can actually be manifested by the existence of one or more LAS fixed points and possibly more complex dynamics. While this is worthy of further investigation, we limit our attention on imposing co-existence when it is not natural.

We now assume that there exists a LAS (possibly globally asymptotically stable GAS) fixed point in which only m species co-survive and the remaining $n - m$ species perish. Without loss of generality we can assume that this fixed point is $E_{1,2,\dots,m}$. As in the simplified Leslie/Gower model, we can choose to have a positive feeding for all species, or to limit the feeding to the weaker species that are not able to survive on their own. We start with positive feeding ($h_i \geq 0$) and consider the system

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + x_i(t) + \sum_{j \neq i} c_{ij} x_j(t)} + h_i, \quad i = 1, \dots, n. \quad (4.5)$$

The following theorem asserts that the dynamics of the general Leslie/Gower model under positive intervention is quite similar to that of the simplified model.

THEOREM 4.2. *Assume that $E_{1,2,\dots,m}$ is either LAS or GAS.*

1) *If $h_i > 0$ for all $i = 1, \dots, n$, then all species survive and for all $i = 1, \dots, n$,*

$$h_i \leq x_i(t) \leq b_i + h_i.$$

2) *If $h_i = 0$ for all $i = 1, \dots, m$, $h_i > 0$ for all $m+1 \leq i \leq n$ and*

$$\sum_{j \neq i} c_{ij}(b_j + h_j) < b_i - 1 \quad \text{for all } 1 \leq i \leq m,$$

then co-existence is possible.

3) *If $h_i = 0$ for all $i = 1, \dots, m$, $h_i > 0$ for all $m+1 \leq i \leq n$ and*

$$\sum_{j=m+1}^n c_{ij} h_j > b_i - 1 \quad \text{for some } 1 \leq i \leq m$$

then co-existence is not possible.

Proof. The first part of the theorem is straightforward. Assume now that $h_i = 0$ for all $i = 1, \dots, m$, and $h_i > 0$ for all $m+1 \leq i \leq n$, then we can easily establish that

$$\frac{b_i x_i(t)}{1 + x_i(t) + \sum_{j \neq i} c_{ij}(b_j + h_j)} < x_i(t+1) < \frac{b_i x_i(t)}{1 + x_i(t) + \sum_{j > m} c_{ij} h_j}$$

for all $1 \leq i \leq m$. In particular, if for some value of $1 \leq i \leq m$ we have $1 + \sum_{j > m} c_{ij} h_j > b_i$, then $\lim_{t \rightarrow \infty} x_i(t) = 0$. On the other hand, if $\sum_{j=1}^n c_{ij}(b_j + h_j) < b_i - 1$ for all $1 \leq i \leq m$, and $\prod_{i=1}^n x_i(0) \neq 0$, then it is simple to show that $\lim_{t \rightarrow \infty} x_i(t) > b_i - 1 - \sum_{j \neq i} c_{ij}(b_j + h_j)$ for all $i = 1, \dots, n$, and thus co-existence is guaranteed. $\square$

We now turn our attention to harvesting the stronger species as a possible strategy for imposing co-existence between the species. We find that tracking the dy-

namics of the general system

$$x_i(t+1) = \frac{b_i x_i(t)}{1 + x_i(t) + \sum_{j \neq i} c_{ij} x_j(t)} - h_i \quad i = 1, \dots, n, \quad (4.6)$$

where $h_i > 0$ for $i = 1, \dots, m$ and $h_i = 0$ for $i = m+1, \dots, n$ is quite a challenging task. In the next section, we concentrate our effort on harvesting the dominant species in a general two dimensional Leslie/Gower model.

5. The two species system

Consider the harvested two species model

$$\begin{cases} x_{n+1} = \frac{b_1 x_n}{1 + x_n + c_1 y_n} - h \\ y_{n+1} = \frac{b_2 y_n}{1 + c_2 x_n + y_n}. \end{cases} \quad (5.1)$$

When $h = 0$, system (5.1) reduces to (3.2) which has been investigated by Cushing et al. in [17, 18]. In particular, it has been shown that if $c_1 < (b_2 - 1)/(b_1 - 1)$ and $c_2 > (b_1 - 1)/(b_2 - 1)$, then the fixed point $E_1 = (b_1 - 1, 0)$ is GAS in $\mathbb{R}_+^2$ [17, 18], and thus species x dominates species y . Obviously, if $h > h_{max} := (\sqrt{b_1} - 1)^2$, then the dominant species x will be extinct in finite time and thus species y will be the only surviving species. In the remaining of this section, we assume that the intensity of harvesting $0 < h < h_{max}$.

System (5.1) can have two, three or four non-negative fixed points depending on the model parameters. Two of these equilibria are $E_1 := (x_r, 0)$ and $\tilde{E}_1 := (x_l, 0)$ where $x_r > x_l$ are the roots of the second degree polynomial

$$x^2 + (h + 1 - b)x + h = 0.$$

The stability of E_1 and $\tilde{E}_1$ is summarized in the next proposition.

PROPOSITION 5.1. Define $h_{min} := \frac{(b_2 - 1)(c_2(b_1 - 1) - (b_2 - 1))}{c_2(c_2 + b_2 - 1)}$ and h_{max} as above. Each of the following holds true.

- (1) If $c_2 < (b_2 - 1)(\sqrt{b_1} + 1)/(b - 1)$, then
 - (i) E_1 is stable for $0 \leq h < h_{min}$ and a saddle for $h_{min} \leq h < h_{max}$.
 - (ii) $\tilde{E}_1$ is unstable for all $0 \leq h < (\sqrt{b_1} - 1)^2$.
- (2) If $c_2 > (b_2 - 1)(\sqrt{b_1} + 1)/(b - 1)$, then
 - (i) E_1 is stable for all $0 \leq h < h_{max}$.
 - (ii) $\tilde{E}_1$ is unstable for all $0 \leq h < h_{min}$ and a saddle for $h_{min} < h < h_{max}$.

A stable co-existence fixed point (x^*, y^*) of (5.1) must satisfy the following conditions.

- C1: $y^* = b_2 - 1 - c_2 x^*$ and $(x^* + h)[(1 - c_1 c_2)x^* + c_1(b_2 - 1) + 1] = b_1 x^*$
- C2: $0 < x^* < (b_2 - 1)/c_2$
- J1: $P(1, x^*, y^*) > 0$
- J2: $P(-1, x^*, y^*) > 0$
- J3: $1 - P(0, x^*, y^*) > 0$,

where $P(\lambda, x^*, y^*)$ is the characteristic polynomial of the linearization matrix

$$J(x^*, y^*) = \begin{bmatrix} \frac{b_1(1+c_1y^*)}{(1+x^*+c_1y^*)^2} & -\frac{b_1c_1x^*}{(1+x^*+c_1y^*)^2} \\ -\frac{b_2c_2y^*}{(1+c_2x^*+y^*)^2} & \frac{b_2(1+c_2x^*)}{(1+c_2x^*+y^*)^2} \end{bmatrix} = \begin{bmatrix} \frac{b_1(1+c_1y^*)}{(1+x^*+c_1y^*)^2} & -\frac{b_1c_1y^*}{(1+x^*+c_1y^*)^2} \\ -\frac{c_2y^*}{b_2} & \frac{(1+c_2x^*)}{b_2} \end{bmatrix}$$

at (x^*, y^*) . Condition C2 guarantees the non-negativity of the fixed point (x^*, y^*) while J1, J2 and J3 are obviously the Jury conditions that have to be satisfied in order for (x^*, y^*) to be stable.

If $c_2 = \frac{1}{c_1}$, then C1 has a unique solution (x^*, y^*) , and

$$P(-1, x^*, b_2 - 1 - \frac{1}{c_1}x^*) = \frac{[c_1(b_2 - 1) - (b_1 - 1)][c_1(b_2 - 1) - x^*]}{b_2c_1(1 + c_1(b_2 - 1))} < 0.$$

Thus, stable coexistence is not possible in this case regardless of the value of h . If $c_2 \neq \frac{1}{c_1}$, then

$$P(1, x^*, y^*) = \frac{-c_2(x^* - x_1^*)(x^* - x_2^*)(x^* - x_3^*)}{b_2(1 + x^* + c_1y^*)^2},$$

where

$$x_1^* = \frac{b_2 - 1}{c_2}, \quad x_j^* = \frac{c_1(b_2 - 1) + 1 - (-1)^j \sqrt{b_1(c_1(b_2 - 1) + 1)}}{c_1c_2 - 1}, \quad j = 2, 3.$$

Using the fact that $x_2^*x_3^* < 0$, elementary but rather tedious computations reveal that J1 is satisfied only if the three following conditions are satisfied

$$\begin{aligned} x_2^* &< x^* < x_1^*, \\ c_2 &< c_2^* := \frac{(b_2-1)(1+\sqrt{b_1(c_1(b_2-1)+1)})}{c_1b_1(b_2-1)+b_1-1} \quad \text{and} \\ h_{min} &< h < h^* := \frac{c_1(b_2-1)+b_1+1-2\sqrt{b_1(c_1(b_2-1)+1)}}{1-c_1c_2}. \end{aligned}$$

Hence, we proved the following result.

THEOREM 5.2. *Constant harvesting of the dominant species in a two dimensional Leslie/Gower model of the form (5.1) with $c_1 < (b_2 - 1)/(b_1 - 1)$ and $c_2 > c_2^*$, does not lead to stable coexistence between the species.*

It is worth mentioning that $\frac{b_2-1}{b_1-1} < c_2^* < \frac{1}{c_1}$ for all $0 \leq c_1 < \frac{b_1-1}{b_2-1}$. Next, assume $\frac{b_2-1}{b_1-1} < c_2 < c_2^*$, then a stable coexistence is achievable as we prove in the next result.

THEOREM 5.3. *If $c_1 < \frac{b_1-1}{b_2-1}$ and $\frac{b_2-1}{b_1-1} < c_2 < c_2^*$, then there exists a harvesting level $h_{min} < h < h_{max}$ such that the Leslie/Gower model (5.1) allows stable coexistence between the two species.*

Proof. When $c_1 < \frac{b_1-1}{b_2-1}$, $\frac{b_2-1}{b_1-1} < c_2 < c_2^*$ and $h_{min} < h < h_{max}$ conditions C1, C2 and J1 are satisfied for a fixed point (x^*, y^*) . To check the second Jury condition J2, we compute $P(-1, x^*, y^*)$ and find that

$$P(-1, x^*, y^*) = \frac{c_1(x^* + h)^2(1 + b_2)y^*}{b_1b_2} + \frac{(b_1 + 2x^*h + x^{*2} + h^2)(b_2 + 1 + c_2x^*)}{b_1b_2},$$

which is obviously positive. Finally, we have to prove that the third Jury condition J3 is satisfied for some $x^* < \frac{b_2-1}{c_2}$ and $y^* > 0$. In fact, we have

$$1 - P(0, x_1^*, 0) = \frac{(b_2 - 1 + c_2)^2 - b_1 c_2^2}{(c_2 + b_2 - 1)^2}$$

which is positive for all values of $c_2 < \frac{(b_2 - 1)(\sqrt{b_1} + 1)}{b_1 - 1}$. Moreover, by continuity, there exist $x^* < x_1^*$, $y^* > 0$ and $h > h_{min}$ such that C1, C2 and all of the Jury conditions are satisfied. $\square$

Figure 5. Graph (a) shows the region where coexistence is achievable by constant harvesting of the dominant species. Graph (b) shows the bifurcation diagram for System 5.1 with two species, where $b_1 = 4$, $b_2 = 3.5$, $c_2 = 1$, $c_1 = 0.1$, and we conditionally harvest x_1 with $x_1^{th} = 1.7$ and h_1 varies between 0 and 1.7. The same graph captures coexistence in constant harvesting when h is between $5/14$ and $35/6 - 20\sqrt{5}/9$.

For clarity, we summarize the results of this section.

1. When $c_1 < \frac{b_1-1}{b_2-1}$, $c_2 > \frac{b_2-1}{b_1-1}$ and $h = 0$ the species x is dominant, and natural stable coexistence is not possible in the system.
2. When $c_1 < \frac{b_1-1}{b_2-1}$ and $c_2 > c_2^*$, no amount of harvesting will lead to stable coexistence between the species; i.e., depending on the value of h and the initial conditions, either species x will continue to dominate or will die in a finite time in which case species y will be the only surviving species.
3. When $c_1 < \frac{b_1-1}{b_2-1}$ and $c_2 < c_2^*$, then stable coexistence between the species is possible when the harvesting level $h_{min} < h < h^*$. The range of parameters c_1 and c_2 is shown in part (a) of Fig. 5. Part (b) of the same figure shows that it is possible to obtain stable coexistence, and that conditional harvesting of the strong species can also lead to periodic and chaotic behavior as it was the case for the simpler system (3.1).

6. Conclusion

When the competitive nature of the environment threatens the survival of some of the species humans must intervene in order to prevent the extinction of some species. Harvesting and stocking are widely used as management tools in ecology, and are the first tools that come to mind. In this paper, we have studied a simple

Leslie/Gower model in which the growth rates of n different populations are equally affected by interspecies competition, and have found that for this model stocking all species, carefully stocking the weaker species, and carefully stocking the weaker species while harvesting the strong species are possible strategies that can prevent the extinction of the weaker species. Harvesting the strong species by itself does not solve the extinction problem as it is the case in harvesting predators in predator-prey models. We also have found that conditional harvesting is a viable strategy with interesting dynamics. For a more general Leslie/Gower model, we investigated a 2-species model supporting competitive exclusion and have found that constant harvesting of the dominant species can achieve co-existence between the species under certain conditions on the model parameters, while no coexistence can be achieved otherwise.

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