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Effect of parity on productivity and sustainability of Lotka–Volterra food chains

Bounded orbits in food chains

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Abstract Hairston, Slobodkin, and Smith conjectured that top down forces act on food chains, which opposed the previously accepted theory that bottom up forces exclusively dictate the dynamics of populations. We model food chains using the Lotka–Volterra predation model and derive sustainability constants which determine which species will persist or go extinct. Further, we show that the productivity of a sustainable food chain with even trophic levels is predator regulated, or top down, while a sustainable food chain with odd trophic levels is resource limited, which is bottom up, which is consistent with current ecological theory.

Keywords Sustainability · Lotka–Volterra predator–prey equations · Hairston, Slobodkin, and Smith conjecture · Parity of food chains

Mathematics Subject Classification (2000) 92D25 · 37N25 · 34C11

1 Introduction

Ecological food chains are discrete delineations where species higher on the food chain can significantly impact the populations of species below them. Prior to 1960, the productivity of food chains was thought to be governed by bottom up forces, where

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the populations are resource limited by the lowest-level species. In 1960, Hairston, Slobodkin, and Smith (HSS) (Hairston et al. 1960) conjectured that top down forces also impact food chain productivity. They considered a food chain with three trophic levels (carnivores, herbivores and plants) where the carnivores (predators) regulate the herbivore (prey) population, which in turn allows plants to flourish. A well documented ecological example that supports the HSS conjecture is the removal of wolves from Yellowstone National Park. When the wolves were removed, the elk no longer experienced the harmful effects of predation, and the landscape of the park changed. The elk were able to graze freely and woody vegetation in the park was destroyed. When the wolves were reintroduced, the elk were forced to change their grazing patterns and the vegetation began to grow back. Willow trees have grown taller since the wolves returned, and this growth actually supported a colony of beavers to move into the area (Smith 2005).

Ecological evidence of both top down and bottom up regulation of food chain dynamics has stimulated much ecological research. Fretwell generalized HSS to any integer number of trophic levels by combining the ideas of top down and bottom up forces (Polis and Strong 1996), while Oksanen et al. (1981) expanded on Fretwell's idea and suggested that the influence of top down versus bottom up dynamics was related to the parity of the number of species in the food chain. The exploitation ecosystem hypothesis (EEH) (Oksanen et al. 1981) describes that in more productive environments, herbivores regulate the plant biomass, while in less productive environments there are not enough resources to support herbivores so plant biomass is not regulated by predation. Wollrab et al. (2012) considers a similar model with two separate food chains are linked at the bottom by a shared limiting nutrient, whereas Heath et al. (2013) considers density dependent parameters in the presence of a chemostat regulated nutrient resource at the bottom of the chain. Other models which include mass constraints have also been studied from the perspective of bottom-up versus top-down control in food chains of various lengths (DeAngelis 1992).

To illustrate these ideas, extend the three trophic levels (primary carnivore, herbivore, plants) to four levels by adding a secondary carnivore that preys on the primary carnivores, who in turn prey on herbivores who prey on plants. Using the same assumptions made in HSS, this implies that the secondary carnivore is limited by the density of the primary carnivore population. Since the primary carnivores are limited by the predation of the secondary carnivores, they cannot limit the herbivore population. This implies, from the underlying assumptions of HSS, that the herbivore population, not limited by predation, must be limited by the density of the plant population (Fretwell 1977). Therefore, the plant population is regulated by the predation of herbivores. This contrasts with the case of three trophic levels where plants were not regulated by the herbivore population. Thus, the introduction of a secondary carnivore has freed the herbivores from predation and subsequently introduced predation regulation for the plant species. This alternating pattern of predator limitation and prey density limitation can be described for a food chain of any length (Fretwell 1977). Therefore, we would expect to see evidence of top down regulation of productivity in food chains with an even number of species, while bottom up regulation of productivity is found in a food chain with an odd number of species. This manuscript details how models of food chains corroborate these hypotheses.

To understand the effects of parity on the bottom up vs. top down regulation of productivity in food chains, we model food chains using Lotka–Volterra predation equations. The main assumptions of the Lotka–Volterra predation equations are that the predator feeds only on one species of prey and that the prey grows exponentially in absence of the predator (Lotka 1925; Volterra 1931). This model accurately predicted the fluctuations in the well-known Hudson Bay trading data for lynx and hare pelts (Odum 1953). The predation equations operate under different assumptions than the Lotka–Volterra competition equations, which say that both species experience negative effects from interactions because they are competing for the same resources. Unlike some Lotka–Volterra predation models, we do not assume a carrying capacity on the bottom level species, hence the results of Harrison (1979) that guarantee the existence of a positive asymptotically stable equilibrium do not apply. Instead we turn to results of Volterra who proved that for food chains with an even number of species, all orbits with positive initial conditions have bounded orbits. Many have provided their own extensions to the first model introduced by Lotka and Volterra, and continue to study the stability of such systems [(see, for example, (Gopalsamy 1984; Gard and Hallam 1979; Harrison 1979; Roy and Solimano 1987; Chauvet et al. 2002; Harris et al. 2005)].

We characterize food chains as sustainable if all species persist and do not limit to zero. We define a sustainability constant, which corresponds to a particular combination of parameters that appears in the co-ordinates of the equilibria, whose sign classifies behavior of the food chain as either sustainable, critically sustainable for odd length food chains, or unsustainable. If a food chain is unsustainable, then certain species in the food chain become extinct. For sustainable food chains with an even number of species or critically sustainable food chains with an odd number of species, all solutions with positive initial conditions persist and remain bounded, even without the presence of a logistic term on the bottom level species. We show that this corresponds to top down behavior. For sustainable food chains with an odd number of species, our model exhibits unbounded solutions. Since our model places no resource limitation on the first level species in the food chain, unbounded growth in our model corresponds to a species being only limited by availability of resources (bottom up). Unbounded solutions indicate that the food chain has enough resources to support additional species.

In Sect. 2, we will introduce the Lotka–Volterra predation model and describe the equilibria for chains of n species. We also introduce sustainability constants that indicate whether all species in the chain persist, that is, if the chain is sustainable. In Sect. 3 we define K_n, which corresponds to an invariant surface for n even, and use that to show that sustainable food chains have bounded solutions, indicating top down behavior of the food chain. Section 4 discusses non-sustainable food chains and further describes the corresponding cascade of extinction. In Sect. 5, we show that sustainable food chains with an odd number of species have unbounded solutions, and hence demonstrate bottom up behavior. Section 6 contains numerical examples for both even and odd food chains that illustrate the appropriate limiting behavior. Finally, in Sect. 7, we discuss the biological implications of our results.

2 Model properties

Lotka (1925) and Volterra (1931) independently developed what has become known as the Lotka–Volterra equations as a model of populations of a predator and its prey. In this section, we expand Lotka and Volterra's model to a food chain of arbitrary length, while maintaining the same structure of the two-dimensional Lotka–Volterra predation chain. The general model for n interacting species is given by

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1(a_1 - b_1 x_2)\\
\frac{dx_2}{dt} &= x_2\left(-a_2 - b_2 x_3 + c_2 x_1\right)\\
&\vdots\\
\frac{dx_j}{dt} &= x_j\left(-a_j - b_j x_{j+1} + c_j x_{j-1}\right)\\
&\vdots\\
\frac{dx_n}{dt} &= x_n\left(-a_n + c_n x_{n-1}\right)
\end{aligned} \tag{1}$$

where a_i, b_i, and c_i are all assumed to be positive. Here a_i corresponds to the net growth rate of species i, b_i corresponds to the negative effect of predation on species i and c_i is associated with the positive benefit received by species i from preying on species $i-1$.

Since, we are modeling populations, we will restrict ourselves to the domains $\{x_i \geq 0, i = 1, 2, \ldots, n\} \subset \mathbb{R}^n$ and $\mathbb{R}^n_+ = \{x_i > 0, i = 1, 2, \ldots, n\}$. The structure of the differential equations has x_i as a factor in each $\frac{dx_i}{dt}$, which results in the surfaces $x_i = 0$ being invariant.

We begin by making several observations concerning positive equilibria of equation (1) for fixed chain length n. The second and $(n-1)$st co-ordinates of a positive equilibria are determined solely by the parameters in the first and last equations, respectively. Specifically, the second co-ordinate of a positive equilibrium is exclusively determined by the parameters that appear in the equation for the bottom species. Similarly, the fourth co-ordinate of a positive equilibrium depends on the second co-ordinate together with the parameters appearing in the third differential equation. In general, the even co-ordinates of a positive equilibrium only depend upon the parameters that appear in all previous odd differential equations. A symmetric argument holds beginning at the $(n-1)$st co-ordinate and proceeding downward. The $(n-1)$st component of a positive equilibrium is determined by the parameters in the nth differential equation. The $(n-3)$rd component only depends on the parameters that appear in the the $(n-2)$nd and nth differential equation, and so on. This also implies that equilibrium co-ordinates are related to other co-ordinates that have the same parity. If there are an even number of species in the chain, then the even co-ordinates of a positive equilibrium will only depend on the parameters that appear in the equations corresponding to the odd species. Similarly, the odd co-ordinates of a positive equilibrium will only depend on the parameters appearing in the equations corresponding to the even species. If, on the other hand, there are an odd number of species in the chain, then a positive equilibrium will only exist for one particular combination of the parameters involving the odd differential equations in (1).

Understanding the equilibria is a first step in studying any dynamical system, but in this case we are also interested in the evolution of the equilibrium points as n, the number of species, increases. In general, we classify equilibria of this system as either an interior equilibrium, if all co-ordinates of the equilibrium point are positive, or a boundary equilibrium, which means that at least one co-ordinate of the equilibrium point is zero. We will show that for n even the interior equilibrium point is isolated, whereas for n odd, it is possible to get a line of interior equilibria. An equilibrium on the boundary planes, i.e., some co-ordinate of the equilibrium, $x_i = 0$, means that at least one species is extinct while others persist. An equilibrium in $\mathbb{R}^n_+$ means that all species persist.

System (1) has many nonnegative equilibria, the first and most obvious being $(0, 0, \ldots, 0)$ which we label as P^0. Linear analysis verifies that this is always a saddle point with unstable manifold the x_1 axis. The next fixed point of interest is $P^2 = \left(\frac{a_2}{c_2}, \frac{a_1}{b_1}, 0 \ldots, 0\right)$ which corresponds to the fixed point in the classical two species predator–prey model in the $x_1 - x_2$ plane.

Note that if a fixed point of system (1) has $(j-1)$st co-ordinate equal to zero, then equation j becomes

$$\frac{dx_j}{dt} = x_j\left(-a_j - b_j x_{j+1}\right)$$

which is zero only when $x_j = 0$ (since, we assume $x_{j+1} \geq 0$). Thus, when searching for non-negative fixed points, we will always have $x_1 > 0$ and $x_2 > 0$ until the first zero co-ordinate, after which all subsequent co-ordinates must equal zero.

Next, we search for possible fixed points with nonzero first three co-ordinates, with the rest zero (assuming $n > 2$). In this case, we again see that $x_2 = \frac{a_1}{b_1}$ from the first equation. From the third equation we have that (since x_3 is assumed nonzero) $c_3 x_2 - a_3 = 0$ or $\frac{a_1 c_3}{b_1} - a_3 = 0$. This implies that a fixed point of this type will only exist when the parameters are such that $\frac{a_1 c_3}{b_1} - a_3 = 0$. Moreover, from the second equation in the system, we must have $-a_2 - b_2 x_3 + c_2 x_1 = 0$. Thus, $x_1 = (a_2 + b_2 x_3)/c_2$. Setting x_3 as a free parameter s, we have a line of fixed points given by $\left(\frac{a_2+b_2 s}{c_2}, \frac{a_1}{b_1}, s, 0, \ldots, 0\right)$ for $s > 0$. These fixed points only occur when $\frac{a_1 c_3}{b_1} - a_3 = 0$. We label these fixed points as P^3, when they exist.

For possible fixed points with nonzero first four co-ordinates, with the rest zero (assuming $n > 3$), again we have $x_2 = \frac{a_1}{b_1}$, and from the third differential equation:

$$x_4 = \frac{1}{b_3}\left(c_3 \frac{a_1}{b_1} - a_3\right) = \frac{a_1 c_3 - a_3 b_1}{b_1 b_3}.$$

Of course, for this fixed point to be of interest requires that $a_1 c_3 - a_3 b_1 > 0$. (If $a_1 c_3 - a_3 b_1 = 0$, we reduce to the previous case.) The other co-ordinates are readily solved by the equations for x_4 and x_2 which yield $x_3 = a_4/c_4$ and $x_1 = (a_2c_4 + a_4b_2)/(c_2c_4)$. Thus, assuming $a_1c_3 - a_3b_1 > 0$, there exists a fixed point of the form

$$\left(\frac{a_2c_4 + a_4b_2}{c_2c_4}, \frac{a_1}{b_1}, \frac{a_4}{c_4}, \frac{a_1c_3 - a_3b_1}{b_1b_3}, 0, \ldots 0\right),$$

which we label as P^4.

In general, to find a fixed point with the first $m = 2j$ co-ordinates non-zero (and the rest zero) is similar to the work presented above. Namely, $x_2 = \frac{a_1}{b_1}$ and (from the differential equation for x_3) $x_4 = \frac{a_1c_3 - a_3b_1}{b_1b_3}$ and (from the differential equation for x_5), $x_6 = \frac{a_1c_3c_5 - a_3b_1c_5 - a_5b_1b_3}{b_1b_3b_5}$. Moreover for any $k < j$ if we make the assumption that

$$\begin{aligned} x_{2k} = \frac{1}{\rho_{2k-1}} &(a_1c_3 \ldots c_{2k-1} - a_3b_1c_5 \ldots c_{2k-1} - \ldots \\ &- a_{2k-3}b_1 \ldots b_{2k-5}c_{2k-1} - a_{2k-1}b_1 \ldots b_{2k-3}) \end{aligned} \tag{2}$$

where $\rho_{2k-1} = b_1b_3 \ldots b_{2k-1}$ then it can be shown (from the $2k + 1$st differential equation) that

$$\begin{aligned} x_{2k+2} &= \frac{1}{b_{2k+1}} (-a_{2k+1} + c_{2k+1}x_{2k}) \\ &= \frac{1}{\rho_{2k+1}} (a_1c_3 \ldots c_{2k+1} - a_3b_1c_5 \ldots c_{2k+1} - \ldots - a_{2k-3}b_1 \ldots b_{2k-5}c_{2k+1} \\ &\quad - a_{2k-1}b_1 \ldots b_{2k-3}c_{2k+1} - a_{2k+1}b_1 \ldots b_{2k-1}) \end{aligned}$$

where $\rho_{2k+1} = b_1b_3 \ldots b_{2k+1}$. Thus, formula (2) holds for all $k \leq j$. Since all constants are positive, and by our assumption $x_{2j} > 0$, we have that the numerators of each x_{2k} are positive for all $k \leq j$. By inspection, if the numerator of $x_{2j} > 0$ then the numerator of all x_{2i} for all $2 \leq i \leq j$ will be positive. Thus, we only require that the numerator of x_{2j} be positive, namely

$$a_1c_3 \ldots c_{2j-1} - a_3b_1c_5 \ldots c_{2j-1} - \ldots - a_{2j-1}b_1b_3 \ldots b_{2j-3} > 0.$$

To compute the odd indexed co-ordinates, we start at the $m = 2j$-th equation and see that $x_{m-1} = \frac{a_m}{c_m}$, since $x_i = 0$ for all $i > m$. We then use equation $(m - 2)$ to see that $x_{m-3} = \frac{a_{m-2}c_m + a_mb_{m-2}}{c_{m-2}c_m}$. Again, we can show inductively for $k < j$ that

$$\begin{aligned} x_{m-2k+1} = \frac{1}{\gamma_{m-2k+2}} &(a_{m-2k+2}c_{m-2k+4}c_{m-2k+6} \ldots c_m \\ &+a_{m-2k+4}b_{m-2k+2}c_{m-2k+6} \ldots c_m \\ &+a_{m-2k+6}b_{m-2k+2}b_{m-2k+4}c_{m-2k+8} \ldots c_m + \ldots \\ &+a_{m-2}b_{m-2k+2}b_{m-2k+4}b_{m-2k+6} \ldots b_{m-4}c_m \\ &+ a_mb_{m-2k+2}b_{m-2k+4} \ldots b_{m-2}) \end{aligned}$$

where $\gamma_{m-2k+2} = c_{m-2k+2}c_{m-2k+4}\ldots c_m$. From the $(m-2k)$th differential equation we obtain:

$$x_{m-2k-1} = \frac{1}{c_{m-2k}}\left(a_{m-2k} + b_{m-2k}x_{m-2k+1}\right), \tag{3}$$

so

$$\begin{aligned}x_{m-2k-1} = \frac{1}{\gamma_{m-2k}} &(a_{m-2k}c_{m-2k+2}c_{m-2k+4}\ldots c_m + a_{m-2k+2}b_{m-2k}c_{m-2k+4}\ldots c_m \\ &+a_{m-2k+4}b_{m-2k}b_{m-2k+2}c_{m-2k+6}\ldots c_m + \ldots \\ &+a_{m-2}b_{m-2k}b_{m-2k+2}b_{m-2k+4}\ldots b_{m-4}c_m \\ &+a_m b_{m-2k}b_{m-2k+2}\ldots .b_{m-2})\end{aligned}$$

where $\gamma_{m-2k} = c_{m-2k}c_{m-2k+2}\ldots c_m$. Thus, we can inductively solve for each of the odd co-ordinates (which are each always positive) all the way down to $m-2k-1 = 1$.

To see how to apply this, for $m = 6$ solving for P^6, the fixed point with exactly six positive entries. The second, fourth, and sixth co-ordinates are:

$$\frac{a_1}{b_1}, \quad \frac{a_1c_3 - a_3b_1}{b_1b_3}, \quad \frac{a_1c_3c_5 - a_3b_1c_5 - a_5b_1b_3}{b_1b_3b_5}$$

while the fifth, third, and first are:

$$\frac{a_6}{c_6}, \quad \frac{a_4c_6 + a_6b_4}{c_4c_6}, \quad \frac{a_2c_4c_6 + a_4b_2c_6 + a_6b_2b_4}{c_2c_4c_6}.$$

To understand the case where there are exactly $m = 2j+1$ odd non-zero co-ordinates, we proceed as before. In particular, we again note that $x_2 = \frac{a_1}{b_1}$ and that again the even co-ordinates are obtained as before from formula (2). Since, $m = 2j+1$ is odd, the mth differential equation will yield $x_{m-1} = \frac{a_m}{c_m}$. But ,since m is odd, $m-1$ is even and we have the additional constraint $x_{m-1} = x_{2j}$ as given by (2). Thus, for such fixed points to exist, we must have

$$\begin{aligned}&\frac{a_{2j+1}}{c_{2j+1}} \\ &= \frac{a_1c_3c_5\ldots c_{2j-1} - a_3b_1c_5\ldots c_{2j-1} - a_5b_1b_3c_7\ldots c_{2j-1} - \ldots - a_{2j-1}b_1b_3\ldots b_{2j-3}}{b_1b_3b_5\ldots b_{2j-1}}\end{aligned}$$

or

$$\begin{aligned}&a_1c_3c_5\ldots c_{2j+1} - a_3b_1c_5\ldots c_{2j+1} - \ldots - a_{2j-1}b_1b_3\ldots b_{2j-3}c_{2j+1} \\ &\quad -a_{2j+1}b_1b_3\ldots b_{2j-1} = 0.\end{aligned}$$

As in the P^3 case, we can assume that the mth-co-ordinate of P^m is a free variable s and generate the other odd co-ordinates using (3).

Table 1 Table of equilibrium points as a function of chain length

Label	Equilibrium	Sustainability constant
P^0	$(0, 0, \dots, 0)$	n/a
P^2	$(\frac{a_2}{c_2}, \frac{a_1}{b_1}, 0, \dots, 0)$	n/a
P^3	$(\frac{a_2+b_2 s}{c_2}, \frac{a_1}{b_1}, s, 0, \dots, 0)$	$\alpha_2 = a_1c_3 - a_3b_1 = 0,\ s > 0$
P^4	$(\frac{a_2c_4+a_4b_2}{c_2c_4}, \frac{a_1}{b_1}, \frac{a_4}{c_4}, \frac{a_1c_3-a_3b_1}{b_1b_3}, 0, \dots, 0)$	$\alpha_2 = a_1c_3 - a_3b_1 > 0$
P^5	$(\frac{a_2c_4+a_4b_2+b_2b_4s}{c_2c_4}, \frac{a_1}{b_1}, \frac{a_4+b_4s}{c_4}, \frac{a_1c_3-a_3b_1}{b_1b_3}, s, 0, \dots, 0)$	$\alpha_3 = a_1c_3c_5 - a_3b_1c_5 - a_5b_1b_3 = 0,\ s > 0$
P^6	$(\frac{a_2c_4c_6+a_4b_2c_6+a_6b_2b_4}{c_2c_4c_6}, \frac{a_1}{b_1}, \frac{a_4c_6+a_6b_4}{c_4c_6}, \frac{a_1c_3-a_3b_1}{b_1b_3}, \frac{a_6}{c_6}, \frac{a_1c_3c_5-a_3b_1c_5-a_5b_1b_3}{b_1b_3b_5}, 0, \dots, 0)$	$\alpha_3 = a_1c_3c_5 - a_3b_1c_5 - a_5b_1b_3 > 0$

The last column of the table displays the sustainability constant. The parameter s in rows labelled P^3 and P^5 represent the density of the chain's top species, and mathematically corresponds to an equilibrium point for each value of s

In the particular case of $m = 7$ (where $n \geq 7$) we must have $a_1c_3c_5c_7 - a_3b_1c_5c_7 - a_5b_1b_3c_7 - a_7b_1b_3b_5 = 0$ and the second, fourth, and sixth co-ordinates are:

$$\frac{a_1}{b_1}, \quad \frac{a_1c_3 - a_3b_1}{b_1b_3}, \quad \frac{a_1c_3c_5 - a_3b_1c_5 - a_5b_1b_3}{b_1b_3b_5}$$

while the seventh, fifth, third, and first are:

$$s, \quad \frac{a_6 + b_6 s}{c_6}, \quad \frac{a_4c_6 + b_4(a_6 + b_6 s)}{c_4c_6}, \quad \frac{a_2c_4c_6 + b_2\left(a_4c_6 + b_4(a_6 + b_6 s)\right)}{c_2c_4c_6},$$

where $s > 0$. Note that this is a parametric line of equilibria in 7-space.

Henceforth, we label P^k_j to be the jth co-ordinate of the fixed point P^k and for each j with $2 \leq 2j - 1 \leq n$ we label the quantities

$$\alpha_j = a_1c_3c_5 \dots c_{2j-1} - a_3b_1c_5c_7 \dots c_{2j-1} - a_5b_1b_3c_7 \dots c_{2j-1} - \\ \dots - a_{2j-3}b_1b_3 \dots b_{2j-5}c_{2j-1} - a_{2j-1}b_1b_3 \dots b_{2j-3}$$

which we will refer to as *sustainability constants*. In particular, we say that system (1) is *sustainable* if $\alpha_j > 0$ for all $2 \leq 2j - 1 \leq n$. In other words, a food chain with $n = 2k$ species is sustainable if P^n is positive, and a food chain with $n = 2k - 1$ species is sustainable if the $n + 1$ even species chain is sustainable. We call an odd food chain with n species *critically sustainable* if P^n exists (i.e., $\alpha_{\frac{n+1}{2}} = 0$). If none of the above applies to a food chain, we call it *unsustainable*.

Table 1 contains equilibrium points for P^m. The last column contains the parameter conditions that ensure components of the equilibria are positive.

3 Sustainable even chains and critically sustainable odd chains

For sustainable food chains with an even number of species, Volterra proved that all species persist and remain bounded, which corresponds to top down effects dictating the dynamics of the food chain. In this section, we present a proof similar to Volterra's to illustrate the boundedness of all solutions for any food chain where P^n exists and is positive. The fixed point(s) P^n will allow us to define surfaces which will be useful to show the boundedness and extinction of species.

From the equilibria found above, we define a function that corresponds to Volterra's constants of motion for an even number of species (Volterra 1931). For a sustainable food chain with n species, we define surface K_n as follows:

$$K_n(x_1, \ldots, x_n) = x_1 - P_1^n \ln x_1 + \frac{b_1}{c_2} x_2 - \frac{b_1}{c_2} P_2^n \ln x_2 + \frac{b_1 b_2}{c_2 c_3} x_3 - \frac{b_1 b_2}{c_2 c_3} P_3^n \ln x_3 + \ldots + \frac{b_1 \ldots b_{n-1}}{c_2 \ldots c_n} x_n - \frac{b_1 \ldots b_{n-1}}{c_2 \ldots c_n} \ln x_n \quad (4)$$

where P_j^n is the jth co-ordinate of the equilibrium P^n. For convenience, we define $P_n^{n+1} = 0$ and $P_n^0 = 0$.

Proposition 1 *Assume an interior fixed point exists, that is, that n is even with $\alpha_{\frac{n}{2}} > 0$ or in the case n odd when $\alpha_{\frac{n+1}{2}} = 0$. If each $P_j^n > 0$ for $1 \leq j \leq n$ then the function* (4) *is invariant.*

Proof To show that K_n is invariant, we need to show that $dK_n/dt = 0$ for any solution of (1). The derivative is

$$\begin{aligned}\frac{dK_n}{dt} = &\left(1 - \frac{P_1^n}{x_1}\right)\dot{x_1} + \frac{b_1}{c_2}\left(1 - \frac{P_2^n}{x_2}\right)\dot{x_2}\\ &\vdots\\ &+ \frac{b_1 b_2 \ldots b_{j-2}}{c_2 c_3 \ldots c_{j-1}}\left(1 - \frac{P_{j-1}^n}{x_{j-1}}\right)\dot{x}_{j-1} + \frac{b_1 b_2 \ldots b_{j-1}}{c_2 c_3 \ldots c_j}\left(1 - \frac{P_j^n}{x_j}\right)\dot{x}_j\\ &+ \frac{b_1 b_2 \ldots b_j}{c_2 c_3 \ldots c_{j+1}}\left(1 - \frac{P_{j+1}^n}{x_{j+1}}\right)\dot{x}_{j+1}\\ &\vdots\\ &+ \frac{b_1 b_2 \ldots b_{n-2}}{c_2 c_3 \ldots c_n}\left(1 - \frac{P_{n-1}^n}{x_{n-1}}\right)\dot{x}_{n-1} + \frac{b_1 b_2 \ldots b_{n-1}}{c_2 c_3 \ldots c_n}\left(1 - \frac{P_n^n}{x_n}\right)\dot{x}_n. \quad (5)\end{aligned}$$

After substituting for $\dot{x}_j$ from (1), we will consider three different types of terms in the above sum: terms with the product $x_j x_{j+1}$, terms containing only x_j, and constant terms. To show that $dK_n/dt = 0$ we will show that the coefficient of each type of term is 0.

First, we will show that all the terms containing only x_j will cancel out. We obtain a term of the form

$$-\frac{b_1 \dots b_{j-1}}{c_2 \dots c_j} a_j x_j$$

by multiplying the 1 in $(1 - \frac{P_j^n}{x_j})$ by the first term in $\dot{x}_j$ in (5). Next, we obtain a term of the form

$$\frac{b_1 \dots b_{j-1}}{c_2 \dots c_{j-1}} P_{j-1}^n x_j$$

by multiplying $-\frac{P_{j-1}^n}{x_{j-1}}$ by the second term in $\dot{x}_{j-1}$ in (5). Lastly, we have a term of the form

$$-\frac{b_1 \dots b_j c_{j+1}}{c_2 \dots c_{j+1}} P_{j+1}^n x_j$$

by multiplying $-\frac{P_{j+1}^n}{x_{j+1}}$ by the last term of $\dot{x}_{j+1}$. Therefore, the coefficient of x_1 is $a_1 - b_1 P_2^n = 0$ and for $j > 1$ the x_j term is

$$\frac{b_1 \dots b_{j-1}}{c_2 \dots c_{j-1}} \left(-a_j + c_j P_{j-1}^n - b_j P_{j+1}^n \right).$$

The term inside the parentheses is zero by the jth equation in system (1) evaluated at the fixed point.

Next, we will show that all the terms containing $x_{j-1} x_j$ have coefficient zero. These terms are obtained in two ways. First, by multiplying the 1 in $(1 - \frac{P_{j-1}^n}{x_{j-1}})$ by $\dot{x}_{j-1}$ to obtain a coefficient of $-(b_1 \dots b_{j-2} b_{j-1})/(c_2 \dots c_{j-1})$ for $x_{j-1} x_j$ and by 1 in $(1 - \frac{P_j^n}{x_j})$ by $\dot{x}_j$ to obtain a coefficient of $(b_1 \dots b_{j-2} b_{j-1})/(c_2 \dots c_{j-1})$. So these coefficients are again zero.

Lastly, we analyze the sum of the constant terms in (5). These terms all arise from multiplying $\frac{P_j^n}{x_j}$ by $\dot{x}_j$ and all amount to

$$P_1^n a_1 - \frac{b_1}{c_2} P_2^n a_2 - \frac{b_1 b_2}{c_2 c_3} P_3^n a_3 - \dots - \frac{b_1 b_2 \dots b_{n-1}}{c_2 c_3 \dots c_n} P_n^n a_n$$

Note that the linear combination: $\dot{x}_1 + \frac{b_1}{c_2} \dot{x}_2 + \frac{b_1 b_2}{c_2 c_3} \dot{x}_3 + \dots + \frac{b_1 b_2 \dots b_{n-1}}{c_2 c_3 \dots c_n} \dot{x}_n$ from system (1) reduces to

$$x_1 a_1 - \frac{b_1}{c_2} x_2 a_2 - \frac{b_1 b_2}{c_2 c_3} x_3 a_3 - \dots - \frac{b_1 b_2 \dots b_{n-1}}{c_2 c_3 \dots c_n} x_n a_n$$

since all of the $x_j x_{j+1}$ terms cancel.

Note that when we evaluate the above linear combination at $(P_1^n, \ldots, P_n^n)$, we must get zero (since each $\dot{x}_j = 0$) so we also must have that

$$P_1^n a_1 - \frac{b_1}{c_2} P_2^n a_2 - \frac{b_1 b_2}{c_2 c_3} P_3^n a_3 - \ldots - \frac{b_1 b_2 \ldots b_{n-1}}{c_2 c_3 \ldots c_n} P_n^n a_n = 0$$

as desired. Therefore the function K_n is invariant, so its level sets are invariant. □

For the next theorem, we will use Volterra's constant of motion to prove the following (which was also shown by Volterra).

Theorem 1 *For any sustainable food chain with an even number of species ($n = 2k$ with $\alpha_k > 0$), or odd food chain $n = 2k - 1$ with $\alpha_{\frac{n+1}{2}} = 0$, all solutions with positive initial conditions (i.e., in $\mathbb{R}_+^n$) remain bounded and with all co-ordinates bounded away from 0.*

Proof As shown in the previous theorem, the level sets defined by $K_n(x_1, \ldots, x_n)$ are invariant. Let $(x_1^0, \ldots, x_n^0) \in \mathbb{R}_+^n$ and $K_n(x_1^0, \ldots, x_n^0) = K^0$. We show the set $K_n(x_1, \ldots, x_n) = K^0$ is bounded.

To see this, consider functions of the form $f(x) = ax - b \ln x$ where $a, b > 0$. These functions have an absolute minimum at $\frac{b}{a}$. We utilize the fact that K_n is the sum of functions of the form $f_i(x_i) = A_i x_i - B_i \ln x_i$ where $A_i = \frac{b_1 \ldots b_{i-1}}{c_2 \ldots c_i} > 0$, $B_i = \frac{b_1 \ldots b_{i-1}}{c_2 \ldots c_i} P_i^n > 0$. These functions have global minima at $x_i = B_i / A_i = P_i^n$ and also tend to infinity as $x_i \to 0^+$ and as $x_i \to \infty$. Thus K_n has an absolute minimum in $\mathbb{R}_+^n$ at $(P_1^n, \ldots, P_n^n)$.

Moreover, if the solution with initial condition $(x_1^0, \ldots, x_n^0)$ is such that $N_i \to 0$ or $x_i \to \infty$, then $K_n(x_1, \ldots, x_n)$ would necessarily have to limit to ∞ since the other functions $f_j(x)$ are all bounded below. However, this contradicts the fact that $K_n(x_1, \ldots, x_n)$ is constantly equal to K^0. So solutions must remain bounded and all species persist and are bounded away from zero. □

In conclusion, for a sustainable even food chain or a critically sustainable odd food chain, all species persist and none are unbounded. These types of food chains are therefore top down in behavior. No logistic term is needed in such models, indeed, including such a term changes the cause of the bounded behavior from predator limited to resource limited.

Furthermore, we make the observation that each of the even co-ordinates of all equilibria agree. That is P_{2j}^m is the same as P_{2j}^n assuming $2j \leq m$ and $2j \leq n$. Whereas, for the odd co-ordinates $P_{2j+1}^m < P_{2j+1}^n$ for $m < n$. For instance,

$$P_1^2 = \frac{a_2}{c_2} < P_1^4 = \frac{a_2 c_4 + a_4 b_2}{c_2 c_4}.$$

Basically, this implies that (at least with regard to the fixed point solutions) adding species to obtain a sustainable even length food chain from a smaller length even food chain can only benefit the odd-level species, while having no effect on the even-level species. Thus, with regard to the equilibria solutions, adding species can be beneficial to odd-level species lower in the food chain while remaining neutral to even level species. This implies that in sustainable even food chains, the odd-level species are limited by predation, since introducing additional predators alleviates some of the predation effects on these species, allowing them to increase. Thus, top down forces affect the odd-level species.

Additionally, if we increase the productivity in this chain by increasing a_1, the amount of sunlight for example, then the benefits are only seen in the even level species. Consider, the table of equilibria (Table 1). Notice that the second co-ordinate of each equilibrium point is a_1/b_1. Thus, as a_1 increases, so to does the second co-ordinate of the equilibrium point. Similarly, all the even co-ordinates of the equilibrium points increase as a_1 increases, but the odd ones remain unchanged. So increasing productivity of the bottom species only benefits the predators, i.e. the even species are resource limited (i.e., they are affected by bottom up forces).

4 Nonsustainable food chains

In this section we consider food chains that are not sustainable. For all, k such that $3 \leq 2k - 1 \leq n$, we define functions of the form

$$F_{2k-1} = x_1 x_3^{\beta_1} \dots x_{2k-1}^{\beta_{2k-3}}, \tag{6}$$

where $\beta_{2j-1} = (b_1 b_3 \dots b_{2j-1})/(c_3 c_5 \dots c_{2j+1})$ and whose derivative is

$$\frac{dF_{2k-1}}{dt} = \begin{cases} \alpha_k F_{2k-1} & \text{if } n = 2k-1 \\ \alpha_k F_{2k-1} - \beta_{2k-3} b_{2k-1} x_{2k} F_{2k-1} & \text{if } 2k-1 < n \end{cases} \tag{7}$$

The function G_{2k-1}

$$\begin{aligned} G_{2k-1} = x_1 - P_1^{2k-2} \ln x_1 + \frac{b_1}{c_2}(x_2 - P_2^{2k-2} \ln x_2) + \dots \\ + \frac{b_1 \dots b_{2k-3}}{c_2 \dots c_{2k-2}}(x_{2k-2} - P_{2k-2}^{2k-2} \ln x_{2k-2}) + \frac{b_1 \dots b_{2k-2}}{c_2 \dots c_{2k-1}} x_{2k-1} \end{aligned} \tag{8}$$

with derivative

$$\frac{dG_{2k-1}}{dt} = \begin{cases} \alpha_k \frac{b_2 b_4 \dots b_{2k-2}}{c_2 c_4 \dots c_{2k-2}} x_{2k-1} & \text{if } n = 2k-1 \\ \alpha_k \frac{b_2 b_4 \dots b_{2k-2}}{c_2 c_4 \dots c_{2k-2}} x_{2k-1} - \frac{b_1 b_2 \dots b_{2k-1}}{c_2 c_3 \dots c_{2k-1}} x_{2k-1} x_{2k} & \text{if } 2k-1 < n \end{cases} \tag{9}$$

will also be used in the proof of the following theorem.

Theorem 2 *For any n chain, suppose that $\alpha_j < 0$ but $\alpha_{j-1} > 0$ for $2j - 1 \leq n$. Then, species x_i for $2j - 1 \leq i \leq n$ all die off, while species x_i for $i < 2j - 1$ all persist and remain bounded. Finally, when $\alpha_j = 0$, for some $2j - 1 \leq n$, then species*

x_i for $i > 2j-1$ all die off, while species x_i for $i \leq 2j-1$ all persist and remain bounded.

Proof When $\alpha_j < 0$, we have $dF_{2j-1}/dt < 0$. Since, F_{2j-1} is decreasing and bounded below by 0, we must have $dF_{2j-1}/dt \to 0$. This implies that at least one x_{2i-1} goes to 0 for $i = 1,2,\ldots, j$. We will show that $x_{2j-1} \to 0$. Note that since $\alpha_j < 0$, and $\alpha_{j-1} > 0$, we have P^{2j-2} is positive. Therefore, consider G_{2j-1} which is strictly decreasing. Since each component of G_{2j-1} of the form $A_i x_i - B_i \ln x_i$ has a global minimum at $x_i = B_i/A_i$ the function G_{2j-1} is bounded below and decreasing, so it must have a limit, moreover $\frac{dG_{2j-1}}{dt}$ must also limit to zero, which implies that $x_{2j-1} \to 0$. Using this fact we can show, by contradiction, that none of x_i for $i = 1, 2, \ldots, 2j-2$ can limit to 0 or ∞. Suppose that, $x_1 \to 0$ or to ∞. This implies $x_1 - P_1^{2j-2} \ln x_1$ goes to ∞. Since G_{2j-1} is always decreasing, some other component must go to $-\infty$ to compensate. However, recall that each component of G_{2j-1} is bounded below so this is impossible. Thus, x_1 cannot go to 0 or ∞. Similar arguments show that no x_i can go to 0 or ∞ for $i = 1, 2, \ldots, 2j-2$. Recall, since $dF_{2j-1}/dt \to 0$ we must have $x_{2j-1} \to 0$.

We next show that this implies that $x_{2j} \to 0$. Recall from (1)

$$\frac{dx_{2j}}{dt} = -a_{2j}x_{2j} - b_{2j}x_{2j}x_{2j+1} + c_{2j}x_{2j}x_{2j-1}.$$

Thus, if $x_{2j-1} \to 0$, then eventually $dx_{2j}/dt < 0$ which causes $x_{2j} \to 0$ as well. Similarly, all species x_i with $i > 2j$ will limit to zero. This implies that solutions limit to some bounded solution in the $2j-2$ species subchain where the remaining species $x_1,\ldots,x_{2j-2}$ all persist (uniformly bounded away from zero) and are bounded.

In the special case when $\alpha_j = 0$, the degenerate fixed points P^{2j-1} exist. For the particular fixed point with $s = a_{2j}/c_{2j}$ we construct

$$\begin{aligned} G_{2j} &= x_1 - P_1^{2j-1} \ln x_1 + \frac{b_1}{c_2}(x_2 - P_2^{2j-1} \ln x_2) + \ldots \\ &\quad + \frac{b_1 \ldots b_{2j-2}}{c_2 \ldots c_{2j-1}}(x_{2j-1} - P_{2j-1}^{2j-1} \ln x_{2j-1}) + \frac{b_1 \ldots b_{2j-1}}{c_2 \ldots c_{2j}} x_{2j}. \end{aligned}$$

Again, we can show that

$$\frac{dG_{2j}}{dt} = -\frac{b_1 \ldots b_{2j}}{c_2 \ldots c_{2j}} x_{2j}x_{2j+1}$$

which implies that G is strictly decreasing. By a similar argument, we see that $x_{2j} \to 0$ while all lower-level species remain bounded away from 0 and ∞ while all species higher than x_{2j} go extinct. □

5 Sustainable chains with an odd number of species

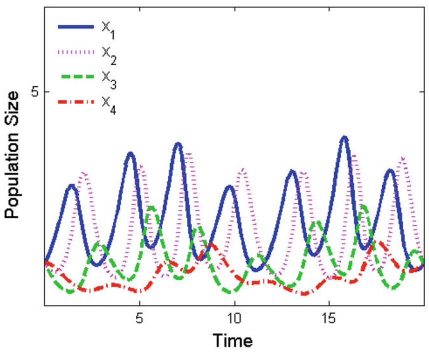
We now prove for a sustainable food chain with an odd number of species that is not critically sustainable, that all positive solutions are unbounded, by this we mean that any solution with positive initial conditions will have one or more co-ordinates which are unbounded. Let $n = 2k-1$, and suppose the sustainability constant $\alpha_k > 0$. Recall from (6) that F_n is the product of the odd level species. Thus, when F_n is increasing, it implies some odd level species x_{2j-1} is unbounded. This implies that at least one of $x_1, x_3, \ldots$, and x_{2k-1} is unbounded. Biologically, this implies that the chain will be limited only by resources and not predator regulated.

We note here that numerical evidence suggests that the even level species actually approach a limiting value after exhibiting oscillations. In this case, the odd level species limit to infinity, which is stronger than simply being unbounded.

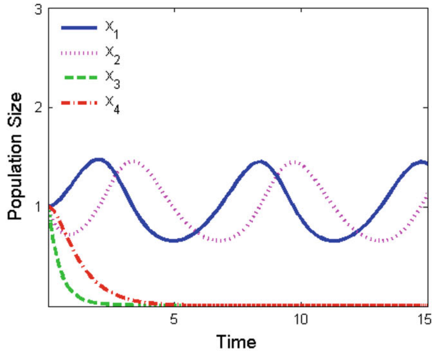
6 Examples

We illustrate the different types of behavior that can be seen for both a food chain with an even number of species, and an odd number of species using numerical examples. Consider, for example, a chain of $n = 4$ species. Figure 1 illustrates for a particular set of initial conditions the different types of behavior that can occur in a food chain with an even number of species. In Fig. 1a, the sustainability constant $\alpha_2 > 0$ and all species persist and remain bounded. We note that the size of the oscillations in Fig. 1a will increase as the initial condition increases in distance from the equilibrium point. Figure 1b corresponds to $\alpha_2 < 0$ and shows a cascade of extinction with the top two species x_3 and x_4 going to zero, while x_1 and x_2 persist and remain bounded. Finally, for $\alpha_2 = 0$, x_4 dies off, while x_1, x_2 and x_3 persist and remain bounded. In the case of $n = 4$, the food chain can only support four species if $\alpha_2 > 0$, while for $\alpha_2 \leq 0$ some species go extinct. This result is consistent with Volterra's result for even food chains (Volterra 1931), and also supports the ecological theory that the productivity of food chains with an even number of species are predator regulated, or top down.

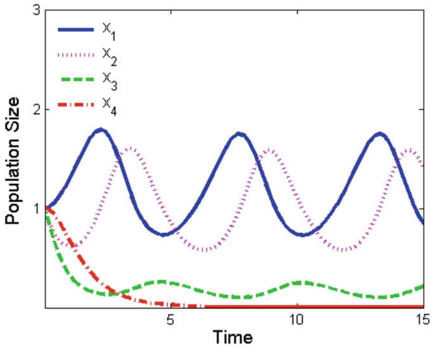
We illustrate the different types of behavior that a food chain with an odd number of species can exhibit, using $n = 3$ as an example. Figure 2 shows the range of behaviors for different sustainability constants. Figure 2a shows that for $\alpha_2 > 0$, trajectories corresponding to x_1 and x_3 grow unbounded, while x_2 limits to a positive value. In Fig. 2b, for $\alpha_2 < 0$, x_3 dies off, while x_1 and x_2 persist and remain bounded, which reflects the dynamics of the classical two species Lotka–Volterra predator–prey model. The food chain is critically sustainable for $\alpha_2 = 0$, and all orbits persist and remain bounded, as can be seen in Fig. 2c. Thus, for $\alpha_2 \geq 0$, all species persist, hence the food chain is sustainable. In the case $\alpha_2 > 0$, the orbit with unbounded x_1 and x_3 co-ordinates indicate that the food chain could sustain an additional species. Moreover, limiting behavior is not predator limited in this model, which suggests that odd level food chains are only limited by resources. These results generalize the work of Chauvet et al. (2002) for the three species case and support the ecology hypothesis that productivity of food chains with an odd number of species is resource limited, or bottom up.



(a) $a_1 = 1.7,\ a_3 = b_1 = c_3 = 1, \alpha_2 > 0$



(b) $a_1 = b_1 = c_3 = 1,\ a_3 = 2, \alpha_2 < 0$



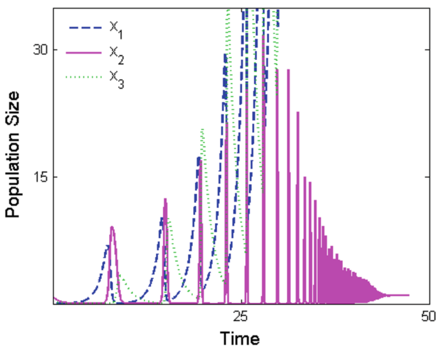
(c) $a_1 = a_3 = b_1 = c_3 = 1, \alpha_2 = 0$

Fig. 1 Plots of solutions for the three cases of parameter values with initial condition [1, 1, 1, 1]

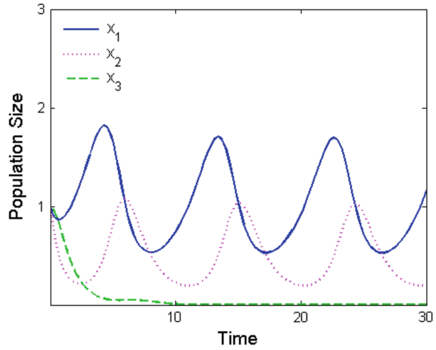
Another way to look at productivity of food chains is in terms of the species that the food chain cannot support, that is those species that become extinct. We call this phenomena cascades of extinctions. Figure 3 illustrates sustainability, or cascades of extinction, for a food chain with $n = 5$ species. Sustainability or extinction is indicated by the sustainability constants. For $n = 5,\ \alpha_3 \geq 0$, all species persist. If $\alpha_3 < 0$, then x_5 dies off and there are four species remaining. The dynamics of these four species is determined by the sign of α_2. For $\alpha_2 \leq 0$, additional species die off, but for $\alpha_2 > 0$, the remaining four species persist. Thus, the sustainability constants predict the cascades of extinction for a food chain of any length.

7 Conclusions

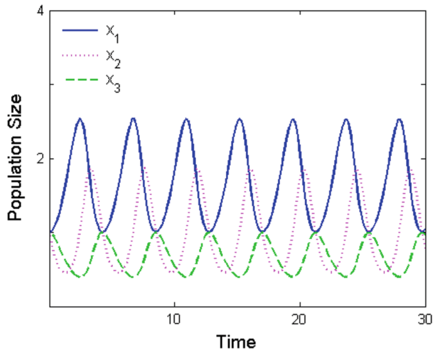
Parity of the number of species in a food chain has been known to affect the dynamics of that chain. Ecologists conjectured that plant biomass could only accumulate in food chains with an odd number of species (Persson et al. 1992), because for an even number of species, predation by herbivores always limits the plant population,



(a) $a_1 = c_3 = 1,\ a_3 = b_3 = 0.75,\ \alpha_2 > 0$



(b) $a_1 = 0.5,\ a_3 = b_1 = c_3 = 1, \alpha_2 < 0$



(c) $a_1 = a_3 = b_1 = c_3 = 1, \alpha_2 = 0$

Fig. 2 Plots of solutions for the three cases of parameter values with the initial condition [0.01, 0.8, 0.15] for (**a**) and [1, 1, 1] for figures (**b**) and (**c**)

making unbounded growth impossible (Fretwell 1977). Using Lotka–Volterra predation models, we showed that sustainability of a food chain can be determined by the sustainability constants, we define in terms of net growth rates and competition rates. These sustainability constants indicate whether a chain of n species can support n species without extinction, or, in contrast, if the productivity of that same chain can support additional species.

The qualitative behavior of a sustainable odd food chain is different from that of a sustainable even food chain. Sustainable even level food chains have bounded orbits, and thus cannot experience unbounded accumulation so must be regulated by predation. Sustainable odd food chains, however, are limited by resources, as evidenced by unbounded orbits in our model. Unbounded orbits do not appear in natural ecosystems because an abundance of resources would be consumed by additional species, hence we interpret unbounded orbits as a measure of the productivity of the ecosystem and as an indication that the system can support additional species.

Further analysis revealed that additional species can affect the odd co-ordinates of the equilibrium differently than the even co-ordinates. To illustrate this phenomenon,

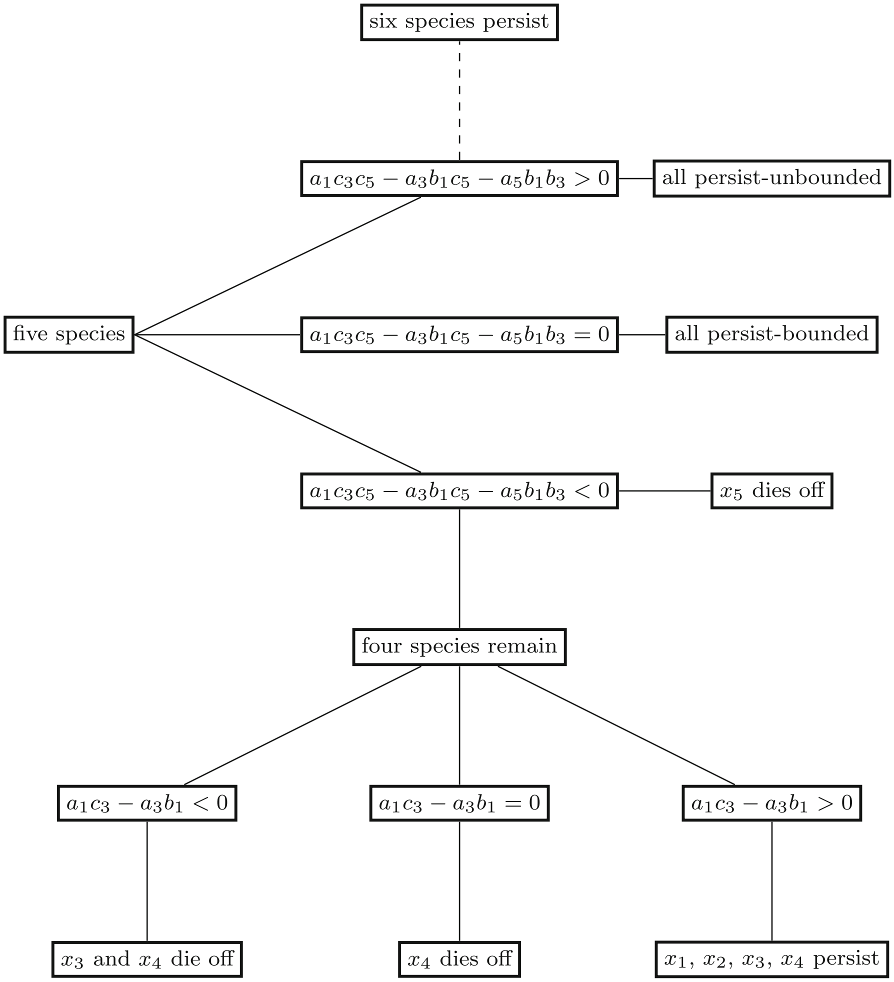


Fig. 3 Illustration of possible cascades of extinction for a five species food chain. If α_3 and $\alpha_2 < 0$ then species x_5, x_4, and x_3 die off in succession. If $\alpha_3 > 0$ the odd level species grow unbounded which indicates a sixth species could be supported (indicated by the *dashed line*). All possible parameter cases are considered and the species that persist are listed

consider two food chains, one with $2n$ species and the other with $2n + 2$ species. We noted that although the even components of the equilibria are the same for $m \leq 2n$, the odd co-ordinates of the food chain with $2n + 2$ species are greater than the odd co-ordinates of the food chain with $2n$ co-ordinates. Thus, in terms of equilibrium dynamics, additional species in the food chain benefit the odd-level species lower in the food chain, while there is no effect on the even level species.

The Lotka–Volterra predation model of food chains is consistent with the ecological conjecture that parity of the food chain determines whether the productivity of the food chain is regulated by predation or resources. Food chains with odd parity experience accumulation, whereas food chains with even parity always have bounded orbits, even without the presence of a logistic term. In fact, our research suggests that one should be cautious regarding the inclusion of a logistic term on a sustainable even food chain since such a term may change the cause of the bounded behavior from predator limited to resource limited.

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