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EXTINCTION, WEAK EXTINCTION AND PERSISTENCE IN A DISCRETE, COMPETITIVE LOTKA-VOLTERRA MODEL

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In a discrete Lotka-Volterra model, the set of points where a population remains unchanged over one generation is a hyperplane. Examining the relative position of these hyperplanes, we give sufficient conditions for a group of species to drive another species to extinction. Further using these hyperplanes, we find necessary and sufficient conditions where every ω-limit point of the model has at least one species missing. Building on the work of Hofbauer *et al.* (1987) involving permanence, we obtain a sufficient condition for one or more species to persist. Additionally, in the presence of extinction occurring, we take these persistence results and the previously mentioned extinction results and extend them to subsystems of the full model. Finally, we combine the ideas of persistence and weak extinction to obtain another extinction result.

Keywords: extinction, persistence, weak extinction, Lotka-Volterra model, ω-limit set

1. Introduction

Two important concepts in population modeling are those of persistence and extinction. Much of the current research deals with modeling species on the brink of extinction (Carroll and Lamberson, 1993; Lamberson *et al.*, 1992), and finding ways to prevent it from happening. Other modeling projects deal with disease populations and trying to control their growth (Keeling and Grenfell, 1997).

In this paper, we address the issues of extinction and persistence in a model of Kolmorgorov-type. We will consider the following n-dimensional model where the growth factor of each species is a function of a linear combination of the other species,

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ \vdots \\ x_n(t+1) \end{bmatrix} = F \begin{bmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{bmatrix} = \begin{bmatrix} F_1(x_1(t), x_2(t), \dots, x_n(t)) \\ F_2(x_1(t), x_2(t), \dots, x_n(t)) \\ \vdots \\ F_n(x_1(t), x_2(t), \dots, x_n(t)) \end{bmatrix} \qquad (1)$$

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where

$$F_i(x_1(t), x_2(t), \ldots, x_n(t)) = x_i\lambda_i\Big(\sum_{j=1}^{n} \alpha_{ij}x_j\Big) = x_i \exp\Big(r_i - \sum_{j=1}^{n} \alpha_{ij}x_j\Big).$$

Hofbauer *et al.* (1987) called this model a system of Lotka-Volterra type and showed that it has many of the properties of the Lotka-Volterra differential equations. The one-dimensional version of this model was studied by May (1975). He showed that this system can be chaotic. A two-dimensional version was studied by Comins and Hassell (1976).

Each growth function $\lambda_i : \mathbb{R}_+ \to \mathbb{R}_+$, $\lambda_i(x) = \exp(r_i - x)$, is a decreasing exponential. We will take each $r_i > 0$ so that the population of each species is growing when the population is small. Selgrade and Namkoong (1990) called species with this type of growth function 'pioneer' species. We will also take all the $\alpha_{ij} > 0$. This forces all of the growth rates to decrease with increases in any population and makes this system competitive. Franke and Yakubu (1991) established some extinction results for this system.

We have four goals in this paper. The first is to contrast the ideas of equilibrium populations and weak extinction. One may think of weak extinction occurring if, when one samples the population after many generations, it appears that there are one or more species dying out. We will show that weak extinction is equivalent to having no equilibrium population density where every species is present.

The second goal is to give sufficient conditions where a group of species can drive another species extinct. We will give this condition in terms of weak dominance. The idea is similar to that of one species driving another species to extinction (Chan and Franke, 1999; Franke and Yakubu, 1991; 1992; 1993). In this case, two or more species can cooperate to drive another to extinction.

The third goal is to extend the permanence results of Hofbauer *et al.* (1987) in terms of persistence. They gave sufficient conditions for system (1) to have permanence. We observe that their ideas can also be applied to one or a group of the species and get persistence of each species in the group.

Finally, we extend the above persistence and extinction results to subspaces where we assume that one or more species is going extinct. Here one can apply the theorems on the subspaces on which the system is limiting due to extinction and obtain further extinction or persistence. These tools allow the investigator to predict the long term behavior of system (1) at many levels.

2. Background

In this section, we will define some basic notation and give some basic results for system (1). We define $\mathbb{R}_+ = [0, \infty)$ and $\mathring{\mathbb{R}}^n_+$ to be the interior of $\mathbb{R}^n_+$. $\mathring{\mathbb{R}}^n_+$ is the set of population densities where every species' population is positive. We denote $F^m(\boldsymbol{x})$ as the m-th iteration of F, which represents the population densities after m generations. Further, $F^m_j(\boldsymbol{x})$ represents the population density of the j-th species at the m-th generation. Throughout the paper, we will use $\omega(x)$ to represent the ω-limit set of a point x.

Using the competitive nature of system (1), Franke and Yakubu (1991) established that populations stay bounded. For $x \in \mathbb{R}^n_+$, let $\mathcal{O}^+(x) = \{F^m(x)\}_{m=0}^{\infty}$ be its forward orbit. Each forward orbit is a bounded set. Note that $\mathbf{0}$, the origin, is a fixed point for system (1) and $\mathbb{R}^n_+ \backslash \mathbf{0}$ is forward invariant, i.e., $F(\mathbb{R}^n_+ \backslash \mathbf{0}) \subset \mathbb{R}^n_+ \backslash \mathbf{0}$.

A subset $\mathcal{X}$ of $\mathbb{R}^n_+ \backslash \mathbf{0}$ is absorbing if it is positively invariant, and $\mathcal{O}^+(x) \cap \mathcal{X} \neq \emptyset$ for $x \in \mathbb{R}^n_+ \backslash \mathbf{0}$. We say a plane P is above another plane Q if on each axis the intercepts of P are above the intercepts of Q. The following proposition, which follows directly from the work of Chan and Franke (1999), establishes the existence of a compact absorbing set.

Proposition 1. *(Chan and Franke, 1999) Let $F : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ be the dynamical system (1). Then there are planes $P_{\max}$ and $P_{\min}$ which intersect each positive axis with $P_{\max}$ above $P_{\min}$ such that if $\mathcal{X}$ is the region on and in between them, then $\mathcal{X}$ is positively invariant. Moreover, if $x \in \mathbb{R}^n_+ \backslash \mathbf{0}$, then there exists an $n_0 = n_0(x)$ such that $F^{n_0}(x) \in \mathcal{X}$.*

In fact, this shows that $\mathcal{X} \cup \{\mathbf{0}\}$ is absorbing for all $\mathbb{R}^n_+$. In this sense, we say $\mathcal{X} \cup \{\mathbf{0}\}$ is a global attractor for (1) which implies that the system is dissipative by definition (Hofbauer *et al*, 1987). In this model, the origin is a repelling fixed point, and starting at any other point in the system, that point is attracted to $\mathcal{X}$. Hofbauer *et al.* (1987) use a global bounded attractor X to prove their results. For our system, we can consider $X = \mathcal{X} \cup \{\mathbf{0}\}$.

Define $N(\lambda_i) = \{x \in \mathbb{R}^n_+ \mid \lambda_i(\sum_{j=1}^n a_{ij}x_j) \geq 1\}$. $N(\lambda_i)$ is the set of population densities where the population density of species i is nondecreasing. We define $\overset{\circ}{N}(\lambda_i) = \{x \in \mathbb{R}^n_+ | \lambda_i(\sum_{j=1}^n a_{ij}x_j) > 1\}$ which is the set of population densities where species i is strictly increasing. So $\partial N(\lambda_i)$ is the set of population densities where species i remains constant in the following generation. For this model $\partial N(\lambda_i)$ is part of a hyperplane which we will denote as P^i. Thus,

$$P^i = \left\{x \in \mathbb{R}^n \mid r_i - \sum_{j=1}^{n} \alpha_{ij}x_j = 0\right\},$$

and $\partial N(\lambda_i) = P^i \cap \mathbb{R}^n_+$. Since all parameters are positive, each P^i intersects each positive axis and so cuts $\mathbb{R}^n_+$ into two pieces, one of which is bounded.

We say that the i-th species, or species i, goes extinct if for all $x \in \overset{\circ}{\mathbb{R}}{}^n_+$, the i-th component of every ω-limit point of x is zero, i.e., if $p \in \omega(x)$, then $p_i = 0$. If one or more species go extinct, then the system exhibits extinction.

We say a system exhibits *weak extinction* if for every $x \in \overset{\circ}{\mathbb{R}}{}^n_+$ and for each $y \in \omega(x)$ we have $y \in \partial\mathbb{R}^n_+$, i.e. for each $y \in \omega(x)$ there exists a j such that the j-th component of y is zero. Thus each ω-limit point is a situation where at least one species is missing. It is easy to see that extinction implies weak extinction, but weak extinction covers many more cases and so the converse does not hold, see Example 2 in Section 3.

We say a species i weakly dominates another species j, if $N(\lambda_j) \subset \overset{\circ}{N}(\lambda_i)$. Additionally, we say a group of species $1, 2, \ldots, l-1$ weakly dominates a species l if $N(\lambda_l) \subset \cup_{i=1,\ldots,l-1} \overset{\circ}{N}(\lambda_i)$. This gives us that when species l is not shrinking at least one of the other species is growing.

Example 1. In the following system, species 1 does not weakly dominate species 3, nor does species 2 weakly dominate species 3. Together, though, species 1 and species 2 weakly dominate species 3.

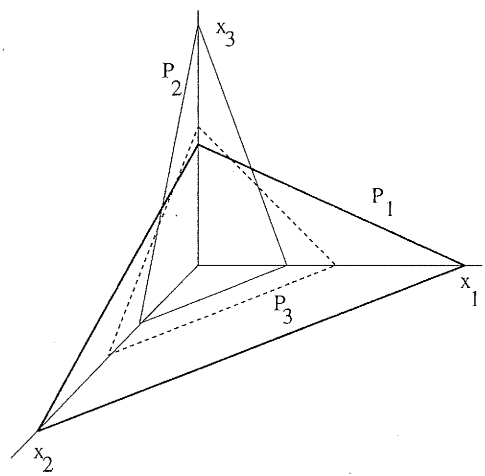

Fig. 1. Two species weakly dominating a third.

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{bmatrix} = \begin{bmatrix} x_1(t)\exp(1 - .5x_1(t) - .5x_2(t) - 1.1x_3(t)) \\ x_2(t)\exp(1 - 1.5x_1(t) - 1.5x_2(t) - .5x_3(t)) \\ x_3(t)\exp(1 - x_1(t) - x_2(t) - x_3(t)) \end{bmatrix}. \quad (2)$$

For this example we have the following planes as seen in Fig. 1.

$$P^1 = \{\boldsymbol{x} = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - .5x_1 - .5x_2 - 1.1x_3 = 0\},$$
$$P^2 = \{\boldsymbol{x} = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - 1.5x_1 - 1.5x_2 - .5x_3 = 0\},$$
$$P^3 = \{\boldsymbol{x} = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - x_1 - x_2 - x_3 = 0\}.$$

♦

A species l persists or is persistent, if there exists an $\eta > 0$ such that for each $\boldsymbol{x} \in \overset{\circ}{\mathbb{R}}{}^n_+$ we have

$$\liminf_{m\to\infty} F_l^m(\boldsymbol{x}) > \eta.$$

Biologically, this means that species l grows to a minimum level and stays above that level. If all of the species persist, then we say that the system exhibits permanence.

Many of the proofs in the following sections use Lyapunov or Lyapunov-type arguments. In these arguments, we will use a particular function called a Lyapunov function. A Lyapunov function for a dynamical system F with respect to a positively invariant set W is a positive, continuous function that decreases along orbits in W. An eventually Lyapunov function is a positive, continuous function that, after a finite number of iterations along an orbit, decreases on the remainder of the orbit. One of the useful results for Lyapunov or eventually Lyapunov functions is the following.

Lemma 1. *Let X be a metric space. If V is an eventually Lyapunov function for a discrete dynamical system, $F : X \to X$, with respect to a positively invariant set $W \subset X$ and $\boldsymbol{q} \in W$, then for all $\boldsymbol{p} \in \omega(\boldsymbol{q})$, $\boldsymbol{p} \notin W$.*

Proof. Let $\boldsymbol{q} \in W$ and $\boldsymbol{p} \in \omega(\boldsymbol{q})$. Suppose $\boldsymbol{p} \in W$. Then there is a k such that for $\boldsymbol{p}' = F^k(\boldsymbol{p})$ we get

$$V(F(\boldsymbol{p}'))/V(\boldsymbol{p}') < 1. \tag{3}$$

Note that since $\boldsymbol{p}'$ is in the orbit of $\boldsymbol{p}$, $\boldsymbol{p}' \in \omega(\boldsymbol{q})$. From (3), we can conclude that $F(\boldsymbol{p}') \neq \boldsymbol{p}'$. Let $3\epsilon = V(\boldsymbol{p}') - V(F(\boldsymbol{p}'))$. Let B_1 and B_2 be open balls with radii δ_1 and δ_2 about the points $\boldsymbol{p}'$ and $F(\boldsymbol{p}')$, respectively. Choose δ_1 and δ_2 such that $B_1 \cap B_2 = \emptyset$ and for $\boldsymbol{x}_1 \in B_1$, $|V(\boldsymbol{x}_1) - V(\boldsymbol{p}')| < \epsilon$ and for $\boldsymbol{x}_2 \in B_2$, $|V(\boldsymbol{x}_2) - V(F(\boldsymbol{p}'))| < \epsilon$. We can do this since V is a continuous function.

Now note that the orbit of $\boldsymbol{q}$ must enter B_1, then B_2, and then B_1 again since $\boldsymbol{p}'$ and $F(\boldsymbol{p}')$ are in $\omega(\boldsymbol{q})$. This would imply that V increases, which is a contradiction. Thus $\boldsymbol{p}'$ and $\boldsymbol{p} \notin W$. ■

In obtaining our extinction results, we utilized a few aspects of convex cones. A subset K of $\mathbb{R}^n$ is a convex cone if

1. $\alpha K \subset K$ for scalars $\alpha \geq 0$, and
2. $K + K \subset K$.

K is a solid cone if its interior is not empty. One may construct a convex cone K by starting with a convex set A and use all the rays from the origin which go through points in A.

3. Weak Extinction

In this section, we will prove that, if system (1) has no equilibrium population density with all species present, then the system exhibits weak extinction. This implies that the ω-limit set of every interior point is a subset of the boundary. In order to prove this, we need some results from cone theory. The main result is the following which is due to Berman and Ben-Israel (Berman 1973), in which the range of A is denoted by $R(A)$.

We can rewrite this system as the matrix equation

$$Ax = r,$$

where A is an $l \times n$ matrix, and x and r are $n \times 1$ and $l \times 1$ vectors, respectively. Using Corollary 1, we see that either $r \notin R(A)$, or there exists a c such that $0 \neq A^T c \in K^*$ and $\sum_{i=1}^{l} c_i r_i \leq 0$.

Suppose that $r \notin R(A)$. Since $l \leq n$, A cannot be of full rank; thus A must be degenerate. If A is degenerate, then there exists a $c = (c_1, c_2, \ldots, c_l)$ such that

$$\sum_{k=1}^{l} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) = 0 \tag{4}$$

for all $x \in \mathbb{R}^n$. Furthermore, since any fewer rows of A are consistent, we have that for each $1 \leq i \leq l$, $c_i \neq 0$. Note that the first $l-1$ equations are consistent, and so have a solution $\bar{x} \in \overset{\circ}{K}$, which satisfy the first $l-1$ equations. Thus

$$\sum_{k=1}^{l-1} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} \bar{x}_j \Big) = \sum_{i=1}^{l-1} c_i r_i.$$

But the system of l equations is not consistent in $\overset{\circ}{K}$. Since (4) is true for all $x \in \overset{\circ}{K}$, and in particular at $\bar{x}$, we must have

$$\sum_{k=1}^{l} c_k r_k \neq 0.$$

Otherwise, $\bar{x}$ would have to satisfy the l-th equation and the system would be consistent, which is a contradiction.

From (4), since the c_i's are nonzero and the α's are positive, there must be an i and j where $c_i > 0$ and $c_j < 0$. Without loss of generality, assume that

$$\sum_{k=1}^{l} c_k r_k < 0,$$

otherwise negate c. This gives us that

$$\sum_{k=1}^{l} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) > \sum_{k=1}^{l} c_k r_k.$$

On the other hand, if there exists a c such that $0 \neq A^T c \in K^*$ and

$$\sum_{i=1}^{l} c_i r_i \leq 0, \tag{5}$$

then for this c using a cone property we have for all $x \in \overset{\circ}{K}$,

$$c^T A x = \sum_{k=1}^{l} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) > 0. \tag{6}$$

Note that if there exists an $1 \leq i \leq l$ where $c_i = 0$, then the system of equations not including the i-th equation is consistent. So there exists an $x \in \overset{\circ}{K}$ where

$$c^T Ax = \sum_{k=1}^{l} c_k r_k.$$

Thus, we must have $c_i \neq 0$ for all $1 \leq i \leq l$. Note that from (5) we have that there exists an i where $c_i < 0$ and from (6) we have a j where $c_j > 0$. Putting (5) and (6) together, we again obtain

$$\sum_{k=1}^{l} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) > \sum_{k=1}^{l} c_k r_k.$$

Now for either case we let $c_i = 0$ for $l+1 \leq i \leq n$, this gives us

$$\sum_{k=1}^{n} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) > \sum_{k=1}^{n} c_k r_k.$$

This completes the proof. ■

In fact in the above proof, we actually prove a stronger result which is the following.

Corollary 2. *Let $K \supset \mathbb{R}^n_+$ be a convex cone and $P^i = \{x \in \mathbb{R}^n \mid r_i - \sum_{j=1}^n \alpha_{ij} x_j = 0\}$. If*

$$\bigcap_{i=1}^{l} P^i \cap \overset{\circ}{K} = \emptyset$$

but

$$\bigcap_{i \in A} P^i \cap \overset{\circ}{K} \neq \emptyset$$

for each A, a proper subset of $\{1, 2, \ldots, l\}$, where $2 \leq l \leq n$, then there exists a $c = (c_1, c_2, \ldots, c_l)$ with $c_i \neq 0$ for $1 \leq i \leq l$ such that

$$\sum_{k=1}^{l} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) > \sum_{k=1}^{l} c_k r_k.$$

Moreover, there exists an $i, j \in \{1, 2, \ldots, l\}$ where $c_i > 0$ and $c_j < 0$.

Now we are ready for the weak extinction result. We show here that, for our system, the lack of an equilibrium distribution with each species present is equivalent to weak extinction. Also we note here that it is not difficult in general to determine whether an equilibrium distribution with all species present exists or not. One can either check to see if $\cap_{i=1}^n P^i \cap \overset{\circ}{\mathbb{R}}{}^n_+$ is empty or not, or check to see if the system $\{\sum_{j=1}^n \alpha_{ij} x_j = r_i\}_{i=1}^n$ is consistent or not relative to $\overset{\circ}{\mathbb{R}}{}^n_+$.

Theorem 3. *System (1) exhibits weak extinction if and only if it does not have an equilibrium population density with all species present.*

Proof. First note that, if system (1) does have an equilibrium population density with all species present, then the system cannot exhibit weak extinction since there would be a point whose ω-limit set is not a subset of the boundary.

On the other hand, if there does not exist an equilibrium population density with all species present, then $\cap_{i=1}^{n} P^i \cap \overset{\circ}{\mathbb{R}}{}^n_+ = \emptyset$. So letting $K = \mathbb{R}^n_+$ we obtain by Theorem 2 a $\boldsymbol{c} = (c_1, c_2, \ldots, c_n)$ where

$$\sum_{k=1}^{n} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) > \sum_{k=1}^{n} c_k r_k \tag{7}$$

is true on $\overset{\circ}{\mathbb{R}}{}^n_+$.

Now define $V : \overset{\circ}{\mathbb{R}}{}^n_+ \to \mathbb{R}_+$ to be

$$V(x_1, x_2, \ldots, x_n) = x_1^{c_1} x_2^{c_2} \cdots x_n^{c_n}$$

We will show that V is a Lyapunov function. For $\boldsymbol{q} \in \overset{\circ}{\mathbb{R}}{}^n_+$, compute the ratio of V applied to $F(\boldsymbol{q})$ and $\boldsymbol{q}$. This gives

$$\frac{V(F(\boldsymbol{q}))}{V(\boldsymbol{q})} = \exp \left(\sum_{k=1}^{l} c_k r_k - \sum_{k=1}^{l} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) \right),$$

but from (7) we get

$$\frac{V(F(\boldsymbol{q}))}{V(\boldsymbol{q})} < 1$$

for all $\boldsymbol{q} \in \overset{\circ}{\mathbb{R}}{}^n_+$. So V is decreasing along orbits in $\overset{\circ}{\mathbb{R}}{}^n_+$. Note that $\overset{\circ}{\mathbb{R}}{}^n_+$ is positively invariant, so by Lemma 1, for all $\boldsymbol{q} \in \overset{\circ}{\mathbb{R}}{}^n_+$, $\omega(\boldsymbol{q}) \subset \partial \overset{\circ}{\mathbb{R}}{}^n_+$. Thus, the system exhibits weak extinction. ∎

This gives a nice condition to determine whether weak extinction occurs, and thus have completed our first goal. At this point we would like to comment on weak extinction. If a system exhibits extinction, then it also exhibits weak extinction. But weak extinction also includes mutual exclusion. In the following section, we will use a slightly stronger hypothesis and prove a particular species goes extinct.

Example 2. The following is an example of weak extinction that does not have extinction. There is no equilibrium points with all species present. This implies the system exhibits weak extinction. Also each of the equilibrium points on the axes z^1, z^2, and z^3 is locally attracting. Hence there are points in $\overset{\circ}{\mathbb{R}}{}^n_+$ which limit on each of the points z^1, z^2, and z^3. Thus, no species goes extinct.

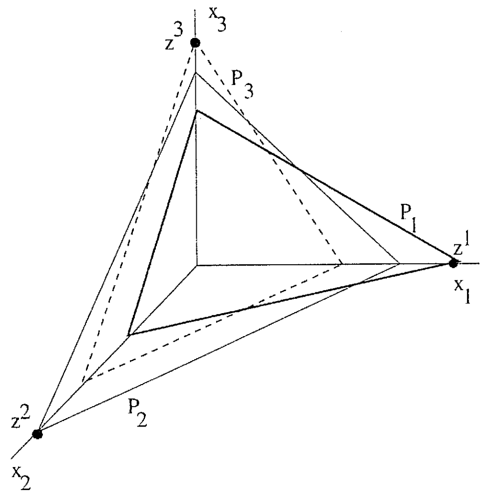

Fig. 2. Weak extinction without extinction.

We have

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{bmatrix} = \begin{bmatrix} x_1(t)\exp(1 - .5x_1(t) - x_2(t) - 1.5x_3(t)) \\ x_2(t)\exp(1 - .7x_1(t) - .5x_2(t) - .7x_3(t)) \\ x_3(t)\exp(1 - 1.5x_1(t) - .75x_2(t) - .5x_3(t)) \end{bmatrix}. \quad (8)$$

For this example we get the following planes as seen in Fig. 2.

$$\begin{aligned} P^1 &= \{x = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - .5x_1 - x_2 - 1.5x_3 = 0\}, \\ P^2 &= \{x = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - .7x_1 - .5x_2 - .7x_3 = 0\}, \\ P^3 &= \{x = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - 1.5x_1 - .75x_2 - .5x_3 = 0\}. \end{aligned}$$

♦

4. Extinction

In this section, we generalize the ideas of Franke and Yakubu (1991) where they showed that if one species weakly dominates another species, then the latter will be driven to extinction. By geometrically describing how a group of species weakly dominates another species, we show how a group of species can cooperate to drive another to extinction. In this case, none of the cooperating species would drive the doomed species to extinction alone. Referring to Example 1 in Section 2, this is an example where the first and second species drive the third to extinction.

To show a species goes extinct, it is necessary to show that the ω-limit set for each interior point of $\mathbb{R}^n_+$ is a subset of one of the faces of $\partial\mathbb{R}^n_+$. Species i goes extinct if $\lim_{m\to\infty} F_i^m(x) = 0$, for every $x \in \overset{\circ}{\mathbb{R}}{}^n_+$. We establish this by finding a particular

Lyapunov function that has enough information to give extinction of a species. The following proposition proves that a Lyapunov function of the form

$$V(x) = x_l^{c_l} \prod_{i=1}^{l-1} x_i^{-c_i},$$

where each $c_i > 0$, is sufficient for this task. For a collection A, we define $\mathbb{R}_A^n = \{x \in \mathbb{R}_+^n \mid \prod_{i \in A} x_i \neq 0\}$. We denote the complement of this set relative to $\mathbb{R}_+^n$ as

$$S_A^n = \Big\{x \in \mathbb{R}_+^n \mid \prod_{i \in A} x_i = 0\Big\}.$$

Note that $S_A^n \cup \mathbb{R}_A^n = \mathbb{R}_+^n$, and that $S_A^n \cap \mathbb{R}_A^n = \emptyset$.

Proposition 2. *Let $F : \mathbb{R}_+^n \to \mathbb{R}_+^n$ be the dynamical system (1) and let $V : \mathbb{R}_{1,\dots,l}^n \to \mathbb{R}_+$ be defined by*

$$V(x_1, x_2, \dots, x_n) = \frac{x_l^{c_l}}{x_1^{c_1} \cdots x_{l-1}^{c_{l-1}}}, \tag{9}$$

where $c_i > 0$ for each i. If V is an eventually Lyapunov function for F with respect to $\mathbb{R}_{1,\dots,l}^n$, $q \in \overset{\circ}{\mathbb{R}}{}_+^n$, and $p \in \omega(q)$, then $p_l = 0$, i.e. the l-th species goes extinct.

Proof. Let $V(x_1, x_2, \dots, x_n) = x_l^{c_l}/(x_1^{c_1} \cdots x_{l-1}^{c_{l-1}})$ be an eventually Lyapunov function for F with respect to $\mathbb{R}_{1,\dots,l}^n$ and let $q \in \mathbb{R}_{1,\dots,l}^n \supset \overset{\circ}{\mathbb{R}}{}_+^n$. Note that each face and subface of $\partial \mathbb{R}_+^n$ is invariant and that no species can go to extinction in finite time, so $\mathbb{R}_{1,\dots,l}^n$ is an invariant set. By assumption, there is a k' such that $k \geq k'$ gives

$$\frac{V(F^{k+1}(q))}{V(F^k(q))} < 1.$$

Now using Lemma 1, if $p \in \omega(q)$ then $p \notin \mathbb{R}_{1,\dots,l}^n$ which implies that $p \in S_{1,\dots,l}^n$. So $\prod_{i=1}^l p_i = 0$, i.e. one or more of the p_j's are zero, where $j \in \{1, 2, \dots, l\}$. Suppose that $p_l \neq 0$ and one or more of the $p_j = 0$ for $j \in \{1, 2, \dots, l-1\}$. Let $\{t_i\}_{i=1}^\infty$ be such that $\lim_{i \to \infty} F^{t_i}(q) = p$. By the nature of V, the set $\{V(F^{t_i}(q)) \mid i = 1, 2, \dots\}$ is unbounded since $p_j = 0$ and $p_l \neq 0$. This is a contradiction since V is eventually decreasing along orbits. Thus we must have $p_l = 0$. ■

In order to use this Lyapunov result, we need to obtain a Lyapunov function in the form of (9). This is achieved by accurately describing the geometry which is involved when a group of species weakly dominate another species. The following several lemmas and theorems describe this geometry which is then finally used in Theorem 6. Theorem 6 is the main theorem in this section and shows how a group of species can drive another species to extinction.

Recall that $\partial N(\lambda_i)$, the set of points where the population of species i remains constant in the following generation, is part of a hyperplane which we denoted by P^i. Hence

$$\partial N(\lambda_i) \subset P^i = \Big\{x \in \mathbb{R}^n \mid r_i - \sum_{j=1}^n \alpha_{ij} x_j = 0\Big\},$$

and $\partial N(\lambda_i) = P^i \cap \mathbb{R}^n_+$. Note P^i divides $\mathbb{R}^n_+$ into two pieces, one piece where the following generation decreases and

$$r_i - \sum_{j=1}^{n} \alpha_{ij} x_j < 0,$$

and the other piece where it increases and

$$r_i - \sum_{j=1}^{n} \alpha_{ij} x_j > 0.$$

The origin is in the latter piece.

We say that point x is covered by a plane P^i, if x is on the side where

$$r_i - \sum_{j=1}^{n} \alpha_{ij} x_j > 0,$$

and so is on the same side as the origin. Similarly, we say a set $\mathcal{S}$ is covered by P^i if

$$r_i - \sum_{j=1}^{n} \alpha_{ij} x_j > 0$$

for each $x \in \mathcal{S}$. A collection $\{P^1, P^2, \ldots, P^l\}$ covers a set $\mathcal{S}$ if for each $x \in \mathcal{S}$ there is an $i \in \{1, 2, \ldots, l\}$ where P^i covers x.

We use this idea of covering a set with a group of planes to define geometrically how a group of species weakly dominates another species. In the following results, we are considering one species being weakly dominated by a group of species. We will relate each species in the group with its corresponding hyperplane P^i and the species which is being dominated by the hyperplane L. So in an n-dimensional model where one species is being weakly dominated by a group of species, the group can be made up at most of $n-1$ species.

We say that a collection of planes $\{P^i\}_{i=1}^k$ is a cover for a plane L relative to a cone K if $L \cap \overset{\circ}{K} \neq \emptyset$ and for each $x \in L \cap \overset{\circ}{K}$ there is a $1 \leq j \leq k$ such that x is covered by P^j. We say that a collection of planes $\{P^i\}_{i=1}^k$ is a minimal cover for a plane L relative to K, if $\{P^i\}_{i=1}^k$ is a cover for L relative to K and if for any proper subset $A \subset \{1, 2, \ldots, k\}$, $\{P^i\}_{i \in A}$ is not a cover for L relative to K. Additionally, a collection of planes $\{P^i\}_{i=1}^l$ is a partial inimal cover for a plane L relative to K, if there exists a minimal cover $\{P^i\}_{i=1}^k$ such that $\{P^i\}_{i=1}^l$ is a proper subset of $\{P^i\}_{i=1}^k$.

It is important to note that, if we have a cover for a plane L relative to K, then there is a subcollection of the cover, which is a minimal cover for L relative to K. Also note that the minimal cover is not necessarily unique and it is possible to have two minimal covers for L relative to K which are of different sizes.

Once we get a minimal cover for L relative to a cone K, we will discuss how L is covered. To do this, we will divide L into sections where in each section we keep track of which planes are covering it. We will denote the sections by the following. Define

$$L_B^A = \{x \in L \cap \overset{\circ}{K} \mid x \text{ is cover by } P^i \text{ each } i \in A \\ \text{and is not covered by } P^j \text{ for each } j \in B \backslash A\},$$

for sets $A \subset B \subset \{1, 2, \ldots, n\}$. So L_B^A is the part of plane L in the cone $\overset{\circ}{K}$ where the planes $\{P^i\}_{i \in A}$ cover it with respect to the (partial) cover $\{P^i\}_{i \in B}$. We will also denote L_B^0 as the part of L which collection B does not cover.

Now using these minimal covers, we have the following useful lemmas. This first lemma deals with some of the properties involving the planes $P^1, P^2, \ldots, P^k$, and L. Note if we only need one plane to cover L, then this case is covered by Theorem 1 in (Franke and Yakubu, 1991).

Lemma 2. *Let K be a convex cone containing $\mathbb{R}^n_+$. Let $\{P^i\}_{i=1}^k$ be a minimal cover for a plane L relative to K and suppose $k > 1$. Then*

1. *$P^i \cap L \cap \overset{\circ}{K} \neq \emptyset$ for all $1 \leq i \leq k$,*
2. *$P^i \cap P^j \cap \overset{\circ}{K} \neq \emptyset$ for all $1 \leq i, j \leq k$,*
3. *$L^0_{1\cdots j}$ for $1 \leq j \leq k-1$ and $L^i_{1\cdots j}$ for $1 \leq j \leq k$ are nonempty, convex sets,*
4. *$L^{1\cdots j}_{1\cdots j}$ is an open set relative to L for all $1 \leq j \leq k$.*

Proof. Part 1: Suppose there exists an $1 \leq i \leq k$ such that $P^i \cap L \cap \overset{\circ}{K} = \emptyset$. Then either P^i covers L or P^i does not cover any point in $L \cap \overset{\circ}{K}$. If P^i coveres L, then $k = 1$, a contradiction. On the other hand, if P^i does not cover any point in $L \cap \overset{\circ}{K}$, then P^i could not be a part of the minimal cover, and thus $P^i \cap L \cap \overset{\circ}{K} \neq \emptyset$.

Part 2: Suppose there exists an i and j such that $P^i \cap P^j \cap \overset{\circ}{K} = \emptyset$. Then we have either P^i covers P^j or vice versa. In either case the lower plane is unnecessary. Thus $P^i \cap P^j \cap \overset{\circ}{K} \neq \emptyset$.

Part 3: Since $\{P^i\}_{i=1}^j$ is a partial minimal cover, some point in $L \cap \overset{\circ}{K}$ is not covered. Hence, $L^0_{1\cdots j}$ must be nonempty. Also for a partial minimal cover or a minimal cover, $L^i_{1\cdots j}$ must be nonempty, for otherwise P^i would be unnecessary and the cover could not be minimal.

To show convexity, first note $L \cap \overset{\circ}{K}$ is a convex set and each hyperplane P^i divides L into two convex sets. Let $x, y \in L^i_{1\cdots j}$ (or $x, y \in L^0_{1\cdots j}$). Then since x and y are in the same section, each is covered and not covered by the same planes. Thus x and y are on the same side of each plane and so the line segment connecting them must also be on the same side. Thus the line segment is covered and not covered by the same planes, so the entire line segment is in $L^i_{1\cdots j}$ (or $L^0_{1\cdots j}$). Therefore $L^i_{1\cdots j}$ and $L^0_{1\cdots j}$ are convex.

Part 4: Note that each P^i splits L into two pieces. The piece it does not cover is L_i^0. The other which it does cover is L_i^i. Since $P^i \cap L \cap \overset{\circ}{K}$ is not covered, it is part of L_i^0. This leaves L_i^i as an open set relative to L since $\overset{\circ}{K}$ is open. $L_{1\cdots j}^{1\cdots j}$ consists of points in $L \cap \overset{\circ}{K}$ which are covered by every plane, so

$$L_{1\cdots j}^{1\cdots j} = \bigcap_{i=1}^{j} L_i^i.$$

Since we have an intersection of open sets, the intersection is also open. This completes the proof. ■

Note that if $k = 1$, Parts 2, 4 and the second part of 3 of Lemma 2 also hold. We will use the brackets, $\langle \cdot \rangle$, to denote the convex hull of a set of points. For example, $\langle x_1, x_2, x_3 \rangle$ is the convex hull of the points x_1, x_2, and x_3. We will use a circumflex, $\hat{\xi}$, in a list to denote the absence of ξ from the list. For instance, $\langle x_1, x_2, \dots, \hat{x}_j, \dots, x_k \rangle$ represents the convex hull $\langle x_1, x_2, \dots, x_{j-1}, x_{j+1}, \dots, x_k \rangle$. The next lemma gives some of the geometry that exists between the $L_{1\cdots j}^i$s.

Lemma 3. *Let K be a convex cone containing $\mathbb{R}_+^n$. Let $\{P^i\}_{i=1}^k$ be a partial minimal cover of a plane L relative to K, and $x_i \in L_{1\cdots j}^i$ for $i = 1, 2, \dots, k$. Then $x_j \notin \langle x_1, x_2, \dots, \hat{x}_j, \dots, x_k \rangle$ for each $1 \le j \le k$.*

Proof. Since $x_j \in L_{1\cdots j}^j$, we have $x_1, \dots, \hat{x}_j, \dots, x_k$ are on one side of P^j and x_j is on the other. Since $x_1, \dots, \hat{x}_j, \dots, x_k$ are on one side of P^j, so is its convex hull $\langle x_1, x_2, \dots, \hat{x}_j, \dots, x_k \rangle$. Thus $x_j \notin \langle x_1, x_2, \dots, \hat{x}_j, \dots, x_k \rangle$. ■

Since $x_j \notin \langle x_1, x_2, \dots, \hat{x}_j, \dots, x_k \rangle$, each x_i is an extreme point of the convex hull (Coppel, 1998). For a convex hull $\langle x_1, x_2, \dots, x_k \rangle$, we can find a smallest dimensional linear subspace which contains it. Relative to this linear subspace, the boundary of the convex hull consists of lower dimensional convex hulls or faces. In particular, these faces can be written as convex hulls with fewer points (Coppel, 1998). With this in mind, we have

$$\partial \langle x_1, x_2, \dots, x_k \rangle \subset \bigcup_{j=1}^{k} \langle x_1, x_2, \dots, \hat{x}_j, \dots, x_k \rangle.$$

If the convex hull has dimension $k-1$, we obtain equality of the above sets.

When adding a new planes P^l to a partial cover, one can look at a convex hull of points $\langle x_1, x_2, \dots, x_{l-1} \rangle$ where $x_i \in L_{1\cdots l-1}^i \cap P^l$. The convex hull, $\langle x_1, x_2, \dots, x_{l-1} \rangle$, is a means of describing how the new plane, which would contain $\langle x_1, x_2, \dots, x_{l-1} \rangle$, fits relative to the partial cover $\{P^1, P^2, \dots, P^{l-1}\}$. With this in mind, we have the following lemma.

Lemma 4. *Let K be a convex cone containing $\mathbb{R}_+^n$. Let $\{P^i\}_{i=1}^k$ be a partial minimal cover of a plane L relative to K, and $x_i \in L_{1\cdots k}^i$ for $i = 1, 2, \dots, k$. Then $\langle x_1, x_2, \dots, x_k \rangle$ cannot contain a point of both $L_{1\cdots k}^0$ and $L_{1\cdots k}^{1\cdots k}$.*

Proof. We will prove this by contradiction. Suppose $p \in L^0_{1\cdots k} \cap \langle x_1, x_2, \ldots, x_k \rangle$ and $q \in L^{1\cdots k}_{1\cdots k} \cap \langle x_1, x_2, \ldots, x_k \rangle$. The ray starting at p and going through q has to pass through $P^1, P^2, \ldots, P^k$ and cannot cross them again. Thus past q, the ray stays in $L^{1\cdots k}_{1\cdots k}$. The ray will eventually hit a face of $\langle x_1, x_2, \ldots, x_k \rangle$. Using Lemma 3 we have each face is in some $L^{1\cdots \hat{j} \cdots k}_{1\cdots k}$ and so misses $L^{1\cdots k}_{1\cdots k}$. This is a contradiction and finishes the proof. ∎

The following lemma gives more geometry involving the pieces of L. Here we show how the sets $L^0_{1\cdots k}$ and $L^{1\cdots k}_{1\cdots k}$ sit relative to each other and the other $L^i_{1\cdots k}$'s.

Lemma 5. *Let K be a convex cone containing $\mathbb{R}^n_+$. Let $\{P^i\}^k_{i=1}$ be a partial minimal cover for L relative to K, $k \geq 1$, and $x_i \in L^i_{1\cdots k}$ for $i = 1, 2, \ldots, k$. If $\langle x_1, x_2, \ldots, x_k \rangle \cap L^0_{1\cdots k} = \emptyset$, then $\langle x_1, x_2, \ldots, x_k \rangle \cap L^{1\cdots k}_{1\cdots k} \neq \emptyset$.*

Proof. We will prove this by induction. Suppose that $k = 1$. Then for $x_1 \in L^1_1$, we have $\langle x_1 \rangle \cap L^1_1 \neq \emptyset$. This proves the case for $k = 1$.

For a better insight into the proof we will provide the case where $k = 2$. Let $x_1 \in L^1_{12}$ and $x_2 \in L^2_{12}$. Since x_1 is covered only by P^1, the line connecting x_1 and x_2, $\langle x_1 x_2 \rangle$, must intersect P^1. Likewise, since x_2 is covered only by P^2, $\langle x_1 x_2 \rangle$ must intersect P^2 as well.

Now consider going from x_1 to x_2; if we intersect P^1 first, then this point of intersection on P^1 is not covered by P^1 by definition. It is not covered by P^2 either and so it is in L^0_{12}. Note that if the line intersects P^1 and P^2 simultaneously, then this point is also on L^0_{12} by definition. So the line must intersect P^2 first and then P^1, so there are points that are covered by both the planes on the line. These points are in L^{12}_{12}. Thus $\langle x_1 x_2 \rangle \cap L^{12}_{12} \neq \emptyset$. This proves the case $k = 2$.

Let $\{P^i\}^k_{i=1}$ be a partial minimal cover for L. Let $x_i \in L^i_{1\cdots k}$. Suppose that $\langle x_1, x_2, \ldots, x_k \rangle \cap L^0_{1\cdots k} = \emptyset$. We would like to show $\langle x_1, x_2, \ldots, x_k \rangle \cap L^{1\cdots k}_{1\cdots k} \neq \emptyset$. Note if $\langle x_1, x_2, \ldots, x_{k-1} \rangle \cap L^0_{1\cdots k-1} \neq \emptyset$, then since these x_i's are not covered by P^k, $\langle x_1, x_2, \ldots, x_{k-1} \rangle \cap L^0_{1\cdots k} \neq \emptyset$. This implies that $\langle x_1, x_2, \ldots, x_{k-1} \rangle \cap L^0_{1\cdots k-1} = \emptyset$, so by the induction hypothesis, we must have $\langle x_1, x_2, \ldots, x_{k-1} \rangle \cap L^{1\cdots k-1}_{1\cdots k-1} \neq \emptyset$.

This gives us that $\langle x_1, x_2, \ldots, x_{k-1} \rangle \cap L^{1\cdots k-1}_{1\cdots k} \neq \emptyset$. Choose y_i as the point on P^k where the line connecting x_i and x_k intersects it. Note $\langle x_i, x_k \rangle$ can only be covered by P^i or P^k. With our hypothesis $\langle x_1, x_2, \ldots, x_k \rangle \cap L^0_{1\cdots k} = \emptyset$, the line must pass through P^k first instead of P^i; otherwise $\langle x_1, x_2, \ldots, x_k \rangle \cap L^0_{1\cdots k} \neq \emptyset$, which is a contradiction. Note that the convex hull $\langle y_1, y_2, \ldots, y_{k-1}, x_k \rangle$ is the part of the convex hull $\langle x_1, x_2, \ldots, x_k \rangle$ which is on or below P^k.

From the above, we have that $y_i \in L^i_{1\cdots k-1}$, since we have only intersected P^k. Thus $\langle y_1, y_2, \ldots, y_{k-1} \rangle \cap L^{1\cdots k-1}_{1\cdots k-1} \neq \emptyset$. Let $z \in \langle y_1, y_2, \ldots, y_{k-1} \rangle \cap L^{1\cdots k-1}_{1\cdots k-1}$, and consider the line $\langle z x_k \rangle$ connecting z and x_k. Now from Lemma 2, $L^{1\cdots k-1}_{1\cdots k-1}$ is an open set, so we can find in L an open ball $B(z, \epsilon)$ centered at z with radius $\epsilon > 0$ which is contained in $L^{1\cdots k-1}_{1\cdots k-1}$. We have that z is on P^k and x_k is below P^k and so $\langle z x_k \rangle \backslash z$ is below P^k. Now $(\langle z x_k \rangle \backslash z) \cap B(z, \epsilon) \neq \emptyset$. Thus, we have $\langle y_1, y_2, \ldots, y_{k-1}, x_k \rangle \cap L^{1\cdots k}_{1\cdots k} \neq \emptyset$. This gives us our lemma. ∎

Next we would like to show the existence of a convex hull that intersects $L_{1\cdots k}^{1\cdots k}$. This will be useful in a later theorem. To do this, we first prove the next two lemmas. The first of these lemmas describes another relationship between the sets $L_{1\cdots k}^{0}$ and $L_{1\cdots k}^{i}$. We show that they sit next to one another by showing they have a common boundary.

Lemma 6. *Suppose $\{P^i\}_{i=1}^{k}$ is a partial minimal cover for L. Then, relative to L,*

$$\partial L_{1\cdots k}^{i} \cap \partial L_{1\cdots k}^{0} \neq \emptyset$$

for each $1 \leq i \leq k$.

Proof. Let $1 \leq i \leq k$, and since $L_{1\cdots k}^{0}$ and $L_{1\cdots k}^{i}$ are nonempty, let $x \in L_{1\cdots k}^{0}$ and $y \in L_{1\cdots k}^{i}$. Consider the line, $\langle x, y\rangle$, connecting x and y. $\langle x, y\rangle$ is above every plane except P^i. Also $\langle x, y\rangle$ must intersect P^i and only P^i. Let $z \in P^i \cap \langle x, y\rangle$. Since $z \in L_{1\cdots k}^{0}$, we have $\langle x, z\rangle \subset L_{1\cdots k}^{0}$, and $\langle z, y\rangle\backslash z \subset L_{1\cdots k}^{i}$. This gives us that $z \in \partial L_{1\cdots k}^{0}$ and $z \in \partial L_{1\cdots k}^{i}$. This completes the lemma. ■

This next lemma shows how the hyperplanes P^i's sit relative to the $L_{1\cdots k}^{i}$'s. We show that each hyperplane makes up part of the boundary of each $L_{1\cdots k}^{i}$ by showing $P^j \cap L_{1\cdots m}^{i} \neq \emptyset$.

Lemma 7. *Suppose $k > 1$. If $\{P^i\}_{i=1}^{k}$ is a minimal cover for L, then for each P^j we have*

$$P^j \cap L_{1\cdots m}^{i} \neq \emptyset$$

for each $1 \leq i \leq k$, $1 \leq m \leq k$, and $i \neq j$.

Proof. First we will show $P^k \cap L_{1\cdots k-1}^{i} \neq \emptyset$ for all $i < k$. If this is not true, then there exists a j such that $P^k \cap L_{1\cdots k-1}^{j} = \emptyset$. Since $L_{1\cdots k-1}^{i}$ is convex, it lies completely on one side of P^k. Also note that, since $\{P^i\}_{i=1}^{k}$ is a minimal cover for L, $L_{1\cdots k-1}^{0}$ is covered by P^k. But $\{P^1, P^2, \ldots, P^{k-1}\}$ is a partial minimal cover for L and by Lemma 6, $\partial L_{1\cdots k}^{i} \cap \partial L_{1\cdots k}^{0} \neq \emptyset$. This implies P^k must also cover $L_{1\cdots k}^{j}$, and thus P^j is obsolete. This contradicts the assumption that $\{P^i\}_{i=1}^{k}$ is minimal. Therefore $P^k \cap L_{1\cdots k-1}^{i} \neq \emptyset$ for $1 \leq i \leq k-1$. Further, since $P^k \cap L_{1\cdots k-1}^{i} \neq \emptyset$, let $x \in P^k \cap L_{1\cdots k-1}^{i}$. Then $x \in L_{1\cdots k}^{i}$. This gives $P^k \cap L_{1\cdots k}^{i} \neq \emptyset$ for $i \neq k$.

Note that $L_{1\cdots k-1}^{i} \subset L_{1\cdots m}^{i}$ for $1 \leq m \leq k-1$. So

$$P^k \cap L_{1\cdots m}^{i} \neq \emptyset$$

for each $1 \leq m \leq k$, and $i \neq k$. Thus P^k has this property. By reordering the hyperplanes, we have this true for all $1 \leq i \leq k$. This proves the lemma. ■

Now we are ready to show the existence of a convex hull which intersects $L_{1\cdots k}^{1\cdots k}$. In fact, putting together this next result and Lemmas 4 and 5, we have that any convex hull made from points located in each $L_{1\cdots k}^{i}$ must intersect either $L_{1\cdots k}^{0}$ or $L_{1\cdots k}^{1\cdots k}$ and not both.

Lemma 8. *Let K be a convex cone containing $\mathbb{R}^n_+$. If $\{P^i\}_{i=1}^k$ is a partial minimal cover for L relative to K with $k \geq 1$. Then there exist $x_i \in L^i_{1\cdots k}$ for $1 \leq i \leq k$ such that $\langle x_1, x_2, \ldots, x_k \rangle \cap L^{1\cdots k}_{1\cdots k} \neq \emptyset$.*

Proof. We will prove this by contradiction. Let $\{P^1, P^2, \ldots, P^k\}$ be a partial minimal cover for L relative to K. We will assume that for all choices of $x_i \in L^i_{1\cdots k}$ we have

$$\langle x_1, x_2, \ldots, x_k \rangle \cap L^0_{1\cdots k} \neq \emptyset.$$

Otherwise, by Lemma 5, we would be done. We assume that L has a minimal cover, say $\{P^1, P^2, \ldots, P^m\}$ where $k < m < n$. Now add P^{k+1}. By Lemma 7, P^{k+1} intersects each $P^i_{i\cdots k}$ for $1 \leq i \leq k$. So let $x_i^* \in P^{k+1} \cap L^i_{1\cdots k} \neq \emptyset$. By assumption we have

$$\langle x_1^*, x_2^*, \ldots, x_k^* \rangle \cap L^0_{1\cdots k} \neq \emptyset.$$

This implies that $\{P^1, P^2, \ldots, P^{k+1}\}$ is not a minimal cover since $P^{k+1} \cap L^0_{1\cdots k} \neq \emptyset$ is not covered.

Now let $y_i \in L^i_{1\cdots k+1}$. Note that $L^i_{1\cdots k+1} \subset L^i_{1\cdots k}$ and so $y_i \in L^i_{1\cdots k}$. This gives

$$\langle y_1, y_2, \ldots, y_k \rangle \cap L^0_{1\cdots k} \neq \emptyset.$$

But since each y_i is not covered by P^{k+1}, $\langle y_1, y_2, \ldots, y_k \rangle$ is not covered by P^{k+1}. Thus

$$\langle y_1, y_2, \ldots, y_k \rangle \cap L^0_{1\cdots k+1} \neq \emptyset,$$

and

$$\langle y_1, y_2, \ldots, y_{k+1} \rangle \cap L^0_{1\cdots k+1} \neq \emptyset.$$

We can add P^{k+2} to the partial cover $\{P^1, P^2, \ldots, P^{k+1}\}$. Again, let $y_i^* \in P^{k+2} \cap L^i_{1\cdots k+1} \neq \emptyset$. From above, we have $P^{k+2} \cap L^0_{1\cdots k+1} \neq \emptyset$ and so $\{P^1, P^2, \ldots, P^{k+2}\}$ is not a minimal cover for L. Repeating this argument, we see that we cannot cover L. This is a contradiction, which completes the proof. ∎

We are interested in the intersection of the P^i planes with L. For a collection $A \subset \{1, 2, \ldots, n\}$, we denote by Γ^A the intersection of the planes $\{P^i\}_{i \in A}$ with L in a cone K. Hence

$$\Gamma^{1\cdots k} = \bigcap_{i=1}^{k} P^i \cap L \cap \overset{\circ}{K}.$$

We want to show that this is nonempty for a partial cover. It would have to be empty for a cover by definition of a cover. We will then use this idea in constructing a Lyapunov function of the form needed to determine extinction as in Proposition 2. The following theorem sets up our main result.

Theorem 4. *Let K be a convex cone containing $\mathbb{R}^n_+$. If $\{P^i\}_{i=1}^k$ is a partial minimal cover for L relative to K with $k \geq 1$, then*

1. $\Gamma^{1\cdots k} = \bigcap_{i=1}^{k} P^i \cap L \cap \overset{\circ}{K}$ *has codimension k in L, and*

2. *For $i = 0, 1, 2, \ldots, k$, if $x_i \in L^i_{1\ldots k}$ and $\langle x_1, x_2, \ldots, x_k\rangle \cap L^{1\cdots k}_{1\ldots k} \neq \emptyset$, then $\langle x_0, x_1, \ldots, x_k\rangle \cap \Gamma^{1\cdots k} \neq \emptyset$.*

Proof. We will prove this by induction. First, let $k = 1$, and so P^1 is a partial cover for L. Then by Lemma 2, $P^1 \cap L \cap \overset{\circ}{K} \neq \emptyset$. Let $x_0 \in L^0_{1\ldots k}$ and $x_1 \in L^1_{1\ldots k}$; then $\langle x_0, x_1\rangle$ must intersect $\Gamma^1 = P^1 \cap L \cap \overset{\circ}{K}$. Since $P^1 \neq L$, $\Gamma^1 = P^1 \cap L \cap \overset{\circ}{K}$ has codimension 1 in L.

Now assume $\{P^i\}_{i=1}^k$ is a partial minimal cover for L and that for any subcollection of $\{P^i\}_{i=1}^k$ the above conditions hold. Using Lemma 8, let $x_i \in L^i_{1\ldots k}$ such that $\langle x_1, x_2, \ldots, x_k\rangle \cap L^{1\cdots k}_{1\ldots k} \neq \emptyset$. Lemma 4 gives $\langle x_1, x_2, \ldots, x_k\rangle \cap L^0_{1\ldots k} = \emptyset$. Note that $x_i \in L^i_{1\ldots k-1}$ for $1 \leq i \leq k-1$. If $\langle x_1, x_2, \ldots, x_{k-1}\rangle \cap L^0_{1\ldots k-1} \neq \emptyset$, then since $\langle x_1, x_2, \ldots, x_{k-1}\rangle$ is not covered by P^k, $\langle x_1, x_2, \ldots, x_{k-1}\rangle \cap L^0_{1\ldots k-1} = \emptyset$. This gives $\langle x_1, x_2, \ldots, x_{k-1}\rangle \cap L^0_{1\ldots k} = \emptyset$. Now using Lemma 5 we obtain $\langle x_1, x_2, \ldots, x_{k-1}\rangle \cap L^{1\cdots k-1}_{1\ldots k-1} \neq \emptyset$.

Since $\langle x_1, x_2, \ldots, x_{k-1}\rangle \cap L^{1\cdots k-1}_{1\ldots k-1} \neq \emptyset$, we have by the induction hypothesis that $\langle x_0, x_1, \ldots, x_{k-1}\rangle \cap \Gamma^{1\cdots k-1} \neq \emptyset$. Since x_i is not covered by P^k for $1 \leq i \leq k-1$, $\langle x_0, x_1, \ldots, x_{k-1}\rangle$ is not covered by P^k. Thus $\langle x_0, x_1, \ldots, x_{k-1}\rangle$ must intersect $\Gamma^{1\cdots k-1}$ above or on P^k.

Since $x_k \in L^0_{1\ldots k-1}$, we also get by the induction hypothesis, $\langle x_1, x_2, \ldots, x_k\rangle \cap \Gamma^{1\cdots k-1} \neq \emptyset$. As in the proof of Lemma 5, let y_i be the point on P^k where the line connecting x_i and x_k crosses P^k. So $\langle y_1, y_2, \ldots, y_{k-1}, x_k\rangle$ is the part of the convex hull $\langle x_1, x_2, \ldots, x_k\rangle$ which is on or below P^k. Since $\langle x_1, x_2, \ldots, x_k\rangle \cap L^0_{1\ldots k} = \emptyset$, $\langle y_1, y_2, \ldots, y_{k-1}, x_k\rangle \cap L^0_{1\ldots k} = \emptyset$. This implies that $\langle y_1, y_2, \ldots, y_{k-1}\rangle \cap L^0_{1\ldots k} = \emptyset$, and $\langle y_1, y_2, \ldots, y_{k-1}\rangle \cap \Gamma^{1\cdots k} = \emptyset$ since $\Gamma^{1\cdots k} \subset L^0_{1\ldots k}$.

By assumption, we have $\langle x_1, x_2, \ldots, x_k\rangle \cap L^{1\cdots k}_{1\ldots k} \neq \emptyset$ which implies $\langle y_1, y_2, \ldots, y_{k-1}, x_k\rangle \cap L^{1\cdots k}_{1\ldots k} \neq \emptyset$, since $\langle x_1, x_2, \ldots, x_{k-1}, y_1, y_2, \ldots, y_{k-1}\rangle$ is on and above P^k and so does not intersect $L^{1\cdots k}_{1\ldots k}$. We also have $\langle y_1, y_2, \ldots, y_{k-1}, x_k\rangle \cap \Gamma^{1\cdots k-1} \neq \emptyset$ by the induction hypothesis. But since $\Gamma^{1\cdots k} \subset L^0_{1\ldots k}$ and $\langle y_1, y_2, \ldots, y_{k-1}\rangle \cap \Gamma^{1\cdots k} = \emptyset$, $\langle y_1, y_2, \ldots, y_{k-1}, x_k\rangle$ must intersect $\Gamma^{1\cdots k-1}$ below P^k. Using this fact and the fact that $\langle x_0, x_1, \ldots, x_{k-1}\rangle$ must intersect $\Gamma^{1\cdots k-1}$ above or on P^k, we obtain

$$\langle x_0, x_1, \ldots, x_k\rangle \cap \Gamma^{1\cdots k} \neq \emptyset.$$

Now since $\langle x_1, \ldots, x_k\rangle$ intersects $\Gamma^{1\cdots k-1}$ below $\Gamma^{1\cdots k}$ and $\langle x_0, x_1, \ldots, x_k\rangle \cap \Gamma^{1\cdots k} \neq \emptyset$, this implies that $\Gamma^{1\cdots k} = \cap_{i=1}^k P^i \cap L$ has codimension one higher than $\Gamma^{1\cdots k-1}$ or codimension k. ∎

Finally, the goal of all the preceding geometry leads to the following theorem that gives us that $\Gamma^{1\cdots k}$ is nonempty for a partial minimal cover.

Theorem 5. *Let K be a convex cone containing $\mathbb{R}^n_+$. Let $\{P^i\}_{i=1}^k$ be a partial minimal cover for L relative to K and suppose that $k \geq 1$. Then*

$$\Gamma^{1\cdots k} = \bigcap_{i=1}^{k} P^i \cap L \cap \overset{\circ}{K} \neq \emptyset.$$

Proof. This follows from the previous theorem. ■

Next, to complete our second goal, we present our main extinction result. This result is an extension to the extinction result of Franke and Yakubu (1991) where one species weakly dominates another species. In the following, we show that two or more species in our competitive system can cooperate to weakly dominate a species and drive that species to extinction. Biologically, this means that if at least one of a group of species is growing whenever some other specified species is not decreasing, the specified species goes extinct.

Theorem 6. *If species $1, 2, \ldots, l-1$ weakly dominate species l, then species l goes extinct.*

Proof. By definition, if species $1, 2, \ldots, l-1$ weakly dominate species l, then

$$N(\lambda_l) \subset \bigcup_{i \in \{1,2,\ldots,l-1\}} \overset{\circ}{N}(\lambda_i).$$

Without loss of generality, assume that for any proper subset $A \subset \{1, 2, \ldots, l-1\}$, $N(\lambda_l) \not\subset \cup_{i \in A} \overset{\circ}{N}(\lambda_i)$. Otherwise, we can find a 'smallest' subset for which it is true and then do a renumbering. Note that $N(\lambda_l) \subset \cup_{i \in \{1,2,\ldots,l-1\}} \overset{\circ}{N}(\lambda_i)$ implies that

$$\bigcap_{i=1}^{l} P^i \cap \mathbb{R}^n_+ = \emptyset,$$

and that $\{P^1, P^2, \ldots, P^{l-1}\}$ forms a minimal cover for P^l relative to $\mathbb{R}^n_+$.

Since $N(\lambda_l)$ is closed relative to $\mathbb{R}^n_+$ and $\cup_{i \in A} \overset{\circ}{N}(\lambda_i)$ is open relative to $\mathbb{R}^n_+$, for each point $x \in \partial N(\lambda_l) = P^l \cap \mathbb{R}^n_+$, there is an ϵ-neighborhood in $\mathbb{R}^n$ of x, call it $\mathcal{N}(x)$, which is covered by $\{P^1, P^2, \ldots, P^{l-1}\}$. Let

$$Z = \bigcup_{x \in \partial N(\lambda_i)} \mathcal{N}(x) \cap P^l.$$

Z is open in P^l and covered by $\{P^1, P^2, \ldots, P^{l-1}\}$. $P^l \backslash Z$ and $\partial N(\lambda_l)$ are closed disjoint sets in P^l with $\partial N(\lambda_l)$ compact, and so there is a minimum distance between the two, say $\delta > 0$. Now construct $D = \delta$-neighborhood of $\partial N(\lambda_l)$ relative to P^l. D is a convex neighborhood of $\partial N(\lambda_l)$ with $\partial N(\lambda_l) \subset \overset{\circ}{D}$ and D is covered by $\{P^1, P^2, \ldots, P^{l-1}\}$.

Construct a cone K using the rays from the origin that go through D. Note $K \supset \mathbb{R}^n_+$ and by construction $\{P^1, P^2, \ldots, P^{l-1}\}$ is a cover for P^l relative to K. In fact, the cover is a minimal cover since $\mathbb{R}^n_+$ is contained in K. Note $\{P^1, P^2, \ldots, P^l\}$ is still inconsistent on K. Now using Corollary 2, we have a $\boldsymbol{c} = (c_1, c_2, \ldots, c_l)$ such that

$$\sum_{k=1}^{l} c_k \Big(\sum_{j=1}^{n} \alpha_{kj} x_j \Big) > \sum_{k=1}^{l} c_k r_k, \tag{10}$$

where $2 \leq l \leq n$, $c_i \neq 0$ for $1 \leq i \leq l$, and there exist $i, j \in \{1, 2, \ldots, l\}$ where $c_i > 0$ and $c_j < 0$.

Now consider the function $V : \mathbb{R}^n_{1,\ldots,l} \to \mathbb{R}_+$ defined by $V(x_1, x_2, \ldots, x_n) = \prod_{i=1}^{l} x_i^{c_i}$. For $\boldsymbol{x} \in \mathbb{R}^n_{1,\ldots,l}$ the ratio of $V(F(\boldsymbol{x}))$ and $V(\boldsymbol{x})$ is

$$\begin{aligned} \frac{V(F(\boldsymbol{x}))}{V(\boldsymbol{x})} &= \frac{x_1^{c_1} \exp(c_1(r_1 - \sum_{j=1}^{n} \alpha_{1j} x_j)) \cdots x_l^{c_l} \exp(c_l(r_l - \sum_{j=1}^{n} \alpha_{lj} x_j))}{x_1^{c_1} \cdots x_l^{c_l}} \\ &= \exp\left(\sum_{i=1}^{l} c_i \Big(r_i - \sum_{j=1}^{n} \alpha_{ij} x_j \Big) \right). \end{aligned} \tag{11}$$

Note that (11) is a continuous extension of $V(F(\boldsymbol{x}))/V(\boldsymbol{x})$ to all of K. From (10), we have

$$\sum_{i=1}^{l} c_i \Big(r_i - \sum_{j=1}^{n} \alpha_{ij} x_j \Big) < 0,$$

for $K \supset \mathbb{R}^n_+$. This implies

$$\frac{V(F(\boldsymbol{x}))}{V(\boldsymbol{x})} = \prod_{i=1}^{l} \lambda_i^{c_i}(\boldsymbol{x}) < 1$$

for $\boldsymbol{x} \in \mathbb{R}^n_{1,\ldots,l}$. Thus V is Lyapunov with respect to $\mathbb{R}^n_{1,\ldots,l}$.

Now $\{P^1, P^2 \ldots, \hat{P}^j, \ldots, P^{l-1}\}$ is a partial minimal cover for P^l. Using Theorem 5, we get $\Gamma^{1\cdots\hat{j}\cdots l-1} \neq \emptyset$. So let $\boldsymbol{x} \in \Gamma^{1\cdots\hat{j}\cdots l-1}$. Note that $\boldsymbol{x}$ is on each plane P^i, $1 \leq i \leq l$, except P^j. It is on P^l and so it must be covered. In fact, it must be covered by P^j since it is on every other plane.

Consider $V(\boldsymbol{x})$. Since $\boldsymbol{x}$ is on each plane except P^j, every species except species j will remain constant in the next generation. Also since $\boldsymbol{x}$ is below P^j, species j will grow. But we have that V is decreasing, thus $c_j < 0$. This gives $c_j < 0$ for $j \in \{1, 2, \ldots, l-1\}$. By Corollary 2, there exists an $i \in \{1, 2, \ldots, l\}$ where $c_i > 0$. We then have $c_l > 0$, and V has the form

$$V(x_1, x_2, \ldots, x_n) = \frac{x_l^{c_l}}{x_1^{c_1} \cdots x_{l-1}^{c_{l-1}}}.$$

Thus by Proposition 2, we have that species l goes extinct. ■

In a following section, we will make use of the Lyapunov function derived in the above proof. The following corollary is immediate from the above proof and will be used later.

Corollary 3. *If* $N(\lambda_l) \subset \cup_{i\in\{1,2,\dots,l-1\}} \overset{\circ}{N}(\lambda_i)$ *in* $\mathbb{R}^n_+$, *then there exists a* $\mathbf{c} = (c_1, c_2, \dots, c_l)$ *with* $c_l > 0$, *and* $c_i > 0$ *for* $i \in A \subset \{1, 2, \dots, l-1\}$ *such that*

$$\lambda_l^{c_l}(x) \prod_{i\in A} \lambda_i^{-c_i}(x) < 1$$

on $\mathbb{R}^n_+ \backslash \mathbf{0}$.

5. Persistence

The following results, dealing with persistence, were motivated by the work done by Hofbauer *et al.* (1987). We extend their work on permanence of a system to persistence of a collection of a species.

We will use notation similar to that used in (Hofbauer *et al*, 1987). Their results considered the dynamics on a compact absorbing set X, which we can take as the union of $\mathcal{X}$ and $\{\mathbf{0}\}$. Recall from Proposition 1 that $\mathcal{X}$ is positively invariant and absorbing for $\mathbb{R}^n_+ \mathbf{0}$. Here we use a function similar to our Lyapunov functions. Let

$$V(x_1, x_2, \dots, x_n) = \prod_{i=1}^{n} x_i^{c_i},$$

where for each $i \in A \subset \{1, 2, \dots, n\}$, $c_i > 0$, and for $i \in \{1, 2, \dots, n\}\backslash A$, $c_i = 0$. Using V, recall that

$$S^n_A = \Big\{ \boldsymbol{x} \in \mathbb{R}^n_+ \,|\, \prod_{i\in A} x_i = 0 \Big\}.$$

So $V : \mathbb{R}^n_+ \to \mathbb{R}_+$ and $V(\boldsymbol{x}) = 0$ if and only if $\boldsymbol{x} \in S^n_A$. Hofbauer *et al.* used V, where each $c_i > 0$, to measure the growth of the system. We will employ our V in a similar way but we will only keep track of part of the system.

In order to keep track of how parts of the system grow over the orbit, we define

$$\alpha(m, \boldsymbol{x}) = V(F^m(\boldsymbol{x}))/V(\boldsymbol{x}), \tag{12}$$

where m is a positive integer and $\boldsymbol{x} \in X\backslash S^n_A$. Further, define

$$\phi(\boldsymbol{x}) = \sum_{i\in A} c_i \lambda_i(\boldsymbol{x}) = \sum_{i\in A} c_i \Big[r_i - \sum_{j=1}^{n} \alpha_{ij} x_j \Big]. \tag{13}$$

Using (12) and (13), we have the following relationship:

$$\alpha(1, \boldsymbol{x}) = \exp\big(\phi(\boldsymbol{x})\big). \tag{14}$$

Since ϕ is defined for all of $\mathbb{R}^n$, (14) is a continuous extension of (12) to X where $m = 1$. Also since $\alpha(m, x) = \prod_{n=0}^{m-1} \alpha(1, F^n(x))$, it has a continuous extension to $\mathbb{R}^n$. Now we define

$$\beta(\boldsymbol{x}) = \sup_{m\geq 1} \alpha(m, \boldsymbol{x}). \tag{15}$$

To show persistence (or for Hofbauer *et al.* to show permanence), we would like to argue that $\alpha(1,x) = V(F(x))/V(x) > 1$ for all x in a neighborhood of S_A^n, but this is not in general satisfied. So instead we show a weaker condition, that $\beta(x) > 1$ on S_A^n. This implies that over some time we see an increase in the growth of the system. This turns out to be sufficient for persistence.

We will use the following topological result which follows from Lemma 2.1 from Hutson (1984). Note that our set X is a locally compact metric space which is assumed in this lemma.

Lemma 9. *(Hutson, 1984) Let U be open with compact closure, and suppose that V is open and positively invariant, where $\bar{U} \subset V \subset X$. Then if $\mathcal{O}^+(x) \cap U \neq \emptyset$ for every $x \in V$, $\mathcal{O}^+(\bar{U})$ is compact and absorbing for V.*

This result will help us show that the orbits of interior points stay away from the boundary or part of the boundary. The next lemma is similar to that of Hofbauer *et al.* (1987) except in one important respect. Hofbauer considered the set $S = X \cap \partial\mathbb{R}_+^n$. This is the set for which the orbit could limit on and not give permanence. For the following, we are interested only in part of the boundary, namely S_A^n, which allows us to show that some of the species persist.

Lemma 10. *Let $K \subset X$ be compact, and suppose that $\beta(x) > 1$ for every $x \in S_A^n \cap X$. Then there is a closed neighborhood W of $S_A^n \cap X$ in $\mathbb{R}_+^n$ such that if for some $y \in X$ we have $\omega(y) \subset W$, then $\beta(y) = +\infty$, and $y \in S_A^n$.*

The proof is similar to that of Hofbauer *et al.* (1987).

Next is the first of the main persistence extensions. Hofbauer *et al.* (1987) showed that if

$$\beta(x) > 1.$$

where each $c_i > 0$ and $x \in S = X \cap \partial\mathbb{R}_+^n$, the system exhibits permanence. We show species i persists if $\beta(x) > 1$ on $S_i^n = \{x \in \mathbb{R}_+^n | x_i = 0\}$. In the following, we consider the case where several species persist and include the proof which is similar to that of Hofbauer *et al.*

Proposition 3. *Consider the dissipative system (1). If $\beta(x) > 1$ for each $x \in X \cap S_{1\cdots l}^n$, then species $1, 2, \ldots, l$ persist.*

Proof. Let $K = S_{1\cdots l}^n \cap X$, so $\beta(x) > 1$ for each $x \in K$. Using Lemma 10, we have a closed neighborhood W of $S_{1\cdots l}^n \cap X$ such that if for some $y \in X$ and $\omega(y) \subset W$, then $y \in S_{1\cdots l}^n$.

Let $N = X \backslash W$. For each $x \in X \backslash S_{1\cdots l}^n$, Lemma 10 gives $\omega(x) \cap N \neq \emptyset$, otherwise the lemma gives $x \in S_{1\cdots l}^n$, which is a contradiction.

Now let $V = X \backslash K$, and $U = X \backslash N$, using the relative topology $\overline{U} \subset V \subset X$, and for each $x \in V$, $\mathcal{O}^+(x) \cap U \neq \emptyset$. This implies from Lemma 9 that $\mathcal{O}^+(\overline{U})$ is a compact, forward absorbing set. Thus species $1, 2, \ldots, l$ persist. ■

Hofbauer *et al.* showed that instead of checking β at every point in S, it is sufficient to check it at all the equilibrium points in S. We have a similar condition where it is only necessary to show that $\beta(x^*) > 1$ where x^* is an equilibrium point in S_A where A is the collection of species whose persistence one wants to demonstrate. To do this, we use an averaging property of our system. We denote by $\bar{x}(m) = (\bar{x}_1(m), \bar{x}_2(m), \ldots, \bar{x}_n(m))$ the average population distribution after m generations, where

$$\bar{x}_i(m) = \frac{1}{m} \sum_{k=0}^{m-1} F_i^k(x).$$

This allows us to rewrite (12) to be

$$\alpha(m, x) = \exp\big(m\, \phi(\bar{x}(m))\big) \tag{16}$$

The following is a useful lemma that relates average populations and equilibrium points.

Lemma 11. *(Hofbauer et al., 1987) Assume that* $x_i > 0$ $(1 \leq i \leq q)$. *Suppose that there are real numbers* $b > 0$ *and* b', *and a sequence* $(k_j) \to \infty$ *such that* $b < F_i^{k_j}(x) < b'$ *for* $1 \leq i \leq q$ *and* $j \geq 1$. *Then there is a subsequence, again denoted by* (k_j), *and an equilibrium point* x^* *such that*

$$\lim_{j \to \infty} \bar{x}(k_j) = x^*.$$

Now we extend their permanence result, which only involves checking the equilibrium points on the boundary. This next result gives persistence of species $1, 2, \ldots, l$ if ϕ evaluated at each equilibrium point in $S^n_{1,2,\ldots,l}$ is positive.

Proposition 4. *Suppose that there exists an* $l \in \{1, 2, \ldots, n\}$ *such that for all* $1 \leq i \leq l$ *there exist real numbers* $c_1, c_2, \ldots, c_l > 0$ *such that*

$$\phi(x^*) = \sum_{i=1}^{l} c_i \Big(r_i - \sum_{j=1}^{n} \alpha_{ij} x_j\Big) > 0$$

for each equilibrium point x^* *in the subspace* $S^n_{1\cdots l}$. *Then for* $1 \leq i \leq l$ *species* i *persists.*

Proof. We will prove this by induction. First note that $S^n_{1\cdots l} = \{x \in \mathbb{R}^n_+ \mid \prod_{i \in A} x_i = 0\} = \cup_{i=1}^{l} S_i^n$, where each S_i^n is a face of $\partial\mathbb{R}^n_+$. Assume that $\phi(x^*) = \sum_{i=1}^{l} c_i(r_i - \sum_{j=1}^{n} \alpha_{ij} x_j^*) > 0$ for each equilibrium point $x^* \in S^n_{1\cdots l}$. Now using (15) and (16), we get $\beta(x^*) > 1$ for each $x^* \in S^n_{1\cdots l}$.

The induction will be done on the dimension of the boundary where the 0-dimensional space is $S^0 = \cap_{i=1}^{n} S_i^n = \{\mathbf{0}\}$, and in general the k-dimensional space is $S^k = \cup_{i \in I} \cap_{j \in E_i} S_j^n$, where the E_i's are the $(n-k)$-element subsets of $\{1, 2, \ldots, n\}$ and are indexed by I. Note that the origin is a repelling fixed point for our model so $\beta(\mathbf{0}) > 1$. Now suppose for some $2 \leq m \leq l-1$, $\beta(x) > 1$ for all $x \in S^m$. Let

$x \in \mathcal{S}^{m+1} \backslash \mathcal{S}^m$. We want to show that $\beta(x) > 1$. Using the invariance of each $\mathcal{S}^i$, $\omega(x) \subset \mathcal{S}^m$ or $\omega(x) \cap \mathcal{S}^{m+1} \backslash \mathcal{S}^m \neq \emptyset$.

If $\omega(x) \subset \mathcal{S}^m$, then using Lemma 10 with $K = \mathcal{S}^m \cap S^n_{1\ldots l}$ we get $\beta(x) > 1$. On the other hand, if $\omega(x) \cap \mathcal{S}^{m+1} \backslash \mathcal{S}^m \neq \emptyset$, let $x' \in \mathcal{S}^{m+1} \backslash \mathcal{S}^m$ and $\{k_j\}$ be a sequence with $\lim_{j\to\infty} F^{k_j}(x) = x'$. Now using Lemma 11, we have that the average $\bar{x}$ converges to an equilibrium point x^*. But using (15) and (16), we again get $\beta(x) > 1$. This completes the proof. ∎

Example 3. This completes our third goal to extend the result of Hofbauer *et al.* We now use these to consider the following example. This is a competitive model with three species of the following form:

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{bmatrix} = \begin{bmatrix} x_1(t)\exp(1 - x_1(t) - x_2(t) - .5x_3(t)) \\ x_2(t)\exp(1 - .7x_1(t) - 1.3x_2(t) - 1.5x_3(t)) \\ x_3(t)\exp(1 - 1.7x_1(t) - .5x_2(t) - x_3(t)) \end{bmatrix}. \quad (17)$$

For this example we have

$$\begin{aligned} P^1 &= \{x = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - x_1 - x_2 - .5x_3 = 0\}, \\ P^2 &= \{x = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - .7x_1 - 1.3x_2 - 1.5x_3 = 0\}, \\ P^3 &= \{x = (x_1, x_2, x_3) \in \mathbb{R}^n \mid 1 - 1.7x_1 - .5x_2 - x_3 = 0\}. \end{aligned}$$

Note that $\cap_{i=1}^3 P^i \cap \mathbb{R}^n_+ = \emptyset$, see Fig. 3. Since there is no equilibrium population density, Theorem 3 gives weak extinction.

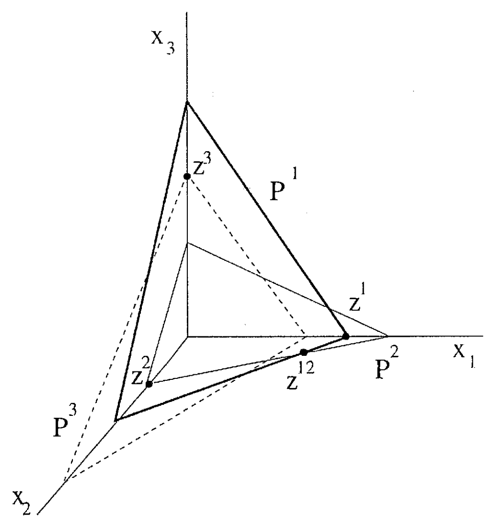

Fig. 3. Relationship of P^1, P^2, and P^3 in system (17).

Next we can use Proposition 4 and check to see if we can show that any species persists. If we choose

$$V(x_1, x_2, x_3) = x_i^{c_i},$$

we see that using the conditions of Proposition 4, species 2 and 3 do not persist on their own. But for species 1, we see that S_1^3 has only two equilibrium points, z^2 and z^3. Further since P^1 is above both z^2 and z^3, using $V(x_1, x_2, x_3) = x_1^{c_1}$, (12), and (15) we see that $\beta(z^2)$ and $\beta(z^3)$ are greater than one. Thus we have that species 1 persists.

Now using this information, we see if there is a combination of species that persist. So for this model, since we know species 1 persists, we can look at

$$V(x_1, x_2, x_3) = x_1^{c_1} x_3^{c_3}.$$

Using this, we see that species 1 and 3 cannot satisfy the conditions at z^{12}. Now trying

$$V(x_1, x_2, x_3) = x_1^{c_1} x_2^{c_2},$$

we want to check the conditions on the equilibrium points in S_{12}^3 which are z^1, z^2, and z^3. Note that P^1 is above z^2 and z^3 and P^2 is above z^1. Since $z^1 \in P^1$ and $z^2 \in P^2$, for any choice of $c_1, c_2 > 0$, β evaluated at z^1 or z^2 would be greater than one. At z^3 though, P^2 is below and P^1 is above, so in order for β evaluated at z^3 to be larger than one, we need $c_2 \gg c_1 > 0$. This will give β evaluated at all the equilibrium points in S_{12}^3 is greater than one at each equilibrium point in S_{12}^3. Proposition 4 gives us that species 1 and 2 persist. But we have that the system exhibits weak extinction, so species 3 must go extinct. ♦

This example, in fact, shows that not only can we deduce some species persist or go extinct but further we can actually determine the long term dynamics of (17). We were able to determine that there was no attractor with each species present, species 1 and 2 persist, and we could conclude that species 3 had to go extinct. So for small r_i's, and thus simple dynamics, we would expect the system to converge to z^{12}. Otherwise, it would converge to some more complicated attractor in the plane $x_3 = 0$.

From another perspective, this example shows that if one can deduce that all but one species persist in a system exhibiting weak extinction, the remaining species must go extinct. So extinction occurred even though in the original system we could not have applied Theorem 6. Using the other theorems of persistence and weak extinction allowed us to show that extinction was actually occurring. Thus we have the following, immediate result.

Theorem 7. *Suppose system (1) exhibits weak extinction and species* $1, 2, \ldots, n-1$ *persist. Then species* n *goes extinct.*

6. Extensions

In this section, we have reached our final goal which is to extend these results to submodels of a full model. Suppose we know or can determine by some means that one or more species are going extinct. In this situation, we can extend Theorem 6 and Proposition 4 to the subsystem by neglecting the species that are going extinct. We are able to apply these tools on these subsystems and still conclude what will happen on the whole system.

We first prove this useful proposition which relates a Lyapunov function with respect to a subsystem with that to the entire system. This allows us to look at the smaller system, which we are limiting on, and determine what will happen on the entire system.

Proposition 5. *In system (1) suppose species* $l+1, l+2, \dots, n$ *are going extinct. Let* $V : \mathbb{R}^n_{1,\dots,l} \to \mathbb{R}_+$ *be defined by* $V(x_1, x_2, \dots, x_n) = \prod_{i=1}^{l} x_i^{c_i}$. *If* $\prod_{i=1}^{l} \lambda_i^{c_i}(\boldsymbol{x}) < 1$ *on* $\mathbb{R}^l_+ \times \{0\} \times \cdots \times \{0\} \backslash \boldsymbol{0}$, *then* V *is eventually Lyapunov with respect to* $\overset{\circ}{\mathbb{R}}{}^n_+$.

Proof. Let $\boldsymbol{q} \in \overset{\circ}{\mathbb{R}}{}^n_+$. Using Proposition 1, let $\mathcal{X}$ be the region between and including the planes $P_{\max}$ and $P_{\min}$ in $\mathbb{R}^n_+$. We have $\omega(\boldsymbol{q}) \subset \mathcal{X}$, and there exists an $m_0 = m_0(\boldsymbol{q})$ so that $F^m(\boldsymbol{q}) \in \mathcal{X}$ for $m > m_0$. Let $f(\boldsymbol{x}) = V(F(\boldsymbol{x}))/V(\boldsymbol{x}) = \prod_{i=1}^{l} \lambda_i^{c_i}(\boldsymbol{x})$. Note that f has a continuous extension to $\mathbb{R}^n_+$. Since $\mathcal{X}$ is compact and does not contain $\boldsymbol{0}$, $\mathcal{X}' = \mathcal{X} \cap \mathbb{R}^l_+ \times \{0\} \times \cdots \times \{0\}$ is also compact.

By hypothesis, for all $\boldsymbol{x} \in \mathcal{X}'$, $f(\boldsymbol{x}) < 1$. Since $\mathcal{X}$ is the region between two planes, given $\delta > 0$ there is an $\epsilon > 0$ such that $\mathcal{X} \cap \mathbb{R}^l_+ \times [0, \epsilon] \times \cdots \times [0, \epsilon]$ is within the δ-neighborhood of $\mathcal{X}'$. By the continuity of f and the compactness of $\mathcal{X}'$, there exists $\epsilon > 0$ so that if $\boldsymbol{x} \in \mathcal{X} \cap \mathbb{R}^l_+ \times [0, \epsilon] \times \cdots \times [0, \epsilon]$, then $f(\boldsymbol{x}) < 1$.

Since the species $l+1, l+2, \dots, n$ are going extinct, for every $\epsilon > 0$ there is a $m_1 > 0$ such that if $m > m_1$,

$$\max_{i \in \{l+1, \dots, n\}} |F_i^m(\boldsymbol{q})| < \epsilon.$$

Let $m^* = \max\{m_0, m_1\}$. Then for $m > m^*$, we have $F^m(q) \in \mathcal{X} \cap \mathbb{R}^l_+ \times [0, \epsilon] \times \cdots \times [0, \epsilon]$ so $f(F^m(\boldsymbol{q})) < 1$. This shows V is eventually Lyapunov with respect to $\overset{\circ}{\mathbb{R}}{}^n_+$. ∎

Next we extend Proposition 4 assuming we have one or more species going extinct. It is important to note that our set S is no longer a face of $\mathcal{X}$. Instead S is now going to be the boundary of a face. So in order to make this clear we will add a superscript to denote what dimensional space we are studying. For example, S_1^l is the boundary of an l-dimensional space where $x_1 = 0$.

Lemma 12. *Let* $S_A^l = \{\boldsymbol{x} \in \mathbb{R}^l_+ \,|\, \prod_{i \in A} x_i = 0\}$ *and suppose the species* $l+1$, $l+2, \dots, n$ *are going extinct. Also assume that there exist positive real numbers*

$c_i > 0$ for $i \in A \subset \{1, 2, \ldots, l\}$ such that for all equilibriums points $\boldsymbol{x}^*$ in $S_A^l \cap X$,

$$\phi(\boldsymbol{x}^*) = \sum_{i \in A} c_i \Big(r_i - \sum_{j=1}^{l} \alpha_{ij} x_j^* \Big) > 0.$$

Then species i persist for each $i \in A$.

Proof. Using a similar argument as in the proof of Proposition 4, we get that if $\phi(\boldsymbol{x}^*) > 0$ for all equilibrium points $\boldsymbol{x}^* \in S_A^l$, then $\beta(\boldsymbol{x}) > 1$ for all $\boldsymbol{x} \in S_A^l \cap X$. Note that for each $\boldsymbol{x}^* \in S_A^l \cap X$, $x_i^* = 0$ for each $i = l+1, l+2, \ldots, n$. This gives

$$\phi(\boldsymbol{x}^*) = \sum_{i \in A} c_i \Big(r_i - \sum_{j=1}^{n} \alpha_{ij} x_j^* \Big) > 0.$$

Further, let $c_i = 0$ for $i \in \{1, 2, \ldots, n\} \backslash A$. Then we have

$$\phi(\boldsymbol{x}^*) = \sum_{i=1}^{n} c_i \Big(r_i - \sum_{j=1}^{n} \alpha_{ij} x_j^* \Big) > 0.$$

Using these c_i's we will consider the function $V : \mathbb{R}_+^n \to \mathbb{R}_+^n$ to be

$$V(\boldsymbol{x}) = \prod_{i=1}^{n} x_i^{c_i},$$

which we use to define α and β.

Next using the notation used in Lemma 10, let $K = S_A^l \cap X$, which is a compact subset of $\mathbb{R}_+^n$. Lemma 10 gives a closed neighborhood W of K where, if for some $\boldsymbol{y} \in X$ we have $\omega(\boldsymbol{y}) \subset W$, then $\boldsymbol{y} \in S_A^l \cap X$. Since W is closed, we can find a closed cylindrical neighborhood $W' \subset W$ that has radius $\delta > 0$. Let $N = \{X \backslash S_A^l\} \cap \overset{\circ}{\mathbb{R}}{}_+^l \times [0, \delta/2) \times \cdots \times [0, \delta/2)$ and let $U = \{X \backslash W\} \cap \overset{\circ}{\mathbb{R}}{}_+^l \times [0, \delta/2) \times \cdots \times [0, \delta/2)$.

Note since species $l+1, l+2, \ldots, n$ go extinct for each $\boldsymbol{x} \in \overset{\circ}{\mathbb{R}}{}_+^n$ and for any $\delta > 0$ there exists an $M = M(\boldsymbol{x})$ such that for all $m > M$,

$$\max_{i \in \{l+1, \ldots, n\}} F_i^m(\boldsymbol{x}) < \delta/2.$$

So we have $\overline{U} \subset V$, V is positively invariant, and $\mathcal{O}^+(\boldsymbol{x}) \cap U \neq \emptyset$ for every $\boldsymbol{x} \in V$ by Lemma 10, we get from Lemma 9 that $\mathcal{O}^+(\overline{U})$ is compact and absorbing for V. Thus each species i persists for $i \in A$. ∎

This extends our persistence result so that we may look for species persisting when we know that one or more species are going extinct. In fact, we can take the above 'global' theorem and get a local theorem. This is done by replacing the assumption that species $l+1, l+2, \ldots, n$ are going extinct with the assumption that there exists an initial population density $\boldsymbol{x}$ with $\omega(\boldsymbol{x}) \subset \mathbb{R}_+^l$ where $l < n$. This gives a similar conclusion.

Theorem 8. *Suppose that species $l+1, l+2, \dots, n$ are going extinct, and on the subspace $\mathbb{R}_+^l$ species l is weakly dominated by species $1, 2, \dots, l-1$. Then species l goes extinct in $\mathbb{R}_+^n$.*

Proof. Consider the subspace $\mathbb{R}_+^l$. Using Corollary 3, there exists an $A \subset \{1, 2, \dots, l-1\}$ such that there is a $\boldsymbol{c} = (c_1, c_2, \dots, c_l)$ with $c_l > 0$, and $c_i > 0$ for $i \in A$ with

$$\lambda_l^{c_l}(\boldsymbol{x}) \prod_{i \in A} \lambda_i^{-c_i}(\boldsymbol{x}) < 1$$

on $\mathbb{R}_+^l \backslash \mathbf{0}$. Now using Proposition 5, we obtain a function $V(x_1, x_2, \dots, x_n) = x_l^{c_l} \prod_{i=A} x_i^{-c_i}$ on $\mathbb{R}_{A,l}^l$ where $A \subset \{1, 2, \dots, l\}$ such that V is eventually Lyapunov with respect to $\mathbb{R}_{A,l}^n$. Using Lemma 1, we have species l goes extinct. ∎

7. Conclusions

For a system of difference equations of Lotka-Volterra type, we have constructed tools that one can use to determine the long term behavior of the system. This is the goal of many biologists since knowing the long-term behavior can answer questions whether a species goes extinct or persists. We have found sufficient conditions for a group of species to drive another to extinction. We proved that if a group weakly dominates another species, then that species will be driven to extinction.

Our persistence results were modeled after the permanence results of Hofbauer *et al.* (1987). We were able to modify their results to get the persistence of one or more species. They were able to show that the region, where one or more species are extinct, was, on average, repelling. This is sufficient for permanence. We noticed that one can apply the same techniques to just part of this region and get that some of the species persist. This can be extremely useful information to the researcher.

The other main result deals with weak extinction. We think of weak extinction as starting with each species present; it eventually appears that one or more species are going extinct. This includes extinction of a species as well as dynamics such as mutual exclusion where a species dies out, but which species may depend on what the initial population density was. We showed that if there was no equilibrium population density where every species was present, the system exhibited weak extinction.

In addition to these results, we showed that the persistence and extinction results were applicable to submodels where one or more species are known to be going extinct. These are ideas similar to those presented in (Chan D.M. and Franke, 1999). So if one is able to determine that a few species will go extinct, the full model can be reduced to the submodel which has the species going extinct removed. Now with this submodel, our persistence and extinction theorems can be applied and still hold for the full model. These extensions to submodels allow researchers to investigate their model to much greater depths, and thus allow for a greater understanding of the dynamics.

Finally, we examined a system in which a species goes extinct without any type of weak dominance. This was shown using the persistence and the weak extinction results. So applying each of the tools to a model, one can deduce the dynamics of the system beyond what each tool itself is capable of describing.

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