On the stabilizing effect of specialist predators on founder-controlled communities

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Abstract

We study a generalized model of $2n$ interacting species consisting of n competing prey and n predators each of which feeds exclusively upon one of the prey species. Under the assumption that the prey community is founder-controlled (the positive equilibria determined by single prey species are asymptotically stable in prey phase space), it is shown that the n predators can mediate uniform persistence when their mortality rates are sufficiently small. When this occurs, a repelling heteroclinic network on the boundary of the positive orthant is formed in which the removal of any predator leads to a system with a globally asymptotically stable equilibrium that only supports a single species.

1 Introduction

A basic question confronting ecologists is: what mechanisms help mediate coexistence amongst species competing for overlapping resources? [1]. One such mechanism, the keystone effect, involves a complex of predators who dynamically readjust the competitive balance of an ecological community [13]. Mathematical studies of this effect herald back to the early work of Slobodkin [16] who showed that the addition of a density-dependent mortality term could mediate coexistence between Lotka-Volterra competitors. Since then, studies of low dimensional communities have focused on various types of predator-mediated coexistence: local stability of an equilibrium [6, 7, 9, 18], uniform persistence [4, 5, 8, 12, 14, 15] and bifurcations to non-equilibrium attractors [11].

Currently, few generalizations to higher dimensional communities exist that answer the following two questions: How many predators does it take to mediate coexistence on n competing species? What is the effect of removing a single predator from these communities? Since competitive systems can have arbitrarily complex dynamics [17], a mathematically complete response is impossible. However, if we restrict our attention to ecologically prominent community and predator types, answers may be forthcoming. With regards to competition, Yodzis [20] distinguished between two community types: founder-controlled and dominance-controlled. In founder-controlled communities, species have roughly equal competitive abilities and the species that establishes itself first prevents other competitors from invading. In dominance-controlled communities, pairwise interactions result in the exclusion of one species. With regard to predation, ecologists often categorize predators into two types: generalists and specialists [1]. As their names suggest, generalists are predators that feed on many different prey while specialists feed exclusively on a single prey species [1].

Wolkowicz [19] studied the issue of predator-mediated coexistence for a community consisting of dominance-controlled prey and specialist predators. Under the assumptions that the prey compete for an essential and non-reproducing resource, the resource uptake is Holling type I or II and the prey uptake is linear, Wolkowicz showed that it takes $n-1$ specialists to mediate coexistence. To understand the effect of predator deletion on this community, we refer to the work of Butler and Wolkowicz [3]. They showed that in the absence of the predators, the prey community has an ordering, say prey $1 < \ldots <$ prey n, where prey i displaces prey j whenever $i > j$. Hence, for the persistent community consisting of n prey and $n-1$ predator species, Wolkowicz [19] showed that the removal of prey i's predator results in the extinction of prey species 1 through $i-1$ and their affiliated predators.

In this article, we focus on how specialist predators can mediate permanence for communities of founder-controlled prey. In contrast to the dominance-controlled community, we will show that it takes n specialist predators to mediate persistence. When this occurs, the removal of any predator results in the collapse of the entire community except for one prey species.

2   Main Result

Consider the following equations of competition for n species

$$\frac{dx_i}{dt} = x_i f_i(\mathbf{x}) \qquad i = 1, \ldots, n \tag{1}$$

where x_i is density of species i, $\mathbf{x} = (x_1, ..., x_n)$, and f_i is the per-capita growth rate of species i. We assume that the f_i satisfy three conditions:

C1 If the density of any species increases, the growth rate of each species decreases. Hence $\frac{\partial f_i}{\partial x_j} < 0$ for $i, j \in \{1, ..., n\}$.

C2 In the absence of the other species, each competitor has a well defined carrying capacity. Hence, for each i there exists $x_i^* > 0$ such that

$$f_i(0, ..., 0, x_i^*, 0, ..., 0) = 0.$$

C3 The community is founder-controlled [20]. In other words,

$$f_j(0, ..., 0, x_i^*, 0, ..., 0) < 0$$

for all $i \neq j$.

To mediate coexistence for founder-controlled communities, we consider adding specialist predators whose functional (the per-capita rate of consumption) and numerical (the per-capita fecundity rate of the predator) responses are C^1 functions, g_i and $h_i : \mathbf{R}_+ \to \mathbf{R}_+$, that satisfy

G1 In the absence of prey, there is no consumption or reproduction. Hence, $h_i(0) = g_i(0) = 0$.

G2 As prey densities increase, the per-capita consumption and the per-capita fecundity rates increase. Hence $g_i'(x)$ and $h_i'(x)$ are strictly positive for all $x \geq 0$.

Responses that satisfy these criteria include Holling's type I, II and III responses [1]. The dynamics of this augmented community are determined by

$$\frac{dx_i}{dt} = x_i f(\mathbf{x}) - y_i g_i(x_i) \tag{2}$$
$$\frac{dy_i}{dt} = y_i h_i(x_i) - m_i y_i$$
$$i = 1, \ldots, n$$

where y_i is the density of predator i and m_i is the per-capita mortality rate for predator i.

Recall that Eq. 2 is *uniformly persistent* [2] or *permanent* [15] if there exists a constant $K > 0$ such that

$$\frac{1}{K} \leq \liminf_{t \to \infty} x_i(t) \leq \limsup_{t \to \infty} x_i(t) \leq K$$

and

$$\frac{1}{K} \leq \liminf_{t \to \infty} y_i(t) \leq \limsup_{t \to \infty} y_i(t) \leq K$$

for any solution $\mathbf{z}(t) = (\mathbf{x}(t), \mathbf{y}(t))$ to Eq. 2 with positive initial conditions. It is easy to check that adding $n-1$ specialists can not mediate uniform persistence as the equilibria corresponding to predator-free prey remain asymptotically stable in the augmented phase space. The following theorem shows that adding n specialists can mediate uniform persistence.

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Theorem 1 *Let $f_i : \mathbf{R}_+^n \to \mathbf{R}$ be C^1 functions that satisfy C1-C3 and $g_i, h_i :$ $\mathbf{R}_+ \to \mathbf{R}_+$ be C^1 functions that satisfy G1-G2. If the m_i are sufficiently small, then Eq. 2 is uniformly persistent and any solution $\mathbf{z}(t) = (\mathbf{x}(t), \mathbf{y}(t))$ to Eq. 2 with $x_i(0) > 0$ for all $i \geq 1$, $y_1(0) = 0$ and $y_i(0) > 0$ for all $i \geq 2$ satisfies*

$$\lim_{t \to \infty} \mathbf{z}(t) = (x_1^*, 0, \dots, 0).$$

In particular Thm. 1 shows that $\partial\mathbf{R}_+^{2n}$ contains a repelling heteroclinic network for Eq. 2 whenever the m_i are sufficiently small.

3   Proof of Theorem 1

Define

$$
\begin{aligned}
\Sigma &= [0, x_1^*] \times \dots \times [0, x_n^*] \subset \mathbf{R}_+^n \\
\alpha &= \max_{i,j,\mathbf{X} \in \Sigma} -\frac{\partial f_j}{\partial x_i}(\mathbf{x}) \\
\beta &= \min_{i,x \in [0, x_i^*]} \{g_i'(x), h_i'(x)\} \\
\gamma &= \max_{i,x \in [0, x_i^*]} \{g_i'(x), h_i'(x)\} \\
\eta &= \min_{i,j,\mathbf{X} \in \Sigma} -\frac{\partial f_j}{\partial x_i}(\mathbf{x}) \\
F &= \max_i \{f_i(\mathbf{0}), 1/f_i(\mathbf{0})\} \\
\lambda &= \min_i \{f_i(x_1^*, \dots, x_n^*)\} \\
m &= \max_i m_i
\end{aligned}
$$

Note that C1, C2 and the fact that the f_i are nonnegative imply that $\Sigma \times \mathbf{R}^n$ is forward invariant for the flow generated by Eq. 2 and that every solution to Eq. 2 eventually enters $\Sigma \times \mathbf{R}^n$.

The first step in the proof of Thm. 1 is to prove there is a global compact attractor for Eq. 2.

Lemma 1 *Given f_i, g_i and h_i as stated in Thm. 1, there exists a constant $C > 0$ such that*

$$\limsup_{t \to \infty} |\mathbf{z}(t)| < C$$

for any solution $\mathbf{z}(t)$ to Eq. 2.

Proof. For positive constants A and B, we have that

$$\sum_{i=1}^n A\dot{x}_i + B\dot{y}_i = \sum_{i=1}^n (x_i f_i(\mathbf{x}) - y_i g_i(x_i))A + (y_i h_i(x_i) - m_i y_i)B \qquad (3)$$

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$$\leq \sum_{i=1}^{n} x_i(f_i(\mathbf{0}) - \eta x_i)A + y_i x_i(B\gamma - A\beta) - m_i y_i B.$$

Given a solution $\mathbf{z}(t) = (\mathbf{x}(t), \mathbf{y}(t))$ for Eq. 2 define $S(t) = \sum_i Ax_i(t) + By_i(t)$. Choose A and B such that $A\beta > B\gamma$ and $\epsilon > 0$ such that $\epsilon < \min_i m_i$. Eq. 3 implies

$$\dot{S} + \epsilon S \leq \sum_{i=1}^{n} x_i A(f_i(\mathbf{0}) + \epsilon - \eta x_i) + y_i x_i (B\gamma - A\beta) - (m_i - \epsilon)By_i$$

$$\leq \sum_{i=1}^{n} x_i A(F + \epsilon - \eta x_i)$$

where the second line follows from the choice of A, B and ϵ. Since the function $s \mapsto s(F + \epsilon - \eta s)$ takes on its maximum value at $\frac{F+\epsilon}{2\eta}$, it follows that

$$\dot{S} + \epsilon S \leq \frac{An(F + \epsilon)^2}{4\eta}$$

and

$$\limsup_{t \to \infty} S(t) \leq \frac{An(F + \epsilon)^2}{4\eta\epsilon} \square$$

To prove that Eq. 2 is uniformly persistent whenever the m_i are sufficiently small we proceed inductively on n. When $n = 1$, Eq. 2 is uniformly persistent provided that $h_1(x_1^*) > m_1$. Since $h_1(x_1^*) > 0$, Eq. 2 is uniformly persistent for sufficiently small m_1.

Assume Eq. 2 is uniformly persistent whenever $n < k$ and the m_i are sufficiently small. We intend to show that Eq. 2 is uniformly persistent when $n = k$ and the m_i are sufficiently small. To do this, we make use of a result due to Hutson [10]. Recall that the limit set of an invariant set K for Eq. 2 equals

$$L^+(K) = \overline{\cup_{z \in K} \omega(z)}$$

where $\omega(z)$ is the omega-limit set for $z \in \mathbf{R}_+^{2n}$.

Theorem (Hutson 1984). *Consider $F(\mathbf{z}) \in C^1(\mathbf{R}_+^{2n}, \mathbf{R}^{2n})$ such that $\partial\mathbf{R}_+^{2n}$ is invariant for the flow of $\dot{\mathbf{z}} = F(\mathbf{z})$. Assume this flow is dissipative and $P \in C^1(int \ \mathbf{R}_+^{2n}, \mathbf{R}_+)$ is bounded below. Define*

$$\phi(\mathbf{z}) = \begin{cases} \frac{<\nabla P(\mathbf{Z}), F(\mathbf{Z})>}{P(\mathbf{Z})} & \text{if } \mathbf{z} \in int \ \mathbf{R}_+^{2n} \\ \liminf_{\mathbf{w} \to \mathbf{z}, \mathbf{w} \in int \ R_+^{2n}} \phi(\mathbf{z}) & \text{else.} \end{cases}$$

Then for any solution $\mathbf{z}(t)$ to $\dot{\mathbf{z}} = F(\mathbf{z})$, $\phi(\mathbf{z}(t))$ is integrable and the system is uniformly persistent provided that

$$\sup_{t>0} \int_0^t \phi(\mathbf{z}(s))ds > 0$$

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for all solutions $\mathbf{z}(t)$ *such that* $\mathbf{z}(0) \in L^+(\partial \mathbf{R}_+^n)$.

To make use of Hutson's Thm., we define

$$P(\mathbf{z}) = \prod_{i=1}^{n} x_i y_i^a$$

where a is a positive constant that remains to be determined. For $\mathbf{z} \in$ int $\mathbf{R}_+^{2n}$, we get

$$\phi(\mathbf{z}) = \sum_{i=1}^{n} f_i(\mathbf{x}) - \frac{g_i(x_i)y_i}{x_i} + ah_i(x_i) - am_i.$$

ϕ extends continuously to $\partial \mathbf{R}_+^{2n}$ as $\lim_{x_i \to 0} \frac{g_i(x_i)}{x_i} = g_i'(0)$.

To simplify the presentation of the proof we introduce the following notations: Given $\mathbf{z}(t)$ a solution to Eq. 2 and a continuous function $\psi : \mathbf{R}^{2n} \to \mathbf{R}$ define

$$\overline{\psi(\mathbf{z})} = \limsup_{T \to \infty} \frac{1}{T} \int_0^T \psi(\mathbf{z}(t))dt$$

and

$$\underline{\psi(\mathbf{z})} = \liminf_{T \to \infty} \frac{1}{T} \int_0^T \psi(\mathbf{z}(t))dt.$$

Since

$$\sup_{t>0} \frac{1}{T} \int_0^T \phi(\mathbf{z}(t))dt \geq \underline{\phi(\mathbf{z})} \tag{4}$$

it is sufficient to show that $\underline{\phi(\mathbf{z})} > 0$ for any solution $\mathbf{z}(t)$ to Eq. 2 with $\mathbf{z}(0) \in L^+(\partial \mathbf{R}_+^{2n})$.

First, consider the zero solution, $\mathbf{z}(t) \equiv \mathbf{0}$. For this solution,

$$\phi(\mathbf{0}) = \sum_{i=1}^{n} f_i(0) - am_i \geq n(1/F - am)$$

and is positive if m is sufficiently small.

To show that $\underline{\phi(\mathbf{z})}$ is positive for other orbits in $L^+(\partial \mathbf{R}_+^{2n})$, we consider two cases: all "active" competitors are predated upon or there are "active" competitors free from predation. To deal with the first case, assume that $\mathbf{z}(t)$ is a solution to Eq. 2 such that $\mathbf{z}(0) \in L^+(\partial \mathbf{R}_+^{2n})$ and $y_i(0) > 0$ whenever $x_i(0) > 0$. Since predators that predate on inactive prey eventually go extinct and $\mathbf{z}(0) \in L^+(\partial \mathbf{R}_+^{2n})$, we have $y_i(0) = 0$ whenever $x_i(0) = 0$. Define the set of active competitors as $\mathcal{A} = \{i : x_i(0) > 0\}$. Lemma 1 implies that

$$
\begin{aligned}
0 &\geq \limsup_{T \to \infty} \frac{1}{T} \ln \frac{y_i(T)}{y_i(0)} \\
&= \overline{h_i(x_i)} - m_i \\
&\geq \beta \overline{x_i} - m_i
\end{aligned}
$$

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for any $i \in \mathcal{A}$. Hence,

$$\overline{x_i} \leq \frac{m}{\beta} \tag{5}$$

for all $i \in \mathcal{A}$.

Now consider $i \notin \mathcal{A}$, Eq. 5 implies that

$$\underline{f_i(\mathbf{x})} \geq f_i(\mathbf{0}) - \sum_{j \in \mathcal{A}} \alpha \overline{x_j} \geq f_i(\mathbf{0}) - \frac{\alpha m |\mathcal{A}|}{\beta}.$$

where $|\mathcal{A}|$ is the cardinality of $\mathcal{A}$. Since $|\mathcal{A}| < n$, induction implies that the subsystem determined by the active competitors and predators is uniformly persistent for sufficiently small m_i. Therefore, for sufficiently small m_i it follows that

$$0 = \lim_{T \to \infty} \frac{1}{T} \ln \frac{x_i(T)}{x_i(0)} = \lim_{T \to \infty} \frac{1}{T} \ln \frac{y_i(T)}{y_i(0)}$$

for all $i \in \mathcal{A}$. Equivalently,

$$0 = \lim_{T \to \infty} \frac{1}{T} \int_0^T f_i(\mathbf{x}(t)) - \frac{g_i(x_i(t)) y_i(t)}{x_i(t)} dt$$

and

$$0 = \lim_{T \to \infty} \frac{1}{T} \int_0^T h_i(x_i(t)) - m_i dt$$

for all $i \in \mathcal{A}$. Thus, a lower bound for $\underline{\phi(\mathbf{z})}$ is given by

$$
\begin{aligned}
\sum_{i \notin \mathcal{A}} \left(\underline{f_i(\mathbf{x})} - am_i \right) &\geq \sum_{i \notin \mathcal{A}} \left(f_i(\mathbf{0}) - \alpha \sum_{j \in \mathcal{A}} \overline{x_j} - am \right) \\
&\geq \left(1/F - |\mathcal{A}| \frac{\alpha m}{\beta} - am \right) (n - |\mathcal{A}|).
\end{aligned}
$$

Since $|\mathcal{A}| < n$, $\phi(\mathbf{z})$ is positive for m sufficiently small.

Next we consider the case when there are more active competitors than predators. Let $\mathbf{z}(t) = (\mathbf{x}(t), \mathbf{y}(t))$ be a solution to Eq. 2 such that $\mathbf{z}(0) \in L^+(\mathbf{R}_+^{2n})$ and for some i, $x_i(0) > 0$ and $y_i(0) = 0$. Since predators that predate on inactive prey eventually go extinct and $\mathbf{z}(0) \in L^+(\partial \mathbf{R}_+^{2n})$, once again we have $y_i(0) = 0$ whenever $x_i(0) = 0$. Define the "active" preys to be $\mathcal{A} = \{i : x_i(0) > 0\}$ and the "active" predators to be $\mathcal{P} = \{i : y_i(0) > 0\}$. Our assumption that there are more active competitors than predators implies that $\mathcal{P}$ is a proper subset of $\mathcal{A}$. Lemma 1 implies there exists a $C > 0$ such that $\overline{y_i} \leq C$ for all $i \in \mathcal{P}$. Therefore we get

$$
\begin{aligned}
\overline{f_i(\mathbf{x})} - \overline{\frac{g_i(x_i) y_i}{x_i}} &\geq f_i(x_1^*, ..., x_n^*) - \gamma \overline{y_i} \\
&\geq \lambda - \gamma C
\end{aligned}
$$

for all $i \in \mathcal{P}$. For $i \in \mathcal{A} \backslash \mathcal{P}$, we have that

$$
\begin{aligned}
0 &\geq \limsup_{T \to \infty} \frac{1}{T} \ln \frac{x_i(T)}{x_i(0)} \\
&= \overline{f_i(\mathbf{x})} \\
&\geq \underline{f_i(\mathbf{0})} - \sum_{j=1}^{n} \alpha \underline{x_j}.
\end{aligned}
$$

Hence, there exists a $j \in \mathcal{A} \backslash \mathcal{P}$ such that

$$
\underline{x_j} \geq \frac{f_i(\mathbf{0})}{\alpha n} \geq \frac{1}{F \alpha n}.
$$

For $i \in \{1, \ldots, n\} \backslash \mathcal{A}$, it also follows that

$$
\underline{f_i(\mathbf{x})} \geq \lambda.
$$

Using these estimates, we get

$$
\begin{aligned}
\underline{\phi(\mathbf{z})} &\geq n(\lambda - am) - |\mathcal{P}| \gamma C + \underline{a h_j(x_j)} \\
&\geq n(\lambda - am) - |\mathcal{P}| \gamma C + \frac{a\beta}{F \alpha n}
\end{aligned}
$$

Therefore $\underline{\phi(\mathbf{z})}$ is positive whenever a is sufficiently large and m is sufficiently small. Hence we have shown that Eq. 2 is uniformly persistent when $n = k$ completing the proof of the first assertion of Thm. 1.

Now we prove the second assertion of Thm. 1. Assume that $\mathbf{z}(t)$ is a solution to Eq. 2 such that $x_i(0) > 0$ for all i, $y_i(0) > 0$ for all $i > 1$, and $y_1(0) = 0$. We have previously shown $\overline{x_i} \leq \frac{m}{\beta}$ for all $i > 1$. Therefore,

$$
\begin{aligned}
0 &\geq \limsup_{T \to \infty} \frac{1}{T} \ln \frac{x_1(T)}{x_1(0)} \\
&= \overline{f_1(\mathbf{x})} \\
&\geq \eta(x_1^* - \overline{x_1}) - \alpha \sum_{i>1} \overline{x_i} \\
&\geq \eta(x_1^* - \overline{x_1}) - \frac{\alpha(n-1)m}{\beta}.
\end{aligned}
$$

Thus,

$$
x_1^* - \overline{x_1} \leq \frac{\alpha(n-1)m}{\beta \eta}. \tag{6}
$$

For $i > 1$,

$$
\begin{aligned}
\overline{f_i(\mathbf{x})} &\leq \overline{f_i(x_1, 0, \ldots, 0)} \tag{7} \\
&\leq \alpha(x_1^* - \overline{x_1}) + f_i(x_1^*, 0, \ldots, 0).
\end{aligned}
$$

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C3 implies that $f_i(x_1^*, 0, ..., 0) < 0$ for $i > 1$. This observation in conjunction with Eqs. 6 and 7 implies that for sufficiently small m, $\overline{f_i(\mathbf{x})}$ is negative for all $i > 1$. Therefore,

$$\limsup_{t \to \infty} \frac{1}{t} \ln\left(\frac{x_i(t)}{x_i(0)}\right) = \frac{\overline{\dot{x}_i}}{x_i} \leq \overline{f_i(\mathbf{x})} < 0$$

and $\lim_{t \to \infty} x_i(t) = 0$ for all $i > 1$.

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