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Generalist and specialist predators that mediate permanence in ecological communities

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Abstract. General dynamic models of systems with two prey and one or two predators are considered. After rescaling the equations so that both prey have the same intrinsic rate of growth, it is shown that there exists a generalist predator that can mediate permanence if and only if there is a population density of a prey at which its per-capita growth rate is positive yet less than its competitor's invasion rate. In particular, this result implies that if the outcome of competition between the prey is independent of initial conditions, then there exists a generalist predator that mediates permanence. On the other hand, if the outcome of competition is contingent upon initial conditions (i.e., the prey are bistable), then there may not exist a suitable generalist predator. For example, bistable prey modeled by the Ayala–Gilpin (θ-Logistic) equations can be stabilized if and only if $\theta < 1$ for one of the prey. It is also shown that two specialist predators always can mediate permanence between bistable prey by creating a repelling heteroclinic cycle consisting of fixed points and limit cycles.

key words: Permanence – Bistability – Competition – Heteroclinic cycles

1 Introduction

Lotka and Volterra when discussing two competing species classified their interactions into three categories: coexistence, competitive dominance and competitive bistability. One species always emerges the victor in the last two categories. When the system exhibits competitive dominance, the victor displaces the other species independent of the initial conditions. When the system is bistable, victory is contingent upon initial conditions. In light of biodiversity issues, mechanisms that mediate coexistence between competing species is of great interest to ecologists. One well studied mechanism, the keystone effect

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(Paine 1966), involves the presence of predators who mediate coexistence by dynamically readjusting the competitive balance of the community.

One of the first people to investigate the theoretical implications of predation on competing species was Slobodkin (1961). He showed that the addition of a density-dependent mortality term to the Lotka–Volterra competition equations could switch the population dynamics from competitive exclusion to coexistence. Later mathematical analyses addressed this question by evaluating the local stability of equilibria for two prey-single predator models (Cramer and May 1972, Fuji 1977, Vance 1978, Hsu 1981, see Yodzis 1989 for further discussion). These analyses equate coexistence with a state of constancy to which all populations return following sufficiently small perturbations. However, "if we are dealing with a system profoundly effected by changes external to it, and continually confronted by the unexpected, the constancy of [the system's] behavior becomes less important than the persistence of its relationships" (Holling 1973). An alternative definition of coexistence introduced by Hutson and Law (1985) is *permanence*: the existence of "a region of phase space (that is, the space occupied by the population vector) at a non-zero distance form the boundary (corresponding to extinction of at least one species), in which all the population vectors must ultimately lie." Permanence addresses Holling's concerns by providing a global criterion that includes coexistence about a non-equilibrium state (e.g. Klebanoff and Hastings 1994).

In the past decade, predator-mediated permanence has been studied for several low-dimensional Lotka–Volterra systems. Hutson and Vickers (1983) showed that a generalist predator could mediate permanence between dominance controlled prey but could not mediate permanence for bistable competitors. Kirlinger (1986) and Hofbauer and Sigmund (1989) showed the addition of two specialist predators or two competitors can stabilize bistable communities. In this article, predator-mediated permanence is studied for a larger class of predator-prey equations to evaluate the robustness of these predictions.

2 Permanence for competing species

Consider the following equations of competition

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(x_1, x_2) \\ \frac{dx_2}{dt} &= x_2 f_2(x_2, x_1) \end{aligned} \tag{1}$$

where x_i is the density of species i and the f_i satisfy three conditions.

C1: If the density of either species increases, then the growth rate of both species decreases. Hence $(\partial f_i / \partial x_j) < 0$ for $i, j \in \{1, 2\}$.

C2: In the absence of the other species, each competitor has a well defined carrying capacity. Hence, for $i \in \{1, 2\}$ there exists a $x_i^* > 0$ such that $f_i(x_i^*, 0) = 0$.

C3: The equilibria of Eq. 1 are hyperbolic.

Recall that an equilibrium or limit cycle for a system of differential equations $dz/dt = G(z)$ is *hyperbolic* if it has no characteristic exponent with real part zero (cf. Guckenheimer and Holmes 1983).

By examining the transversal eigenvalues of the equilibria $(x_1^*, 0)$ and $(0, x_2^*)$ Eq. 1 falls into one of three cases. If both transversal eigenvalues are positive, the competitors *permanently coexist*. If one transversal eigenvalue is negative and the other is positive, the system is *dominance-controlled*. Finally, if both transversal eigenvalues are negative, competition is *bistable*.

We provide two examples that satisfy conditions C1–C3.

Example 1. Ayala et al. (1973) conducted experiments on fruit fly dynamics to test the validity of ten models of competition. One of the models accounting best for the experimental results is given by:

$$f_i(x_i, x_j) = r_i\left(1 - \left(\frac{x_i}{K_i}\right)^{\theta_i} - \alpha_{ij}\frac{x_j}{K_j}\right) \tag{2}$$

where r_i is the intrinsic rate of growth of species, K_i is the carrying capacity of species i, θ_i provides a non-linear measure of intraspecific interference, and α_{ij} provides a measure of interspecific interference. The model defined by Eq. 2 has at most one internal equilibrium. Therefore, the following invasion criteria determine the global dynamics: species j can invade the equilibrium, $(x_i = K_i, x_j = 0)$ with $i \neq j$ if and only if

$$\alpha_{ji} < 1\,. \tag{3}$$

Note 1. When $\theta_i = 1$ Eq. 2 reduces to the Lotka–Volterra competition equations.

Example 2. Schoener (1978) developed mechanistic one-level models of various types of competition (completely overlapping resources, resource partitioning, intra- and interspecific interference). In the case of species that compete for completely overlapping resources and that engage in interspecific interference, Schoener (1978) proposed that

$$f_i(x_i, x_j) = x_i\left(\frac{\beta_i I_0}{Y + \beta_i x_i + \beta_j x_j} - \gamma_{ij}x_j - C_i\right)R_i \tag{4}$$

where I_0 is the rate of net energy input into the system, β_i is the searching efficiency of species i, γ_{ij} is the cost to species i due to interactions with species j, C_i is the per-capita maintenance and replacement costs o f species i, R_i is the number of individuals of species i resulting from conversion of one unit net energy input, and Y is a constant that is inversely proportional to the rate which the individuals can obtain food.

Applying the change of variables $x_i \mapsto (Y/\beta_i)x_i$ and setting $a_i = R_i I_0 \beta_i / Y$, $b_{ij} = R_i \gamma_{ij} Y/\beta_j$ and $c_i = C_i R_i$, Eq. 4 reduces to

$$f_i(x_i, x_j) = \frac{a_i}{1 + x_i + x_j} - b_{ij}x_j - c_i\,. \tag{5}$$

Solving $f_i(x_i^*, 0) = 0$ for x_i^*, we get that $x_i^* = (a_i - c_i)/c_i$. Plugging x_i^* into Eq. 5, we may conclude that species j $(j \neq i)$ can invade the equilibrium $(x_i = x_i^*, x_j = 0)$ if and only if

$$f_j(0, x_i^*) = \frac{a_j}{1 + x_i^*} - b_{ji} x_i^* - c_j > 0\,.$$

Equivalently, species j can invade if and only if

$$\frac{a_i - c_i}{c_i} < \frac{-(b_{ji} + c_j) + \sqrt{(b_{ji} + c_j)^2 + 4(a_j - c_j)b_{ji}}}{2b_{ji}}\,. \tag{6}$$

Notice that an upper bound for Eq. 6 is given by

$$\lim_{b_{ji} \to 0} \frac{-(b_{ji} + c_j) + \sqrt{(b_{ji} + c_j)^2 + 4(a_j - c_j)b_{ji}}}{2b_{ji}} = \frac{a_j - c_j}{c_j}\,.$$

Consequently, Eq. 6 cannot be meet for both species, and coexistence is impossible.

3 Generalist predators that mediate permanence

To mediate permanence between the competing species, we supplement Eq. 1 with a generalist predator:

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(x_1, x_2) - s_1 x_1 g(x_1, x_2, y) \\ \frac{dx_2}{dt} &= x_2 f_2(x_2, x_1) - s_2 x_2 g(x_1, x_2, y) \\ \frac{dy}{dt} &= y F(x_1, x_2, y) \end{aligned} \tag{7}$$

where s_i represents the rate at which the predator encounters prey i while actively searching, and $g(x_1, x_2, y)/y$ is the portion of the predator population that is actively searching (e.g. not handling or digesting prey, interfering with one another, or resting). Although the predator's functional response, $s_i x_i g(x_1, x_2, y)/y$, occurs in an apparently restrictive form, it covers many multiprey-single predator models where the standing ecological assumption is that the predator selects its prey in a frequency independent manner (Begon et al. 1990).

We assume that g and F are C^1 and Eq. 7 satisfies two conditions.

C4: Eq. 7 is *dissipative* (i.e. there exists a constant $K > 0$ such that every solution $\mathbf{v}(t)$ to Eq. 7 satisfies $\limsup_{t \to \infty} |\mathbf{v}(t)| \leqq K$ where $|\cdot|$ is the Euclidean norm).

C5: All equilibria and limit cycles of Eq. 7 that lie in $\{(x_1, 0, y)\colon x_1 \geqq 0, y \geqq 0\}$ or $\{(0, x_2, y)\colon x_2 \geqq 0, y \geqq 0\}$ are hyperbolic.

C4 ensures that species do not grow without bound and C5 rules out non-generic cases that would complicate the statement of our first theorem.

Theorem 1. *Assume f_i are such that C1–C3 are satisfied. There exists a predator (i.e., parameters s_i and functions g and F such that Eq. 7 satisfies C4–C5) that mediates permanence if and only if for some $i \in \{1, 2\}$ there exists a value $\tilde{x}_i \in (0, x_i^*]$ such that*

$$\frac{f_i(\tilde{x}_i, 0)}{f_i(0, 0)} < \frac{f_j(0, \tilde{x}_i)}{f_j(0, 0)} \tag{8}$$

where $j \neq i$. In particular, when Eq. 8 does hold, there exists a Lotka–Volterra predator that mediates permanence.

A proof of Theorem 1 is presented in Sect. 6. The interpretation of Theorem 1 is facilitated by the observation that the predictions are unaffected by a rescaling of the competition equations such that $f_1(0, 0) = f_2(0, 0)$. With this rescaling, Eq. 8 asserts *there exists a suitable predator if and only if there is a density of one of the prey (say prey 1) at which its per-capita growth is positive but less than the invasion rate of prey 2*. When Eq. 8 holds, we construct a Lotka–Volterra predator that mediates permanence and that has a higher searching and conversion efficiency with respect to prey 2 (i.e. $s_2 > s_1$ and $F(0, x, 0) > F(x, 0, 0)$ for all $x > 0$). Eq. 8 always holds when there is a dominant competitor. Hence, the condition of Eq. 8 fails only if the competitors are bistable. However, unlike the Lotka–Volterra results of Hutson and Vickers (1983), bistability does not imply Eq. 8 always fails as shown below.

Revisiting example 1. Consider the Ayala–Gilpin equations (Eq. 2). Suppose competition is bistable (i.e. Eq. 3 fails for both prey). By Theorem 1 there exists a predator that can mediate permanence if and only if there is an $i \in \{1, 2\}$ and $\tilde{x}_i \in (0, K_i]$ such that

$$1 - \left(\frac{\tilde{x}_i}{K_i}\right)^{\theta_i} < 1 - \alpha_{ji}\frac{\tilde{x}_i}{K_j} \tag{9}$$

for $j \neq i$. Eq. 9 holds if and only if $\theta_i < 1$ for some i. In particular, since the Lotka–Volterra equations correspond to $\theta_i = 1$, no predator that selects its prey independent of frequency can mediate coexistence for bistable Lotka–Volterra competitors.

Note 2. Estimates of θ_i for *Drosophila* in the literature suggest that θ_i is typically less than one (see Gilpin and Ayala 1976, Thomas et al. 1980). Furthermore, there is some evidence that for a small subset of these species, pairwise competition is contingent upon initial conditions (Gilpin et al. 1986).

Revisiting example 2. Consider the Schoener model of competition (Eq. 4) and assume that competition is bistable (i.e., Eq. 6 fails for both prey). By Theorem 1 there exists a predator that can mediate permanence if and only if

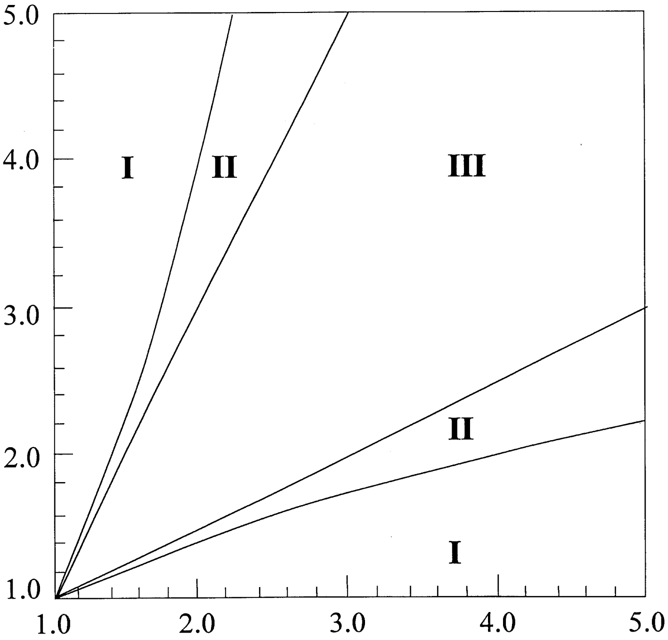

Fig. 1. The bifurcation diagram for the Schoener equations. In this diagram, we vary the a_i between 1 and 5 and hold all other parameters fixed at $b_{ij} = c_i = 1.0$. For parameters in Region I, one species dominates over another and predator-mediated coexistence is possible. In Region II, the competition is bistable and predator-mediated permanence is possible. In Region III, the competition is bistable and predator-mediated coexistence is not possible

there is an $i \in \{1, 2\}$ and an $\tilde{x}_i \in (0, (a_i - c_i)/c_i)$ such that

$$(a_j - c_j)\left(\frac{a_i}{1 + \tilde{x}_i} - c_i\right) < (a_i - c_i)\left(\frac{a_j}{1 + \tilde{x}_i} - b_{ji}\tilde{x}_i - c_j\right) \tag{10}$$

for $j \neq i$. Since

$$(a_j - c_j)\left(\frac{a_i}{1 + x} - c_i\right) = (a_i - c_i)\left(\frac{a_j}{1 + x} - b_{ji}x - c_j\right)$$

is quadratic, it has at most two solutions one of which is $x = 0$. Furthermore, as $\partial^2 f_i/\partial x_i^2(x_i, 0)$ and $\partial^2 f_j/\partial x_i^2(0, x_i)$ are strictly negative, the desired solution to Eq. 10 exists if and only if

$$\begin{aligned}(a_j - c_j)\frac{\partial f_i}{\partial x_i}(0, 0) = (c_j - a_j)a_i &< (c_i - a_i)(a_j + b_{ji}) \\ &= (a_i - c_i)\frac{\partial f_j}{\partial x_i}(0, 0)\,.\end{aligned}$$

Equivalently,

$$\frac{a_i - c_i}{a_i} < \frac{a_j - c_j}{a_j + b_{ji}}\,. \tag{11}$$

(see Fig. 1).

4 Specialist predators that mediate permanence

We consider adding two specialist predators (Begon et al. 1990) whose functional responses (the per-capita consumption rate) and numerical responses (the number of progeny produced per predator at a given prey density) are given by g_i and h_i: $\mathbf{R} \to \mathbf{R}$. We assume that g_i and h_i are C^1 and satisfy $h_i(0) = g_i(0) = 0$ and $g_i'(x)$ and $h_i'(x)$ are positive for all x. In particular, these functions may be a linear, type II, or type III (Holling 1966). With the addition of these specialists Eq. 1 becomes

$$\begin{aligned} \frac{dx_i}{dt} &= x_i f_i(x_i, x_j) - y_i g_i(x_i) \\ \frac{dy_i}{dt} &= y_i h_i(x_i) - m_i y_i \quad i = 1, 2 \end{aligned} \tag{12}$$

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

Theorem 2. *Assume that f_i satisfies C1–C3 and g_i and h_i are as defined above. When the m_i are sufficiently small, the following two statements hold.*

1. *If prey 1 is dominant, the subsystem of Eq. 12 consisting of $x_1 - x_2 - y_1$ is permanent (see Fig. 2a).*
2. *If the prey are bistable, Eq. 12 is permanent. Furthermore, the equilibria, $(x_1 = 0, x_2 = x_2^*, y_1 = 0)$ or $(x_1 = x_1^*, x_2 = 0, y_2 = 0)$, are globally stable for the subsystems, $x_1 - x_2 - y_1$ and $x_1 - x_2 - y_2$, respectively (see Fig. 2b).*

The proof of Theorem 2 is presented in Sect. 7. The first assertion of Theorem 1 generalizes a result of Butler and Wolkowicz (1986) and the second assertion generalizes work of Kirlinger (1986). In the bistable case, predators

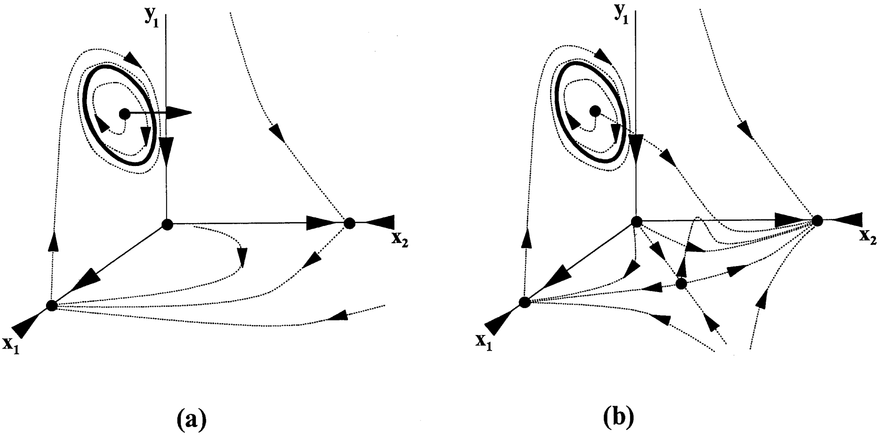

Fig. 2. (a) The limit sets for the subsystem $x_1 - x_2 - y_1$ of Eq. 12 when prey species 1 is dominant. **(b)** The limit sets for the subsystem $x_1 - x_2 - y_1$ of Eq. 12 when the f_i define a bistable community and the m_i are sufficiently small

mediate permanence by creating a repelling heteroclinic cycle: (prey 1) → (prey 1, predator 1) → (prey 2) → (prey 2, predator 2) → (prey 1). Whenever the g_i are saturating functions (e.g., Holling type II or III) and the m_i are sufficiently small, these heteroclinic cycles will alternate between equilibria and limit cycles.

5 Discussion

In addition to providing a simple criterion for predator mediated permanence, Theorem 1 offers two insights into the Lotka–Volterra prediction: a generalist predator cannot mediate permanence between bistable prey. First, Theorem 1 implies (see revisiting Example 1) that no predator who selects its prey in a frequency-independent manner can mediate permanence for bistable Lotka–Volterra prey. Thus, the Lotka–Volterra prediction holds for a large class of predator equations which can introduce non-equilibrium dynamics. Second, Theorem 1 applied to the Ayala–Gilpin equations implies that the Lotka–Volterra prediction is not robust to C^1 perturbations of the prey equations.

Theorem 2 implies that it takes one specialist predator to mediate permanence for dominance controlled prey but it always requires two specialists for bistable communities. The first observation prompts the questions: for larger competitively structured prey communities, how many specialist predators are required to mediate permanence, and what is the effect of removing one of these predators? Since the dynamics of competition can be arbitrarily complex (Smale 1976), a mathematically complete answer is impossible. However, if we restrict our attention to ecologically prominent community types (founder controlled, dominance controlled, etc.), answers are likely to be forthcoming. For example, Wolkowicz (1989) has shown that it takes $n-1$ specialists to mediate coexistence in a chemostat model consisting of n prey competing for a limiting resource. When this community is permanent, the removal of a predator will result in the extinction of 1 to $n-1$ prey species and their affiliated predators. In contrast, extending the proof of Theorem 2 to n dimensions, Schreiber (1996) has shown that a founder-controlled prey community (i.e., pairwise prey interactions are bistable, Yodzis 1989) requires n specialist predators to mediate permanence. When predator-mediated permanence occurs, the dynamics of the linked predator-prey system includes a heteroclinic network and the removal of one predator causes the community to collapse to one species. As many competitively structured communities lie between these two extremes, many interesting questions remain unanswered.

6 Proof of Theorem 1

Assume that

- For all $x \in (0, x_i^*)$ and $i \in \{1, 2\}$ and $j \neq i$,

$$\frac{f_i(x, 0)}{f_i(0, 0)} > \frac{f_j(0, x)}{f_j(0, 0)}\,. \tag{13}$$

- g, F and s_i are such that Eq. 7 is permanent.

Let $\mathbf{v}(t) = (x_1(t), 0, y(t))$ be a periodic or equilibrium solution to Eq. 7 with $x_1(0) > 0$ and $y(0) > 0$. Given a continuous function, h: $\mathbf{R}^3 \to \mathbf{R}$, define

$$\overline{h}(\mathbf{v}) = \lim_{T \to \infty} \frac{1}{T} \int_0^T h(\mathbf{v}(t))\, dt \, .$$

Consider the per-capita growth rate of prey species 1

$$\frac{\dot{x}_1(t)}{x_1(t)} = f_1(\pi \mathbf{v}(t)) - s_1 g(\mathbf{v}(t))$$

where π: $\mathbf{R}^3 \to \mathbf{R}^2$ is projection onto the first two coordinates. Integrating the per-capita growth rate over the interval $[0, T]$ and taking the limit as $T \to \infty$ we obtain

$$\lim_{T \to \infty} \frac{1}{T} \ln \frac{x_1(T)}{x_1(0)}$$

which equals zero since $x_1(t)$ is uniformly bounded above and below for $t > 0$. Hence, $\overline{f_1(\pi \mathbf{v})} = s_1 \overline{g(\mathbf{v})}$.

C5 implies that prey 2 can invade this trajectory if and only if the average per-capita growth rate of prey 2 along $\mathbf{v}$, $\overline{f_2(\pi \mathbf{v})} - s_2 \overline{g(\mathbf{v})}$, is strictly positive. Therefore, prey 2 can invade if and only if

$$\frac{\overline{f_2(\pi \mathbf{v})}}{f_2(0, 0)} > c \, \frac{\overline{f_1(\pi \mathbf{v})}}{f_1(0, 0)} \tag{14}$$

where $c = s_2 f_1(0, 0)/s_1 f_2(0, 0)$. Eqs. 13 and 14 imply that prey 2 can invade only if $c < 1$. Similarly, we can show that prey 1 can invade the prey 2-predator subsystem only if $c > 1$. Hence, either the system is not permanent or Eq. 13 does not hold.

On the other hand, suppose there exists an $i \in \{1, 2\}$ and $\tilde{x}_i \in (0, x_i^*]$ such that Eq. 8 holds. Without loss of generality, we assume that $i = 1$. Continuity of the f_i implies that there exists a constant $c > 1$ such that

$$c \, \frac{f_1(\tilde{x}_1, 0)}{f_1(0, 0)} < \frac{f_2(0, \tilde{x}_1)}{f_2(0, 0)} \, .$$

Continuity of the f_i and C3 implies that there exists $\tilde{x}_2 \in (0, \delta]$ such that

$$c \, \frac{f_1(0, \tilde{x}_2)}{f_1(0, 0)} > \frac{f_2(\tilde{x}_2, 0)}{f_2(0, 0)}$$

where

$$\delta = \min_{x_1, x_2 > 0} \{ x_1 : f_1(x_1, x_2) = f_2(x_2, x_1) = 0 \} \, .$$

Note that C3 implies that δ is positive.

Now, we define our predator. Let $g(x_1, x_2, y) = y$ and $F(x_1, x_2, y) = q_1 s_1 x_1 + q_2 s_2 x_2 - m$. Pick $m > 0$, the value does not matter. Choose s_1 and s_2 such that $s_2/s_1 = cf_2(0,0)/f_1(0,0)$. Define $q_i = m/s_i\tilde{x}_i$. To prove Eq. 7 with these definitions of g, s_i and F is permanent, we use the following theorem

Theorem 3 (Butler and Waltman 1986). *Let $d\mathbf{v}/dt = f(\mathbf{v})$ define a flow on $\mathbf{R}^n_+$ for which $\partial\mathbf{R}^n_+$ is invariant. If this flow is acyclic on $\partial\mathbf{R}^n_+$ and dissipative then it is permanent if and only if*

$$W^s(\gamma) \cap \operatorname{int} \mathbf{R}^n_+ = \emptyset$$

for all omega limit sets, ω, that lie in $\partial\mathbf{R}^n_+$ and where $W^s(\gamma)$ is the stable set of γ.

Consider the dynamics of the predator-prey subsystem,

$$\frac{dx_i}{dt} = x_i f_i(x_i, 0) - s_i x_i y$$

$$\frac{dy}{dt} = y q_i s_i x_i - my\,.$$

Our definitions of F and g imply that
- $(\tilde{x}_i, \tilde{y}_i)$ is the unique internal equilibrium of the predator-prey subsystem.
- The variational matrix for this predator-prey subsystem at equilibrium is given by

$$M = \begin{pmatrix} \tilde{x}_i \dfrac{\partial f_i}{\partial x_i} & -s_i \tilde{x}_i \\ \tilde{y}_i s_i q_i & 0 \end{pmatrix}.$$

  Since trace $M < 0$ and $\det M > 0$, the unique equilibrium of each predator-prey system is asymptotically stable.
- For all x_i and y_i, $\partial/\partial x_i(f_i(x_i, 0) - s_i y_i) < 0$.
- Eq. 7 is dissipative. The proof of this fact is analogous to Lemma 1 in the next section and therefore omitted.

These observations in conjunction with the work of Hastings (1978) imply that the unique equilibrium of this predator-prey system is globally stable. Consequently invasion of i into the predator-prey subsystem, $x_j - y$, occurs if and only if $f_i(0, \tilde{x}_j) > s_i/s_j\, f_j(\tilde{x}_j, 0)$ for all $i \in \{1, 2\}$ and $j \neq i$. Our choice of the s_i and $\tilde{x}_i$ ensure that these inequalities are met. The only omega limit sets for the subsystem $x_1 - x_2$ of Eq. 7 are equilibrium points (see 12.3 in Hirsch and Smale 1974). Our choice of q_i, s_i and m ensure that the predator can invade all these equilibria. Therefore, as Eq. 7 is dissipative and its boundary dynamics are acyclic, Theorem 3 implies that Eq. 7 with $g(y) = y$ and $F(x_1, x_2, y) = q_1 s_1 x_1 + q_2 s_2 x_2 - m$ is permanent. □

7 Proof of Theorem 2

The following definitions will be used throughout the proof of Theorem 2:

$$\Sigma = [0, x_1^*] \times [0, x_2^*]$$

$$\beta = \min_{i, x \in [0, x_i^*]} \{g_i'(x), h_i'(x)\}$$

$$\gamma = \max_{i, x \in [0, x_i^*]} \{g_i'(x), h_i'(x)\}$$

$$\mu = \min_{x_i > 0, x_2 \geqq 0} \{x_1 \colon f_1(x_1, x_2) = f_2(x_2, x_1) = 0\}$$

$$\alpha = \min_{i, j, x \in \Sigma} -\frac{\partial f_i}{\partial x_j}(\mathbf{x})$$

$$\eta = \max_{i, j, x \in \Sigma} -\frac{\partial f_i}{\partial x_j}(\mathbf{x})$$

Given any continuous function, $h \colon \mathbf{R}_+^4 \to \mathbf{R}$, and any solution $\mathbf{v}$ to Eq. 12, we define

$$\underline{h(\mathbf{v})} = \liminf_{T \to \infty} \frac{1}{T} \int_0^T h(\mathbf{v}(t))\, dt$$

and

$$\overline{h(\mathbf{v})} = \limsup_{T \to \infty} \frac{1}{T} \int_0^T h(\mathbf{v}(t))\, dt\ .$$

Our proof of Theorem 2 begins by proving Eq. 12 is dissipative.

Lemma 1. *Given f_i, g_i and h_i as stated in Theorem* 2, *there exists a constant $C > 0$ such that*

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

for any solution, $\mathbf{v}(t)$, *to Eq.* 12 *with* $\mathbf{v}(0) \in \mathbf{R}_+^4$.

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

$$\begin{aligned} \sum_i A\dot{x}_i + B\dot{y}_i &= \sum_i (x_i f_i(x_j, x_i) - y_i g_i(x_i))A + (y_i h_i(x_i) - m_i y_i)B \\ &\leqq \sum_i x_i(f_i(\mathbf{0}) - \alpha x_i)A + y_i x_i(B\gamma - A\beta) - m_i y_i B. \end{aligned}$$

Given a solution, $\mathbf{v}(t)$, for Eq. 12 define $S(t) = \sum_i Ax_i(t) + By_i(t)$. For $A > B\gamma/\beta$ and sufficiently small $\varepsilon > 0$, we get that

$$\dot{S} + \varepsilon S \leqq \sum_i x_i A(f_i(\mathbf{0}) + \varepsilon - \alpha x_i)$$

$$\leqq \frac{A(F+\varepsilon)^2}{2\alpha}\,.$$

From this it follows that

$$\limsup_{t\to\infty} S(t) \leqq \frac{A(F+\varepsilon)^2}{2\alpha\varepsilon}\,. \qquad \square$$

To prove the first assertion of Theorem 2, assume that prey 1 is dominant. Theorem 3 implies that it is sufficient to show that the predator y_1 can invade all equilibria of the form $(x_1, x_2, 0, 0)$ with $x_1 > 0$ and that prey 2 can invade all the equilibria and limit cycles that lie in the positive orthant of the predator-prey subsystem $x_1 - y_1$. C3 implies that there are only a finite number of equilibria of the form $(x_1, x_2, 0, 0)$ and, hence, μ is positive. If we choose m_1 sufficiently small so that $h_1(\mu) > m_1$ then the predator y_1 can invade all of these equilibria. In particular, the predator-prey subsystem, $x_1 - y_1$, is permanent.

Since $g_1(0) = 0$, we have that $g_1(x)$ and $h_1(x)$ are bounded below by βx for $x \in [0, x_1^*]$. Let $\mathbf{v}(t) = (x_1(t), x_2(t), y_1(t), 0)$ be a solution to Eq. 12 such that $y_1(0) > 0$. As Eq. 12 is dissipative (Lemma 1), we have that

$$0 \geqq \limsup_{T\to\infty} \frac{1}{T} \ln \frac{y_1(T)}{y_1(0)}$$

$$= \overline{h_1(x_1)} - m_1$$

$$\geqq \beta \bar{x}_1 - m_1.$$

Hence,

$$\bar{x}_1 \leqq \frac{m_1}{\beta}\,. \tag{15}$$

If $\mathbf{v}(t) = (x_1(t), 0, y_1(t), 0)$ with $y_1(0) > 0$, we have that

$$\underline{f_2(0, x_2)} \geqq f_2(0,0) - \eta \underline{x_1}$$

$$\geqq f_2(0,0) - \eta \frac{m_1}{\beta}$$

which is strictly positive for sufficiently small m_1. Hence, for sufficiently small m_1, Theorem 3 implies assertion 1 of Theorem 2 (i.e., the subsystem $x_1 - x_2 - x_3$ of Eq. 12 is permanent).

To prove the second assertion of Theorem 2, we use the following theorem.

Theorem 4 (Hutson 1984). *Consider $F \in C^1(\mathbf{R}^n_+, \mathbf{R}^n)$ such that $\partial \mathbf{R}^n_+$ is invariant for the flow of $\dot{\mathbf{v}} = F(\mathbf{v})$. Assume $P \in C^1(\operatorname{int} \mathbf{R}^n_+, \mathbf{R}_+)$ is bounded below. Define*

$$\phi(\mathbf{v}) = \begin{cases} \dfrac{\langle \nabla P(\mathbf{v}), F(\mathbf{v}) \rangle}{P(\mathbf{v})} & \text{if } \mathbf{v} \in int\,\mathbf{R}^n_+ \\ \liminf_{\mathbf{u} \to \mathbf{v}, \mathbf{u} \in int\,\mathbf{R}^n_+} \phi(\mathbf{v}) & else\ . \end{cases}$$

Then for any solution $\mathbf{v}(t)$ to $\dot{\mathbf{v}} = F(\mathbf{v})$, $\phi(\mathbf{v}(t))$ is integrable. Furthermore, $\dot{\mathbf{v}} = F(\mathbf{v})$ is permanent if

$$\sup_{T>0} \int_0^T \phi(\mathbf{v}(t))\, dt > 0$$

for all solutions $\mathbf{v}(t)$ such that $\mathbf{v}(0) \in \partial \mathbf{R}^n_+$ lies in an omega limit set of $\dot{\mathbf{v}} = F(\mathbf{v})$.

Define

$$P(x_1, x_2, y_1, y_2) = x_1 x_2 y_1^a y_2^a$$

where a is a positive constant that remains to be determined. For $\mathbf{v} = (x_1, x_2, y_1, y_2) \in \operatorname{int} \mathbf{R}^n_+$, we get

$$\phi(\mathbf{v}) = \sum_i f_i(x_i, x_j) - \frac{g_i(x_i) y_i}{x_i} + a h_i(x_i) - a m_i\,.$$

ϕ extends continuously to $\partial \mathbf{R}^4_+$ as $\lim_{x_i \to 0} g_i(x_i)/x_i = g_i'(0)$. Theorem 4 implies it is sufficient to show that

$$\sup_{T>0} \int_0^T \sum_i f_i(x_i(t), x_j(t)) - \frac{g_i(x_i(t)) y_i(t)}{x_i(t)} + a h_i(x_i(t)) - a m_i\, dt$$

is positive for any solution, $\mathbf{v}(t)$, to Eq. 12 with $\mathbf{v}(0) \in \partial \mathbf{R}^4_+$. To prove this, we begin by examining the boundary dynamics when the m_i are sufficiently small.

Lemma 2. *If m_1 is sufficiently small, then every solution, $\mathbf{v}(t) = (x_1(t), x_2(t), y_1(t), 0)$, to Eq. 12 with $x_1(0)$, $x_2(0)$ and $y_1(0)$ positive satisfies*

$$\lim_{t \to \infty} \mathbf{v}(t) = (0, \mathbf{x}_2^*, 0, 0)\ .$$

Proof. The proof of assertion 1 of Theorem 2 implies that y_1 can invade all the equilibria of the competition equations for which x_1 is positive, and prey 2, can invade the predator-prey subsystem, $x_1 - y_1$, whenever m_1 is sufficiently small.

Since the basin of attraction of $(0, x_2^*, 0, 0)$ includes a set $U \times \mathbf{R}_+$ where U is a neighborhood in $\mathbf{R}^2_+$ of the positive x_2 axis, it suffices to show that $\lim_{t \to \infty} x_1(t) = 0$.

Lemma 1 and Eq. 15 implies that along an orbit $\mathbf{v}(t)$

$$\begin{aligned} 0 &\geqq \limsup_{T\to\infty} \frac{1}{T} \ln \frac{x_2(T)}{x_2(0)} \\ &= \overline{f_2(x_2, x_1)} \\ &\geqq \alpha(x_2^* - \overline{x_2}) - \eta\overline{x_1}) \\ &\geqq \alpha(x_2^* - \overline{x_2}) - \frac{\eta m_1}{\beta} \end{aligned}$$

Hence

$$x_2^* - \overline{x_2} \leqq \frac{\eta m_1}{\alpha\beta}. \tag{16}$$

Since

$$\alpha x_2^* + f_1(0, x_2^*) - \alpha x_2 \geqq f_1(0, x_2)$$

we have that along the orbit $\mathbf{v}(t)$

$$\begin{aligned} \overline{f_1(x_1, x_2)} &\leqq \overline{f_1(0, x_2)} \\ &\leqq \alpha x_2^* + f_1(0, x_2^*) - \alpha\overline{x_2} \\ &= \alpha(x_2^* - \overline{x_2}) + f_1(0, x_2^*). \end{aligned}$$

As $f_1(0, x_2^*)$ is negative, Eq. 16 implies that $\overline{f_1(x_1, x_2)}$ is strictly negative for sufficiently small m_1. Hence

$$\limsup_{T\to\infty} \frac{1}{T} \ln\left(\frac{x_1(T)}{x_1(0)}\right) = \overline{\frac{\dot{x}_1(\mathbf{v})}{x_1(\mathbf{v})}} \leqq \overline{f_1(x_1, x_2)} < 0$$

and $\lim_{t\to\infty} x_1(t) = 0$. □

Now we need to show that ϕ has the desired properties on the boundary limit sets. We have that

- At $(0, 0, 0, 0)$, $\phi(0, 0, 0, 0) = f_1(0, 0) + f_2(0, 0) - am_1 - am_2$.
- At $\mathbf{v} = (x_1^*, 0, 0, 0)$ or $\mathbf{v} = (0, x_2^*, 0, 0)$, $\phi(\mathbf{v}) = f_j(0, x_i^*) + ah_i(x_i^*) - am_i$ where $i \neq j$.
- At equilibria of the form $\mathbf{v} = (x_1, x_2, 0, 0)$ with $x_i > 0$ for $i = 1, 2$, $\phi(\mathbf{v}) = a(h_1(x_1) + h_2(x_2) - m_1 - m_2) \geqq a\beta\mu - 2m$ where $m = \max_i m_i$.
- At orbits of the form $\mathbf{v}(t) = (x_1(t), 0, y_1(t), 0)$ or $(0, x_2(t), 0, y_2(t))$ with $x_i(0) > 0$ and $y_i(0) > 0$ for $i = 1$ or $i = 2$, respectively,

  $$\sup_{T>0} \frac{1}{T} \int_0^T \phi(\mathbf{v}(t))\,dt \geqq \overline{\phi(\mathbf{v})} \geqq \overline{f_j(0, x_i)} - am_i \geqq f_j(0, 0) - \eta\frac{m_j}{\beta} - am_i$$

  where $i \neq j$.

Hence, the conditions of Theorem 4 are met whenever the a is sufficiently large and the m_i are sufficiently small. In which case, the heteroclinic cycle is repelling and the system is permanent. □

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