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Coexistence for species sharing a predator[☆]

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Abstract

A class of equations describing the dynamics of two prey sharing a common predator are considered. Even though the boundary and internal dynamics can exhibit oscillatory behavior, it is shown these equations are permanent if only if they admit a positive equilibrium. Going beyond permanence, a subclass of equations are constructed that are almost surely permanent but not permanent; there exists an attractor in the positive orthant that attracts Lebesgue almost every (but not every) initial condition.

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1. Introduction

The processes and mechanisms underlying coexistence in ecological communities can be understood by examining specific modular based interactions. One module that has attracted interest is known as “apparent competition.” Unlike exploitative competition that involves two species competing for a limiting resource, this module involves two prey species that share a common natural enemy. Using differential and difference equation models, Holt [12–14] has shown that the introduction of the alternate prey into a predator-prey subsystem leads to a reduction in the other prey’s equilibrium density. To an observer unaware of the shared predator, the two prey species appear to be competing. Since its introduction, apparent competition has been recognized as an important indirect interaction that structures ecological communities. A recent search for “apparent competition” on

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Cambridge Scientific Abstracts yields 101 papers since 1991 making use of the term. Most of these articles provide experimental and field studies illustrating apparent competition. For instance, in field experiments on nesting birds, Hoi and Winkler [10] showed that predation rate increased with nest density when only a single prey was present and an increase in the density of one nest type increased the predation rate on another type. In grape vineyards, Karban [18] and colleagues found releases of economically unimportant Willamette mites alone, or of predatory mites alone, failed to significantly reduce populations of the damaging Pacific spider mite. However, where both herbivorous Willamette mites and predatory mites were released together populations of Pacific mites were reduced. They concluded that “apparent competition between Willamette mites and Pacific mites, mediated through their shared predator, can be an important force in the agroecosystems.”

In this article, we investigate two forms of coexistence for models of two species sharing a common natural enemy. The first form of coexistence corresponds to *robust permanence*: the existence of a global attractor in the positive cone that persists following sufficiently small structural perturbations. The second form of coexistence is what Jansen and Sigmund [17] called *almost sure permanence*: there exists a positive attractor whose basin of attraction is Lebesgue almost every point in the positive cone. The remainder of this article is structured as follows. In Section 2, we introduce the class of equations of interest, prove several facts about their equilibria, introduce some dynamical systems terminology, and verify the equations are dissipative. In Section 3, we show these equations are robustly permanent if only if they admit a positive equilibrium. In Section 4, we construct a class of equations that are not permanent, but are almost surely permanent. In Section 5, we make some concluding remarks and pose an open question.

2. Assumptions and background

Consider the dynamics of two non-interacting prey consumed by a single predator

$$\begin{aligned} \frac{dx_i}{dt} &= x_i f_i(x_i) - a_i x_i y g(x_1, x_2) =: x_i p_i(x_1, x_2, y) \quad i = 1, 2, \\ \frac{dy}{dt} &= y h(x_1, x_2), \end{aligned} \quad (1)$$

where x_i is the density of prey i , y is the predator density, $f_i(x_i)$ is the per-capita growth rate of prey i in the absence of the predator, $a_i > 0$ is the searching efficiency of the predator with respect to prey i , $g(x_1, x_2)$ is the fraction of predators actively searching (i.e. the unsatiated predators), and $h(x_1, x_2)$ is the per-capita growth rate of the predator. The functions $p_i(x_1, x_2, y)$ with $i = 1, 2$ are the per-capita growth rates of the prey.

Eq. (1) defines a differential equation on the non-negative cone of \mathbf{R}^3 ,

$$C = \{x = (x_1, x_2, y) \in \mathbf{R}^3 : x_1 \geq 0, x_2 \geq 0, y \geq 0\}.$$

The interior of this non-negative cone is the positive cone

$$\mathbf{C}_+ = \{x = (x_1, x_2, y) \in \mathbf{C} : x_1 x_2 y > 0\}$$

and the boundary of \mathbf{C} corresponding to one or more species being extinct is given by

$$\partial\mathbf{C} = \{x = (x_1, x_2, y) \in \mathbf{C} : x_1 x_2 y = 0\}.$$

2.1. Standing assumptions

A function $f : [0, \infty) \rightarrow \mathbf{R}$ is *concave* if

$$f(\alpha x + (1 - \alpha)y) \geq \alpha f(x) + (1 - \alpha)f(y) \quad (2)$$

for all $x, y \in [0, \infty)$ and $\alpha \in (0, 1)$. f is *strictly concave* if the \geq in (2) is replaced by a $>$. About (1) we make the following assumptions for the remainder of this article.

- A1.** The functions $x_i p_i(x_1, x_2, y)$ and $h(x_1, x_2)$ are continuously differentiable.
- A2.** $f_i(0) > 0$. In other words, the intrinsic rate of growth rate of each prey is positive.
- A3.** $f_i(x_i)$ are decreasing concave functions.
- A4.** There exist $K_i > 0$ such that $f_i(K_i) = 0$; K_i corresponds to the carrying capacity of prey i .
- A5.** $g(x_1, x_2)$ is a positive function non-increasing both in x_1 and x_2 . In other words, the number of satiated predators does not decrease in the presence of more prey.
- A6.** $h(x_1, x_2)$ increases in both x_1 and x_2 , and $h(x_1, 0)$ and $h(0, x_2)$ are concave.
- A7.** $h(0, 0) < 0$ and there exists $L > 0$ such that $h(L, 0) > 0$ and $h(0, L) > 0$. In other words, in the absence of any prey, the predators are doomed to extinction and when each prey is sufficiently abundant, the predator's per-capita growth rate is positive.

2.2. Examples

Two important families of equations that satisfy these assumptions are Lotka–Volterra equations and θ -Logistic–Holling predator–prey equations.

Lotka–Volterra equations. The functions $f_i(x_i) = r_i(1 - x_i/K_i)$, $g(x_1, x_2) = 1$, and $h(x_1, x_2) = b_1 x_1 + b_2 x_2 - c$ give the Lotka–Volterra equations

$$\frac{dx_i}{dt} = r_i x_i (1 - x_i/K_i) - a_i x_i y \quad i = 1, 2,$$

$$\frac{dy}{dt} = b_1 x_1 y + b_2 x_2 y - cy, \quad (3)$$

where b_i/a_i is the efficiency at which the predator converts prey i eaten to new predators and c is the predator per-capita mortality rate. The dynamics of these equations were investigated by Vandermeer [24].

θ-Logistic-Holling equations. The functions $f_i(x_i) = r_i(1 - (x_i/K_i)^{\theta_i})$ with $\theta_i \geq 1$, $g(x_1, x_2) = \frac{1}{1+b_1x_1+b_2x_2}$, and $h(x_1, x_2) = \frac{c_1x_1+c_2x_2}{1+b_1x_1+b_2x_2} - d$ give the θ -Logistic-Holling [6,11] equations

$$\frac{dx_i}{dt} = r_i x_i (1 - (x_i/K_i)^{\theta_i}) - \frac{a_i x_i y}{1 + b_1 x_1 + b_2 x_2} \quad i = 1, 2,$$

$$\frac{dy}{dt} = \frac{y(c_1 x_1 + c_2 x_2)}{1 + b_1 x_1 + b_2 x_2} - dy,$$

where c_i/a_i is the efficiency at which the predator converts prey i eaten to new predators, b_i/a_i is the time it takes the predator to handle prey i , and d is the per-capita predator mortality rate.

2.3. The equilibria

Prior to studying the dynamics of (1), we prove several properties about the equilibria. The first property is well-known and corresponds to the fact if the predator has a positive per-capita growth rate when a prey is at its carrying capacity, then the predator–prey pair can coexist at a unique equilibrium.

Lemma 1. *If $h(K_1, 0) > 0$ (respectively $h(0, K_2) > 0$), then there exists a unique positive equilibrium (x_1^*, y_1^*) (resp. (x_2^*, y_2^*)) for (1) in the x_1 - y (resp. x_2 - y) plane.*

Proof. Since $h(x_1, 0)$ is increasing, $h(0, 0) < 0$, and $h(K_1, 0) > 0$, there exists a unique $x_1^* > 0$ such that $h(x_1^*, 0) = 0$. Since any equilibrium (x_1^*, y_1^*) in the x_1 - y plane must satisfy $p_1(x_1^*, 0, y^*) = f_1(x_1^*) - a_1 y_1^* g(x_1^*, 0) = 0$, $y_1^* = f_1(x_1^*) / (a_1 g(x_1^*, 0))$ is uniquely defined. □

Next we prove two lemmas concerning equilibria that support all three species. These lemmas characterize under what conditions such an equilibrium exists. They also reiterate an observation (i.e. $x_1^{**} < x_1^*$ and $x_2^{**} < x_2^*$) made by Holt [12] which lead to his original formulation of “apparent competition.”

Lemma 2. *Assume $h(K_1, 0) > 0$ and $h(0, K_2) \leq 0$. Eq. (1) has an equilibrium $(x_1^{**}, x_2^{**}, y^{**})$ in C_+ if and only if $f_2(0)/a_2 > f_1(x_1^*)/a_1$. Moreover, when this equilibrium $(x_1^{**}, x_2^{**}, y^{**})$ exists, it is unique and satisfies $x_1^{**} < x_1^*$ and $x_2^{**} < K_2$.*

Proof. Since h is increasing with respect to both arguments, implicit differentiation implies that there is a decreasing function $\bar{x}_2(x_1)$ defined on the interval $[0, x_1^*]$ satisfying $h(x_1, \bar{x}_2(x_1)) = 0$, $\bar{x}_2(0) \geq K_2$ and $\bar{x}_2(x_1^*) = 0$. Define the function $k(x_1) = f_1(x_1)/a_1 - f_2(\bar{x}_2(x_1))/a_2$. Since any positive equilibrium $(x_1^{**}, x_2^{**}, y^{**})$ must satisfy $f_i(x_i^{**}) - a_i y^{**} g(x_1^{**}, x_2^{**}) = 0$ for $i = 1, 2$, it follows that $k(x_1^{**}) = 0$. Since $k'(x_1) = f_1'(x_1)/a_1 - f_2'(\bar{x}_2(x_1))\bar{x}_2'(x_1)/a_2 < 0$, there exists at most one value of x_1 such that

$k(x_1) = 0$. Since $k(x_1^*) = f_1(x_1^*)/a_1 - f_2(0)/a_2$ and $k(0) = f_1(0)/a_1 - f_2(\bar{x}_2(0))/a_2 \geq f_1(0)/a_1 - f_2(K_2)/a_2 = f_1(0)/a_1 > 0$, there exists a solution to $k(x_1) = 0$ with $x_1 \in (0, x_1^*)$ if and only if $f_1(x_1^*)/a_1 < f_2(0)/a_2$. When this solution x_1^{**} exists, we have $x_2^{**} = \bar{x}_2(x_1^{**}) > 0$ and $y^{**} = f_1(x_1^{**})/(a_1 g(x_1^{**}, x_2^{**}))$. \square

Lemma 3. *Assume $h(K_1, 0) > 0$ and $h(0, K_2) > 0$. Eq. (1) has an equilibrium $(x_1^{**}, x_2^{**}, y^{**})$ in \mathbf{C}_+ if and only if $f_2(0)/a_2 > f_1(x_1^*)/a_1$ and $f_1(0)/a_1 > f_2(x_2^*)/a_2$. Moreover, when this equilibrium exists, it is unique and satisfies $x_1^{**} < x_1^*$ and $x_2^{**} < x_2^*$.*

Proof. The proof of this lemma is very similar to proof of Lemma 2. Implicit differentiation implies there exists a decreasing function \bar{x}_2 defined on $[0, x_1^*]$ such that $h(x_1, \bar{x}_2(x_1)) = 0$, $\bar{x}_2(0) = x_2^*$, and $\bar{x}_2(x_1^*) = 0$. Define $k(x_1) = f_1(x_1)/a_1 - f_2(\bar{x}_2(x_1))/a_2$. $k(x_1)$ is decreasing and x_1^{**} must satisfy $k(x_1^{**}) = 0$. Without loss of generality, we may assume that $f_1(0)/a_1 \geq f_2(0)/a_2$. Since $f_2(x_2)$ is a decreasing function, it follows that $f_1(0)/a_1 > f_2(x_2^*)/a_2$. Hence $k(0) = f_1(0)/a_1 - f_2(x_2^*)/a_2 > 0$. Therefore, $k(x_1)$ equals zero on the interval $(0, x_1^*)$ if and only if $0 > k(x_1^*) = f_1(x_1^*)/a_1 - f_2(0)/a_2$. When this solution $x_1^{**} \in (0, x_1^*)$ to $k(x_1) = 0$ exists, we have $x_2^{**} = \bar{x}_2(x_1^{**}) > 0$ and $y^{**} = f_1(x_1^{**})/(a_1 g(x_1^{**}, x_2^{**}))$. \square

2.4. Dynamical background and dissipativeness

Standard theorems of differential equations imply that solutions to (1) define a (local) flow $\phi : U \rightarrow \mathbf{C}$ for some open subset $U \subset \mathbf{R} \times \mathbf{C}$. Let $\phi_t(x) = \phi(t, x)$. Given sets $I \subseteq \mathbf{R}$ and $K \subseteq \mathbf{C}$, let $\phi_I K = \{\phi_t x : t \in I, x \in K\}$. A set $K \subseteq \mathbf{C}$ is called *invariant* if $\phi_t K = K$ for all $t \in \mathbf{R}$. The *omega limit set* of a set $K \subseteq \mathbf{C}$ equals $\omega(K) = \bigcap_{t \geq 0} \overline{\phi_{[t, \infty)} K}$. The *alpha limit set* of a set $K \subseteq \mathbf{C}$ equals $\alpha(K) = \bigcap_{t \leq 0} \overline{\phi_{(-\infty, t]} K}$. Given an invariant set K , $A \subset K$ is called an *attractor* for $\phi|_K$ provided there exists an open neighborhood $U \subseteq K$ of A such that $\omega(U) = A$. The *basin of attraction* of A for $\phi|_K$ is the set of points $x \in K$ such that $\omega(x) \subseteq A$. The flow ϕ is *dissipative* if there exists a compact attractor $A \subset \mathbf{C}$ for ϕ whose basin of attraction is \mathbf{C} .

Using a standard argument, the following lemma proves that (1) is dissipative.

Lemma 4. *Eq. (1) is dissipative.*

Proof. Since $p_i(x_1, x_2, y) < 0$ whenever $x_i > K_i$, all solutions to (1) eventually enter $[0, K_1] \times [0, K_2] \times [0, \infty)$. Choose $\alpha > 0$ sufficiently large so that $-\alpha g(x_1, x_2)(a_1 x_1 + a_2 x_2) + h(x_1, x_2) < 0$ for all (x_1, x_2) in $[0, K_1] \times [0, K_2]$. Define $S(x_1, x_2, y) = \alpha(x_1 + x_2) + y$. Then for $\varepsilon > 0$ sufficiently small and $C > 0$ sufficiently large we get $\dot{S} + \varepsilon S \leq C$ for $(x_1, x_2, y) \in [0, K_1] \times [0, K_2] \times [0, \infty)$. Thus, all solutions eventually enter and remain in the compact set $S^{-1}([0, 2C/\varepsilon])$. \square

3. Permanence

A strong notion of coexistence is *permanence* that ensures populations persist despite large perturbations of the initial conditions. More formally, Eq. (1) is *permanent* if (1) is dissipative and admits a compact attractor $K \subset \mathbf{C}_+$ whose basin of attraction is \mathbf{C}_+ [15,16,23]. Permanence for dissipative systems is also known as uniform persistence [1,2,5]. As any sensible definition of coexistence should be robust to sufficiently small perturbations of the governing equations themselves, (1) is called *robustly permanent* if there exists a C^1 neighborhood of (1) in the C^1 Whitney topology (see, e.g., [7]) such that every vector field in this neighborhood is permanent. In this section, we provide sufficient and necessary conditions for robust permanence of (1).

Theorem 1. *Assume $h(K_1, 0) > 0$ and $h(0, K_2) \leq 0$. Eq. (1) is robustly permanent if and only if $f_2(0)/a_2 > f_1(x_1^*)/a_1$ (see Fig. 1(a)).*

Theorem 2. *Assume $h(K_1, 0) > 0$ and $h(0, K_2) > 0$. Eq. (1) is robustly permanent if and only if $f_2(0)/a_2 > f_1(x_1^*)/a_1$ and $f_1(0)/a_1 > f_2(x_2^*)/a_2$ (see Fig. 1(b)).*

Even though the predator–prey subsystems may exhibit periodic solutions, these theorems imply that permanence is determined solely by invasion criteria evaluated at the equilibria. Furthermore, combining Theorems 1 and 2 with Lemmas 2 and 3, we get the following simple characterization of robust permanence.

Theorem 3. *Eq. (1) is robustly permanent if and only if there exists an equilibrium in \mathbf{C}_+ .*

Proof. Suppose (1) is robustly permanent. By the Permanence Index Theorem [9], there exists an equilibrium in \mathbf{C}_+ . On the other hand, suppose there is a positive equilibrium in \mathbf{C}_+ . Lemmas 2 and 3 imply that the conditions of either Theorem 1 or Theorem 2 are satisfied. Hence, (1) is robustly permanent. \square

To prove Theorems 1 and 2, we use an earlier result on robust permanence. Recall, a compact invariant set K is called *isolated* if there exists a neighborhood V of K such that K is the maximal compact invariant set in V . A collection of sets $\{M_1, \dots, M_k\}$ is a *Morse decomposition* for a compact invariant set K if M_1, \dots, M_k are pairwise disjoint, compact isolated invariant sets for $\phi|_K$ with the property that for each $x \in K$ there are integers $l = l(x) \leq m = m(x)$ such that $\alpha(x) \subseteq M_m$ and $\omega(x) \subseteq M_l$ and if $l = m$ then $x \in M_l = M_m$. Theorem 4.3 of the author [22] implies

Theorem 4. *Let $p_3(x_1, x_2, y) := h(x_1, x_2)$ and $A \subset \partial\mathbf{C}$ be the maximal compact invariant set for the flow of (1) restricted to $\partial\mathbf{C}$. If A admits a Morse decomposition*

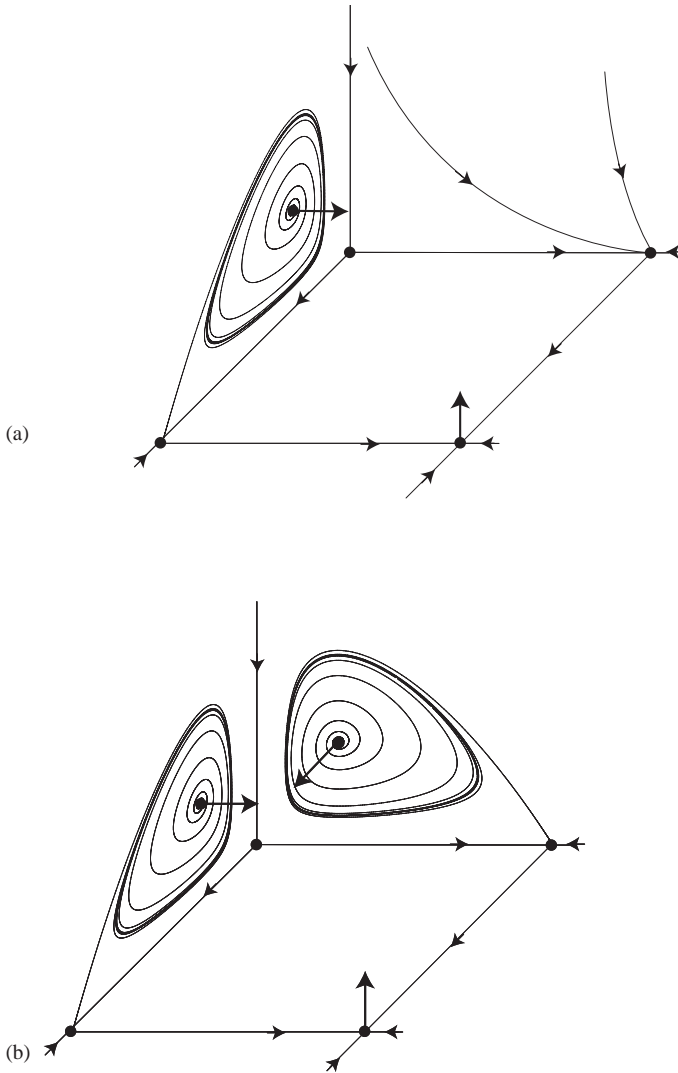


Fig. 1. Boundary dynamics of (1) for Theorems 1 and 2.

$\{M_1, \dots, M_k\}$ such that for all $1 \leq j \leq k$ there exists an $1 \leq i \leq 3$ satisfying

$$\inf_{x \in M_j} \liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T p_i(\phi_t x) dt > 0, \tag{4}$$

then (1) is robustly permanent.

Proof of Theorem 1. Assume $f_2(0)/a_2 > f_1(x_1^*)/a_2$. Lemma 4 implies there is a global attractor A for $\phi|_{\partial C}$ which is contained in $[0, K_1] \times [0, K_2] \times [0, \infty)$. Since the predator-prey subsystem x_1 - y is permanent, there exists a compact attractor A in the positive quadrant of the x_1 - y plane such that A 's basin of attraction is the positive quadrant of the x_1 - y plane. On the other hand, since all solutions of (1) in the x_2 - y plane eventually enter and remain in the strip $[0, K_2] \times [0, \infty)$, $h(0, K_2) \leq 0$ and $h(0, x_2)$ is a decreasing function of x_2 , A intersected with the x_2 - y plane is contained in the interval $[0, K_2]$ on the x_2 axis. Since (1) is uncoupled in the x_1 - x_2 plane, the equilibrium $(K_1, K_2, 0)$ is an attractor in the x_1 - x_2 plane whose basin of attraction is the positive quadrant of the x_1 - x_2 plane. These facts imply that a Morse Decomposition for A is given by $(0, 0, 0)$, $(K_1, 0, 0)$, $(0, K_2, 0)$, $(K_1, K_2, 0)$ and A (see Fig. 1(a)).

We will show that each component of this Morse decomposition satisfies (4) for an appropriate choice of $1 \leq i \leq 3$. Since $p_1(0, 0, 0) = p_1(0, K_2, 0) > 0$ and $p_3(K_1, K_2, 0) = h(K_1, K_2) > p_3(K_1, 0, 0) = h(K_1, 0) > 0$, the equilibria $(0, 0, 0)$, $(0, K_2, 0)$, $(K_1, 0, 0)$, and $(K_1, K_2, 0)$ satisfy (4) with $i = 1$ and 3. To show that A satisfies (4) for $i = 2$, we need the following lemma.

Lemma 5. Assume $h(K_1, 0) > 0$. If $x(t) = (x_1(t), 0, y(t))$ is a solution to (1) with $x_1(0) > 0$ and $y(0) > 0$, then

$$\liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T p_2(x(t)) dt \geq p_2(x_1^*, 0, y_1^*) = f_2(0) - \frac{a_2}{a_1} f_1(x_1^*).$$

Furthermore, the inequality is a strict if $h(x_1, 0)$ is strictly concave and $(x_1^*, 0, y_1^*) \notin \omega(x(0))$.

Proof. Let $x(t) = (x_1(t), 0, y(t))$ be a solution to (1) with $x_1(0) > 0$ and $y(0) > 0$. Since A only contains a single equilibrium, the Poincaré–Bendixson theorem implies that the ω -limit set of $x(0)$ is either a periodic orbit or contains the equilibrium $(x_1^*, 0, y_1^*)$. Hence, for any continuous function $p: C \rightarrow R$, the limit

$$\overline{p(x(t))} := \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T p(x(t)) dt$$

exists. Since A is compact and is contained in the positive quadrant of the x_1 - y plane,

$$0 = \lim_{T \rightarrow \infty} \frac{1}{T} \ln \left(\frac{x_1(T)}{x_1(0)} \right) = \frac{\overline{x_1'(t)}}{x_1(t)} = \overline{p_1(x(t))}$$

and

$$0 = \lim_{T \rightarrow \infty} \frac{1}{T} \ln \left(\frac{y(T)}{y(0)} \right) = \frac{\overline{y'(t)}}{y(t)} = \overline{p_3(x(t))}.$$

Jensen’s inequality and concavity of $h(x_1, 0)$ imply that $0 = \overline{p_3(x(t))} = h(x_1(t), 0) \leq h(x_1(t), 0)$. The inequality is strict if $(x_1^*, 0, y_1^*) \notin \omega(x(0))$ and $h(x_1, 0)$ is strictly concave. Since h is increasing in its first argument and $h(x_1^*, 0) = 0$, $\overline{x_1(t)} \geq x_1^*$. Concavity of f_1 and Jensen’s inequality implies that $\overline{f_1(x_1(t))} \leq f_1(\overline{x_1(t)}) \leq f_1(x_1^*)$. Since $\overline{p_1(x(t))} = \overline{f_1(x_1(t))} - a_1 \overline{y(t)g(x_1(t), 0)} = 0$ and $f_1(x_1^*) = a_1 y_1^* g(x_1^*, 0)$,

$$\begin{aligned} \overline{p_2(x(t))} &= f_2(0) - a_2 \overline{y(t)g(x_1(t), 0)} \\ &= f_2(0) - \frac{a_2}{a_1} \overline{f_1(x_1(t))} \\ &\geq f_2(0) - \frac{a_2}{a_1} f_1(x_1^*) = p_2(x_1^*, 0, y_1^*). \quad \square \end{aligned}$$

The assumption $p_2(x_1^*, 0, y_1^*) = f_2(0) - a_2 f_1(x_1^*)/a_1 > 0$ in conjunction with Lemma 5 implies that (4) holds for A with $i = 2$. Applying Theorem 4 completes the proof. \square

Proof of Theorem 2. Proof of this theorem is very similar to the previous theorem. The main difference is that the Morse decomposition of A has an additional component consisting of a compact set in the interior of the x_2 - y plane (see Fig. 1(b)). The details are left to the reader. \square

4. Non equilibrium coexistence

The previous results imply that permanence and equilibrium coexistence are equivalent. However, these results do not rule out non-equilibrium coexistence in the absence of a positive equilibrium. In this section, we show there is an open class of equations that are not permanent, have no positive equilibria, and have an attractor in C_+ whose basin of attraction is almost every point in C . The approach we take is similar conceptually to the work of McGehee and Armstrong [19] who constructed an example of non-equilibrium coexistence for competing species by perturbing several times a system of Lotka–Volterra equations. The approach taken here differs in several key ways. It begins with an unstable and non-dissipative system. This system contains a line segment of equilibria that passes through the positive orthant and that is a normally hyperbolic repeller. Dissipativeness is added one prey–predator subsystem at a time in a somewhat delicate way to ensure that (1) the perturbed line segment turns into a connecting orbit between the positive equilibria in the predator–prey subsystems, (2) all positive equilibria are destroyed, and (3) the missing prey can invade the periodic orbits for each predator–prey subsystem.

Theorem 5. *Let $f : [0, \infty) \rightarrow \mathbf{R}$ be a continuously differentiable decreasing concave function satisfying $f(0) > 0$ and $f(1) = 0$. Let $g : [0, \infty) \rightarrow [0, \infty)$ be a continuously*

differentiable decreasing function. Let $h: [0, \infty) \rightarrow \mathbf{R}$ be a continuously differentiable, strictly convex, increasing function satisfying $h(0) < 0$ and $\infty > \lim_{x_1 \rightarrow \infty} h(x_1) > 0$. Then there exist $K_i > 0$ and $a_i > 0$ for $i = 1, 2$ such that

$$\begin{aligned} \frac{dx_i}{dt} &= x_i f(x_i/K_i) - a_i x_i y g(x_1 + x_2), \\ \frac{dy}{dt} &= y h(x_1 + x_2) \end{aligned} \tag{5}$$

has no equilibria in \mathbf{C}_+ , is not permanent, and admits a compact attractor $A \subset \mathbf{C}_+$ whose basin of attraction is Lebesgue almost every point in \mathbf{C}_+ . Furthermore, these assertions are robust to sufficiently small perturbations to (5) in the C^1 Whitney topology.

To prove this theorem, we recall definitions about attractor/repellor blocks and normally hyperbolic repellors. An *attractor block* $B \subset \mathbf{C}$ is a compact set with non-empty interior such that for each $x \in \partial B$, $\phi_{(0, \infty)} x \subset \text{int}(B)$ where ∂ denotes the boundary and int denotes the interior. It is well-known that every attractor block B contains an attractor given by $\omega(B)$ and every attractor is $\omega(B)$ for some attractor block B [3,4,20]. A *repellor* and *repellor block* is an attractor and attractor block, respectively, for the backward flow ϕ_{-t} .

Let M be a compact, connected C^1 manifold with boundary. M is a *normally hyperbolic repellor* if

- M is invariant
- there exists a continuous $D\phi_t$ -invariant splitting of the tangent bundle of \mathbf{R}^3 restricted to M , $T\mathbf{R}^3|_M = TM \oplus N$
- there exist $\alpha > 1$ and $\beta > 0$ such that

$$\|D\phi_t(x)v\| \geq \beta \alpha^t \|D\phi_t(x)w\|$$

and

$$\|D\phi_t(x)v\| \geq \beta \alpha^t$$

for all $t \geq 0$, $x \in M$, $v \in N_x$ with $\|v\| = 1$, and $w \in T_x M$ with $\|w\| = 1$.

Hirsch et al. [8] have shown that normally hyperbolic repellors persist under sufficiently small C^1 perturbations.

Proof. The proof consists of five steps. The first four steps involve successive perturbations from an initial system of ODEs. The final step proves that the final perturbation gives us a system with the desired properties.

Step 1 (see Fig. 2). Consider the differential equation

$$\begin{aligned} \frac{dx_i}{dt} &= x_i f(0) - x_i y g(x_1 + x_2), \\ \frac{dy}{dt} &= y h(x_1 + x_2). \end{aligned} \tag{6}$$

Given any point $u = (u_1, u_2) \in [0, \infty) \times [0, \infty)$ with $u_1 + u_2 = 1$, define

$$N(u) = \{(\alpha u_1, \alpha u_2, y) : \alpha, y \in \mathbf{R}\}.$$

$N(u) \cap \mathbf{C}$ is invariant for (6) and the dynamics of (6) restricted to $N(u) \cap \mathbf{C}$ are given by

$$\begin{aligned} \frac{d\alpha}{dt} &= \alpha f(0) - \alpha y g(\alpha), \\ \frac{dy}{dt} &= y h(\alpha), \\ (x_1, x_2) &= \alpha(u_1, u_2). \end{aligned}$$

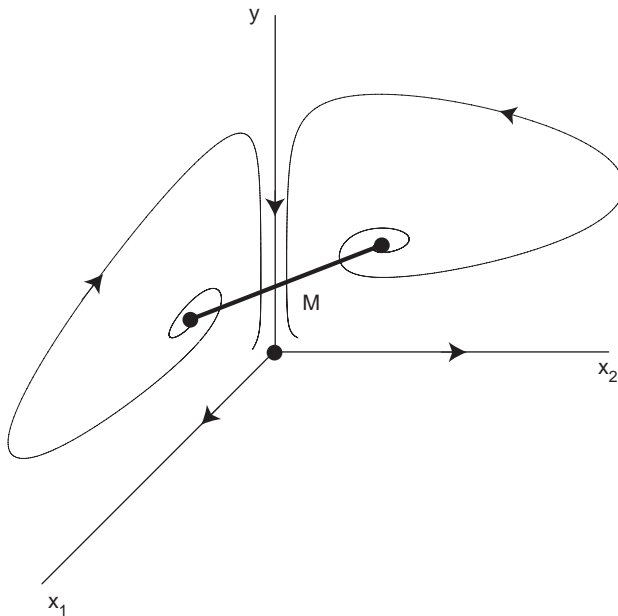


Fig. 2. The dynamics of (6).

This system is not dissipative and has a non-trivial equilibrium given by

$$\begin{aligned} \alpha^* &= h^{-1}(0), \\ y^* &= f(0)/g(\alpha^*). \end{aligned}$$

Since the linearization about this equilibrium is given by

$$\begin{bmatrix} -y^*g'(\alpha^*)\alpha^* & -\alpha^*g(\alpha^*) \\ y^*h'(\alpha^*) & 0 \end{bmatrix}$$

and $g'(\alpha^*) < 0$, the equilibrium (α^*, y^*) is a hyperbolic source.

The line $M = \{(x_1, x_2, y^*) \in \mathbf{C} : x_1 + x_2 = h^{-1}(0)\}$ consists of equilibria for (6). The tangent bundle of \mathbf{R}^3 over M splits continuously as $TM \oplus N$ with $N_x = N(\frac{x_1}{x_1+x_2}, \frac{x_2}{x_1+x_2})$. N is $D\phi_t$ invariant. Since M consists of equilibria, $\|D\phi_t(x)w\| = 1$ for all $x \in M$ and $w \in T_xM$ with $\|w\| = 1$. Alternatively, since $x \in M$ is a hyperbolic source for the flow restricted to N_x , there exist $\alpha > 1$ and $\beta > 0$ such that $\|D\phi_t(x)v\| \geq \beta\alpha^t$ for all $t > 0$ and $v \in N_x$ with $\|v\| = 1$. Hence, M is a normally hyperbolic repeller for (6).

Step 2. First perturbation (see Fig. 3). Consider

$$\begin{aligned} \frac{dx_1}{dt} &= x_1f(x_1/K_1) - x_1yg(x_1 + x_2) \\ \frac{dx_2}{dt} &= x_2f(0) - x_1yg(x_1 + x_2) \\ \frac{dy}{dt} &= yh(x_1 + x_2). \end{aligned} \tag{7}$$

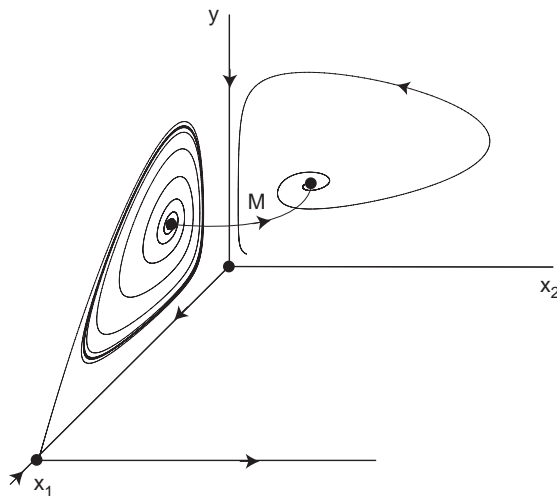


Fig. 3. The dynamics of (7).

Choose $K_1 \gg 0$ sufficiently large so that the one dimensional manifold M of (6) connecting the x_1 - y plane to the x_2 - y plane persists as a normally hyperbolic repellor.

For this system, there is a unique positive equilibrium in the x_1 - y plane given by

$$x_1^* = h^{-1}(0)$$

$$y_1^* = f(x_1^*/K_1)/g(x_1^*).$$

At this equilibrium the per-capita growth rate of prey species 1 is zero:

$$0 = f(x_1^*/K_1) - y_1^*g(x_1^*).$$

In the x_2 - y plane the positive equilibrium remains unchanged. Several key properties about (7) are

- P1.** There is a one-dimensional normally hyperbolic repellor M connecting the positive equilibrium in the x_1 - y plane to the positive equilibrium in the x_2 - y plane.
- P2.** At the positive equilibrium in the x_1 - y plane the per-capita growth rate of prey 2 is positive. This follows from the fact that

$$f(0) - y_1^*g(x_1^*) > f(x_1^*/K_1) - y_1^*g(x_1^*) = 0.$$

- P3.** At the positive equilibrium in the x_2 - y plane, the per-capita growth rates of prey 1 and 2 are both zero.

Step 3. Second perturbation (see Fig. 4). The goal of the second perturbation is to make the entire system dissipative, to preserve properties **P1–P3**, and destroy any positive equilibria. Consider

$$\frac{dx_i}{dt} = x_i f(x_i/K_i) - a_i x_i y g(x_1 + x_2) =: x_i p_i(x_1, x_2, y)$$

$$\frac{dy}{dt} = y h(x_1 + x_2) \tag{8}$$

with $a_2 = 1$, and K_2 and a_1 yet to be defined. For this equation, the unique positive equilibrium in the x_i - y plane is given by

$$x_i^* = h^{-1}(0)$$

$$y_i^* = \frac{f(x_i^*/K_i)}{a_i g(x_i^*)}$$

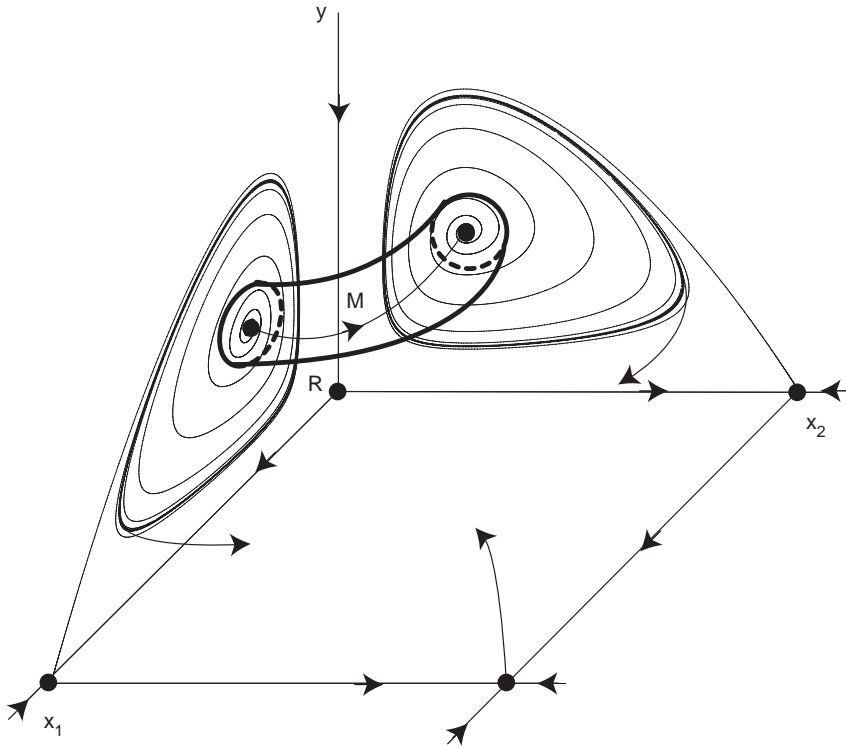


Fig. 4. The dynamics of (8).

for $i = 1, 2$. Given any K_2 (yet to be chosen), define

$$a_1 = \frac{f(0)}{y_2^*g(x_2^*)} = \frac{f(0)}{f(x_2^*/K_2)}.$$

Now choose K_2 sufficiently large (notice this implies that a_1 is close to but not equal to 1) so that **P1–P2** remain true. Since the per-capita growth rate of prey 1 at the (x_2^*, y_2^*) equilibrium is given by $f(0) - a_1 y_2^* g(x_2^*)$, our choice of a_1 implies that **P3** still holds.

Lemma 3 implies that there is no equilibrium for (7) in C_+ . It follows that

P4. For any point on $M \cap C_+$, its ω -limit set is the positive equilibrium in the x_2 - y plane and its α -limit set is the positive equilibrium in the x_1 - y plane.

Since (7) is dissipative and the equilibria (x_i^*, y_i^*) are repellers in the x_i - y planes,

P5. For $i = 1, 2$, there exists a compact attractor A_i in the positive quadrant of the x_i - y plane whose basin of attraction is all points in the positive quadrant of the x_i - y plane except for (x_i^*, y_i^*) .

Our assumption that h is strictly concave, **P3**, and Lemma 5 imply

$$\inf_{x \in A_i} \liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T p_j(\phi_t x) dt > 0 \quad i, j = 1, 2 \quad i \neq j,$$

where ϕ_t denotes the flow of (8). Theorem 1 from the author [21] implies that

P6. There exists a $T > 0$ such that

$$\min_{x \in A_i} \frac{1}{T} \int_0^T p_j(\phi_t x) dt > 0 \quad i, j = 1, 2 \quad i \neq j.$$

Step 4. Final perturbation (see Fig. 4). As a final perturbation, slightly increase the value of a_1 so that **P1**, **P2**, **P4–P6** continue to be satisfied, but instead of **P3** we get

P3*. At the positive equilibrium in the x_2 - y plane, the per-capita growth rate of prey 1 is negative.

Step 5. The attractor.

Let $R \subset \mathbf{C}$ be a neighborhood of the normally hyperbolic repeller that is a repelling block. Since the final system of differential equations is dissipative, there exists a global attractor with an attractor block B_1 . Define the attractor block $B_2 = B_1 \setminus R$ which is homeomorphic to a thickened cylinder. Since all orbits in B_2 intersecting the x_i - y ($i = 1, 2$) planes approach the attractor A_i for which **P6** holds, we can shrink the attractor block B_2 away from these planes to get an attractor block B_3 contained in \mathbf{C}_+ . Furthermore, we can shrink this attractor block in such a way that $\omega(x) \subset B_3$ for all $x \in \mathbf{C}_+ \setminus M$. The attractor $\omega(B_3)$ provides the desired attractor. \square

Numerical example

Fig. 5 illustrates a numerical solution to Logistic-Holling equations for which there is no equilibrium in \mathbf{C}_+ but coexistence about a periodic orbit occurs. In this simulation, we start at a point in \mathbf{C}_+ near $(x_1^*, 0, y^*)$. The simulation illustrates that the solution initially tracks the connecting orbit between $(x_1^*, 0, y_1^*)$ and $(x_2^*, 0, y_2^*)$, then begins to exhibit diverging oscillations between prey 2 and the predator, and then appears to converge toward a periodic orbit that permits coexistence. Notice that in this periodic orbit increasing densities of the predator results in the simultaneous crash of both prey species, a crash in the predator, the recovery of prey 2, the recovery of prey 1, and the recovery of the predator leading once again to the crash of both prey.

5. Conclusions

In this article, we attempt to understand under what conditions two prey sharing a common predator can coexist. We showed that coexistence in the sense of

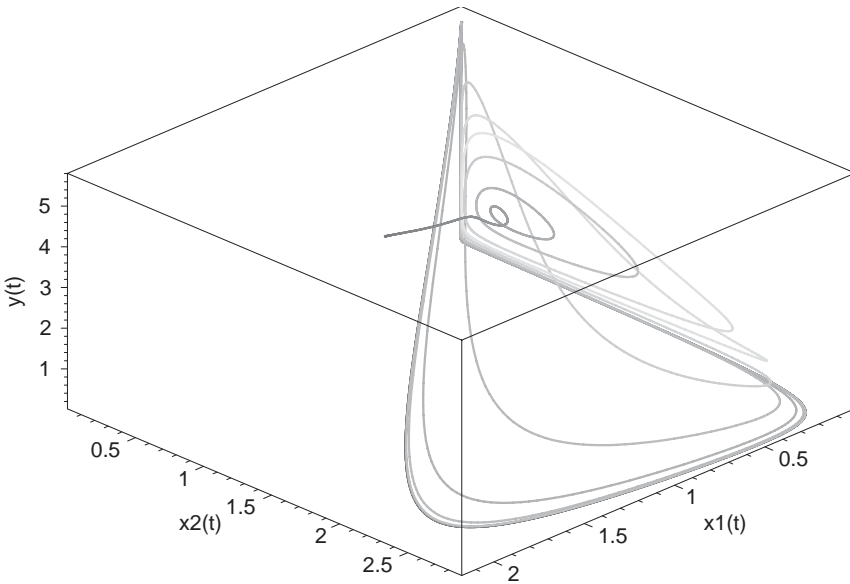


Fig. 5. Nonequilibrium coexistence. Numerical solution to $\frac{dx_i}{dt} = x_i r_i (1 - x_i/3) - \frac{x_i y}{1+x_1+x_2}$, $\frac{dy}{dt} = \frac{y(x_1+x_2)}{1+x_1+x_2} - 0.3y$ with $r_1 = 0.8$, $r_2 = 1.0$, and initial conditions $x_1(0) = x_1^* = 3/7$, $x_2(0) = 1/100$, and $y(0) = y_1^* = 48/49$.

permanence is equivalent to equilibrium coexistence. We showed that even when these systems are not permanent, they can be *almost surely permanence*; there exists a positive attractor whose basin of attraction contains Lebesgue almost every initial condition [17]. The construction of these examples were somewhat delicate and involved controlling the dynamics throughout the non-negative orthant. It would be very interesting to know under what conditions almost sure permanence can be deduced from the boundary behavior of the system. More specifically,

Suppose that $h(K_1, 0) > 0$, $h(0, K_2) < 0$, the positive equilibria (x_1^*, y_1^*) of (1) is unstable in the x_1-y plane, (1) admits no positive equilibrium, and

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T p_2(\phi_t x) dt > 0$$

for all $x = (x_1, 0, y) \neq (x_1^*, 0, y_1^*)$ with $x_1 y > 0$. Can one deduce that (1) is almost surely permanent?

A similar question can be posed when $h(K_1, 0) > 0$ and $h(K_2, 0) > 0$.

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