PERMANENCE OF WEAKLY COUPLED VECTOR FIELDS

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Abstract. Let $F_1, \ldots, F_k$ be $k$ dissipative vector fields on finite dimensional Euclidean spaces that preserve the skeleton of the positive orthant. Permanence of all sufficiently weak couplings of these vector fields corresponds to robust permanence of the uncoupled vector field $F_1 \times \cdots \times F_k$. A sufficient condition for robust permanence of $F_1 \times \cdots \times F_k$ involving unsaturated Morse decompositions is provided. In the case of coupled food chain vector fields and coupled two-dimensional vector fields, this sufficient condition is shown to be necessary. As an illustration, these results are applied to weakly coupled logistic-Holling predator-prey systems.

Key words. permanence, weak coupling, population dynamics

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1. Introduction. Ecological communities are bound together by a web of complex relationships. Data on interaction strengths between species in natural food webs indicate that these interaction strengths are characterized by many weak interactions and a few strong interactions [2, 19, 21, 30]. Consequently, food webs are often viewed as modular [22] in which modules of strongly interacting species are weakly interconnected. Because of this modularity, theoretical ecologists often develop ordinary differential equation models that include strong interactions and ignore weak interactions [11, 24, 25]. One justification for this approach is the belief that weak interactions play a small role on the models dynamics and therefore can be ignored. More recently, however, theoretical ecologists have considered the effects of weak interactions and have found that weak interactions can play important stabilizing and “noise” dampening roles [2, 19, 21] and can magnify spatiotemporal variation in community structure [2]. Furthermore, weak couplings of predator-prey systems with periodic orbits exhibit phase locking and entrainment [28]. To better understand their global dynamics, we investigate permanence of weakly coupled systems.

Population dynamics are frequently modeled by vector fields on the positive orthant of Euclidean space that leave the boundary of this orthant invariant. Stated loosely, such a vector field is permanent provided that the boundary of the positive orthant is repelling [3, 4, 9, 13, 14, 27]. Ecologically this is interpreted as the long-term coexistence of the interacting populations. Reviews of the mathematical progress on studying permanence and its applications can be found in [10, 15, 29]. If we have $k$-vector fields $F_1, \ldots, F_k$ representing $k$ uncoupled systems of interacting populations, then weak couplings of these vector fields correspond to vector fields that are close to the product vector field $F_1 \times \cdots \times F_k$. The goal of this article is to find conditions that ensure all vector fields sufficiently close to the uncoupled vector field $F_1 \times \cdots \times F_k$ are permanent. In other words, determine under what conditions $F_1 \times \cdots \times F_k$ is robustly permanent. After defining these concepts more precisely in section 2, we conjecture that $F_1 \times \cdots \times F_k$ is robustly permanent if and only if for each $1 \leq i \leq k$ the vector field $F_i$ is robustly permanent. If this conjecture is indeed true, then it reduces a
potentially high-dimensional problem (i.e., determining whether $F^1 \times \cdots \times F^k$ has a robustly repelling boundary) to $k$ lower-dimensional problems (i.e., determining for each $1 \leq i \leq k$ whether $F^i$ has a robustly repelling boundary). To prove such a conjecture requires an appropriate characterization of robust permanence and extending it to product vector fields. Results in this direction include the recent work of the author [26] in which it is shown that a vector field is robustly permanent provided that it admits an unsaturated Morse decomposition of its boundary dynamics, and a generalization of this criterion by Hirsch, Smith, and Zhao [8] to semiflows. Recall that a Morse decomposition of an invariant set $K$ is a collection of isolated invariant subsets of $K$ such that collapsing these sets to distinct points results in a gradient-like quotient flow on $K$. On the other hand, an unsaturated equilibrium in a population model is in effect one which can be invaded by some population entering the system at low density. Thus an unsaturated Morse decomposition is one in which the invariant subsets in the decomposition, which may be more complicated than just equilibria, have the analogous property of invasibility by at least one population not already present. In section 3, we discuss these results and prove that if $F^1, \ldots, F^k$ are vector fields that admit an unsaturated Morse decomposition, then $F^1 \times \cdots \times F^k$ admits an unsaturated Morse decomposition and, consequently, is robustly permanent. In section 4, we use the main result of section 3 to prove our conjecture for couplings of two-dimensional vector fields and for couplings of food chain vector fields. In section 5, we prove a technical proposition to make our results more applicable and illustrate our approach with coupled predator-prey systems of the logistic-Holling type.

2. Preliminaries and a conjecture.

**Definition 2.1.** Let $P^r(n)$ be the space of $C^r$ vector fields $F = (F_1, \ldots, F_n) : R^+_n \to R^n$ that satisfy $F_i(x) = 0$ whenever $x_i = 0$.

The extra condition on $F$ corresponds to the fact that in the absence of population $i$, the growth rate of population $i$ is zero. We view $P^r(n)$ as the space of all possible models of $n$-interacting populations and endow $P^r(n)$ with the $C^r$ Whitney topology [7, Chapter 2].

**Definition 2.2.** Let $F = (F_1, \ldots, F_n) \in P^r(n)$ with $r \geq 1$. The per capita growth functions $f = (f_1, \ldots, f_n) : R^+_n \to R^n$ associated with $F$ are the continuous functions defined by

$$f_i(x) = \begin{cases} \frac{F_i(x)}{x_i} & \text{if } x_i \neq 0, \\ \frac{\partial F_i}{\partial x_i}(x) & \text{if } x_i = 0 \end{cases}$$

for any $x = (x_1, \ldots, x_n) \in R^+_n$.

We recall several definitions from dynamical systems theory. Assume $F : R^+_n \to R^n$ is $C^1$ and that $\dot{x} = F(x)$ generates a global flow $\phi : R \times R^+_n \to R^+_n$. Let $\phi_t x = \phi(t, x)$. Given sets $I \subseteq R$ and $K \subseteq R^+_n$, let $\phi_I K = \{\phi_t x : t \in I, x \in K\}$. A set $K \subseteq R^+_n$ is called invariant if $\phi_t K = K$ for all $t \in R$. The omega limit set of a set $K \subseteq R^+_n$ equals $\omega(F, K) = \cap_{t \geq 0} \phi_t K$. The alpha limit set of a set $K \subseteq R^+_n$ equals $\alpha(F, K) = \cap_{t \leq 0} \phi_t K$. $A \subseteq R^+_n$ is called an attractor for $\phi$ provided there exists an open neighborhood $U \subseteq R^+_n$ of $A$ such that $\omega(F, U) = A$. The basin of attraction of $A$ is the set of points $x \in R^+_n$ such that $\omega(F, x) \subseteq A$. The flow $\phi$ is dissipative if there exists a compact attractor $A \subseteq R^+_n$ for $\phi$ whose basin of attraction is $\text{int} R^+_n$.

**Definition 2.3.** $F \in P^r(n)$ is permanent provided that $\dot{x} = F(x)$ generates a dissipative flow $\phi$ and there exists a compact attractor $A \subseteq \text{int} R^+_n$ for $\phi$ whose basin of attraction is $\text{int} R^+_n$. 

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Permanence was originally introduced in [27] and for dissipative vector fields is equivalent to uniform persistence [4]. To talk about permanence of weakly coupled vector fields, the following definition is useful.

**Definition 2.4.** $F \in \mathcal{P}^r(n)$ is $C^r$ robustly permanent if there exists a neighborhood $\mathcal{N} \subseteq \mathcal{P}^r(n)$ of $F$ such that every vector field $G \in \mathcal{N}$ is permanent.

Now suppose that $F^1 \in \mathcal{P}^r(n_1), \ldots, F^k \in \mathcal{P}^r(n_k)$ are vector fields. Define the product vector field $F^1 \times \cdots \times F^k \in \mathcal{P}^r(n_1 + \cdots + n_k)$ by

$$F^1 \times \cdots \times F^k(x^1, \ldots, x^k) = (F^1(x^1), \ldots, F^k(x^k)),$$

where $x^1 \in \mathbb{R}_{+}^{n_1}, \ldots, x^k \in \mathbb{R}_{+}^{n_k}$. If $F^1 \times \cdots \times F^k$ is $C^r$ robustly permanent, then all sufficiently weak $C^r$ couplings of $F^1, \ldots, F^k$ are permanent.

We make the following conjecture.

**Conjecture 1.** Let $F^1 \in \mathcal{P}^r(n_1), \ldots, F^k \in \mathcal{P}^r(n_k)$ with $r \geq 1$ be vector fields that generate dissipative flows. If $F^i$ is $C^r$ robustly permanent for each $1 \leq i \leq k$, then $F^1 \times \cdots \times F^k$ is $C^r$ robustly permanent.

The converse of this conjecture—namely, robust permanence of $F^1 \times \cdots \times F^k$ implies robust permanence of $F^i$ for each $1 \leq i \leq k$—follows immediately from the definitions. The utility of this conjecture, provided that it is true, is that it reduces checking robust permanence of a $n_1 + \cdots + n_k$-dimensional vector field to checking robust permanence of $n_i$-dimensional vector fields for $1 \leq i \leq k$.

### 3. Unsaturated Morse decompositions

In previous work [26], the author developed a sufficient condition for robust permanence. This condition involves the notion of unsaturated Morse decompositions that we discuss now. Let $F \in \mathcal{P}^r(n)$ with $r \geq 1$ generate the dissipative flow $\phi$ and let $f = (f_1, \ldots, f_n)$ denote the per capita growth rate functions associated with $F$. Given a compact invariant set $K$, let $\mathcal{M}_{\text{inv}}(F, K)$ denote the set of $\phi$-invariant Borel probability measures with support in $K$. A compact invariant set $K$ for $\phi$ is unsaturated if

$$\min_{\mu \in \mathcal{M}_{\text{inv}}(F, K)} \max_{1 \leq i \leq n} \int_K f_i \, d\mu > 0.$$

Recall that a compact invariant set $K$ is isolated if there exists a neighborhood $V$ of $K$ such that $K$ is the maximal compact invariant set in $V$. A collection of sets $\{M_1, \ldots, M_k\}$ is a Morse decomposition for a compact invariant set $K$ if $M_1, \ldots, M_k$ 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 $\alpha(F, x) \subseteq M_l$ and $\omega(F, x) \subseteq M_m$ if $l = m$, then $x \in M_l = M_m$. Let $K$ be a compact invariant set. We say that $\{M_1, \ldots, M_k\}$ is an unsaturated Morse decomposition for $K$ if $\{M_1, \ldots, M_k\}$ is a Morse decomposition for $K$ and each $M_j$ is unsaturated. The following sufficient condition for $C^r$ robust permanence was proven by the author.

**Theorem 3.1** (Schreiber [26]). Let $F \in \mathcal{P}^r(n)$ with $r \geq 1$ be such that $\dot{x} = F(x)$ generates a dissipative flow $\phi$. Let $\Lambda \subset \partial \mathbb{R}^n_+$ be the maximal compact invariant set for $\phi|\mathbb{R}^n_+$. If $\Lambda$ admits an unsaturated Morse decomposition, then $F$ is $C^r$ robustly permanent.

As a step toward our conjecture, we prove a direct product of flows that admit unsaturated Morse decompositions admits an unsaturated Morse decomposition.

**Theorem 3.2.** If $F^1 \in \mathcal{P}^r(n_1), \ldots, F^k \in \mathcal{P}^r(n_k)$ with $r \geq 1$ are vector fields such that for each $1 \leq i \leq k$

1. $F^i$ generates a dissipative flow,
2. $F^k$ admits an unsaturated Morse decomposition of the maximal compact invariant set of $\partial \mathbb{R}_+^m$, then $F^1 \times \cdots \times F^k$ is $C^r$ robustly permanent.

The proof of this theorem follows from induction, the following proposition, and the fact that dissipative vector fields are open in the $C^1$ Whitney topology.

**Proposition 3.3.** Let $F \in \mathcal{P}'(n)$ and $G \in \mathcal{P}'(m)$ with $r \geq 1$ generate dissipative flows $\phi_t$ and $\psi_t$, respectively. Let $\Lambda_1 \subset \mathbb{R}_+^n$ and $\Lambda_2 \subset \mathbb{R}_+^m$ be the maximal compact invariant sets for $\phi$ and $\psi$, respectively. If $\Lambda_1 \cap \partial \mathbb{R}_+^n$ admits an unsaturated Morse decomposition for $\phi$ and $\Lambda_2 \cap \partial \mathbb{R}_+^m$ admits an unsaturated Morse decomposition for $\psi$, then $\Lambda_1 \times \Lambda_2 \cap \partial \mathbb{R}_+^{n+m}$ admits an unsaturated Morse decomposition for $\phi \times \psi$.

**Proof.** Let $\{N_1, \ldots, N_k\}$ and $\{M_1, \ldots, M_l\}$ be unsaturated Morse decompositions for $\phi|\Lambda_1 \cap \partial \mathbb{R}_+^n$ and $\psi|\Lambda_2 \cap \partial \mathbb{R}_+^m$, respectively. Theorem 3.1 implies that $\phi$ and $\psi$ are permanent. Hence there exist compact attractors $N_0 \subset \text{int} \mathbb{R}_+^n$ and $M_0 \subset \text{int} \mathbb{R}_+^m$ for $\phi$ and $\psi$, respectively, whose basins of attraction are $\text{int} \mathbb{R}_+^n$ and $\text{int} \mathbb{R}_+^m$, respectively. Hence $\{N_0, \ldots, N_k\}$ and $\{M_0, \ldots, M_l\}$ define Morse decompositions for $\phi|\Lambda_1$ and $\psi|\Lambda_2$, respectively.

Define the collection of sets $\{V_i\}_{i=0}^{(k+1)+l}$ by

$$V_{j+1} = N_i \times M_j, \quad i = 0, \ldots, k, \quad j = 0, \ldots, l.$$ 

We claim that this collection of sets is a Morse decomposition for $\phi \times \psi$ restricted to $\Lambda_1 \times \Lambda_2$. Given any $1 \leq i \leq k$ and $1 \leq j \leq l$, $N_i$ and $M_j$ have isolating neighborhoods for $\phi|\Lambda_1$ and $\psi|\Lambda_2$. The product of these isolating neighborhoods is an isolating neighborhood of $N_i \times M_j$ for $\phi \times \psi|\Lambda_1 \times \Lambda_2$. Hence, $\{V_i\}_{i=0}^{(k+1)+l}$ is a collection of isolated invariant sets for $\phi \times \psi|\Lambda_1 \times \Lambda_2$. Given $z = (x,y) \in \Lambda_1 \times \Lambda_2$, there exist $0 \leq i \leq k$ and $0 \leq j \leq l$ such that $\alpha(F,x) \subset N_i$ and $\alpha(G,y) \subset M_j$. Hence, $\alpha(F \times G, z) \subset V_{j+1}$. Since $\{N_1, \ldots, N_k\}$ and $\{M_1, \ldots, M_l\}$ are Morse decompositions for $F$ and $G$, respectively, there exist $i' \leq i$ and $j' \leq j$ such that $\omega(F,x) \subset M_{j'}$ and $\omega(G,y) \subset N_{i'}$. Furthermore, $i' = i$ only if $x \in N_i$ and $j' = j$ only if $y \in M_j$. Consequently, $\omega(F \times G, z) \subset N_{i'} \times M_{j'} = V_{j+1}$ with $i' \leq j' \leq j(k+1) + i$ only if $z \in V_{j+1}$. Hence, $\{V_i\}_{i=0}^{(k+1)+l}$ is a Morse decomposition for $\phi \times \psi|\Lambda_1 \times \Lambda_2$.

Since $V_0 \subset \text{int} \mathbb{R}_+^{n+m}$ is an attractor for $\phi \times \psi$ with basin of attraction $\text{int} \mathbb{R}_+^{n+m}$, $\{V_i\}_{i=0}^{(k+1)+l}$ defines a Morse decomposition for $\phi \times \psi$ restricted to $\Lambda = (\Lambda_1 \times \Lambda_2) \cap \partial \mathbb{R}_+^{n+m}$. We claim that this Morse decomposition is unsaturated. Let $(f_1, \ldots, f_n)$ and $(g_1, \ldots, g_l)$ be the per capita growth rate functions of $F$ and $G$, respectively. The per capita growth rate functions for $H = F \times G$ are given by

$$(h_1(x,y), \ldots, h_n(x,y), h_{n+1}(x,y), \ldots, h_{n+m}(x,y)) = (f_1(x), \ldots, f_n(x), g_1(y), \ldots, g_m(y)).$$

Let $V_{j+1} = N_i \times M_j$ with $0 \leq i \leq k$ and $0 \leq j \leq l$ be a component of this Morse decomposition. Due to the fact that $j(k+1) + i \geq 1$, we have that either $i \neq 0$ or $j \neq 0$. Assume that $i \neq 0$ as the case $j \neq 0$ can be treated similarly. Since $\mathcal{M}_{\text{inv}}(H, N_i \times M_j)$ is compact in the weak* topology, to show that $V_{j+1}$ is unsaturated reduces to verifying that

$$\max_{1 \leq i \leq n+m} \int_{N_i \times M_j} h_i \, d\mu > 0$$

for every $\mu \in \mathcal{M}_{\text{inv}}(H, N_i \times M_j)$. Let $\mu \in \mathcal{M}_{\text{inv}}(H, N_i \times M_j)$. Define $\pi : \mathbb{R}_+^n \times \mathbb{R}_+^m \to \mathbb{R}_+^n$ by $\pi(x,y) = x$. Let $\pi_* \mu$ be the Borel probability measure on $N_i$ defined by
\[ \pi_*\mu(A) = \mu(\pi^{-1}(A)) \] for all Borel sets \( A \subset N_i \). \( \pi_*\mu \) is invariant for \( \phi \) as for any continuous function \( c : N_i \to \mathbb{R} \) and \( t \in \mathbb{R} \),

\[
\int_{N_i} c \circ \phi_t \, d\pi_*\mu = \int_{N_i \times M_j} c \circ \phi_t \circ \pi \, d\mu = \int_{N_i \times M_j} c \circ \pi \circ \phi_t \times \psi_t \, d\mu
\]

\[
= \int_{N_i \times M_j} c \circ \pi \, d\mu = \int_{N_i} c \, d\pi_*\mu
\]

where the third equality is given by the invariance of \( \mu \). Since \( M_i \) is unsaturated for \( \phi \),

\[ (3.1) \quad \max_{1 \leq i \leq n} \int_{N_i} f_i \, d\pi_*\mu > 0. \]

Since \( \int_{N_i \times M_j} h_i \, d\mu = \int_{N_i} f_i \, d\pi_*\mu \) for \( 1 \leq l \leq n \), \( (3.1) \) implies that

\[ \max_{1 \leq i \leq n+m} \int_{N_i \times M_j} h_i \, d\mu > 0. \]

Hence \( N_i \times M_j \) is unsaturated for \( \phi \times \psi \).

\[
\square
\]

4. Two corollaries. In the next two subsections, we derive two corollaries of Theorem 3.2.

4.1. Weakly coupled two-dimensional systems. The basic building blocks of ecological theory are two-species interactions that include competition, mutualism, and predator-prey interactions [1]. The following corollary of Theorem 3.2 implies that our conjecture is true for couplings of two-dimensional vector fields.

**Corollary 4.1.** Let \( F^1 \in \mathcal{P}^r(2) \), \( \ldots, F^k \in \mathcal{P}^r(2) \) with \( r \geq 1 \) be vector fields that generate dissipative flows. If \( (f^1_1, f^2_1) \) denote the per capita growth rates of \( F^i \) for \( 1 \leq i \leq k \), then \( F^1 \times \cdots \times F^k \) is robustly permanent if and only if for each \( 1 \leq i \leq k \)

1. \( f^1_1(0) > 0 \) or \( f^2_1(0) > 0 \).
2. \( f^1_2(x) > 0 \) for all \( x = (x_1,0) \in \mathbb{R}_+^2 \setminus \{0\} \) such that \( f^1_1(x) = 0 \), and
3. \( f^2_1(x) > 0 \) for all \( x = (0,x_2) \in \mathbb{R}_+^2 \setminus \{0\} \) such that \( f^2_2(x) = 0 \).

**Remark.** Since two-dimensional vector fields can exhibit periodic orbits as well as equilibria, the boundary dynamics of the direct product of several two-dimensional vector fields may exhibit periodic and quasi-periodic orbits. Despite these complications, the corollary implies that robust permanence of uncoupled two-dimensional vector fields is determined by easily verified conditions at equilibria.

**Proof.** First, suppose that each \( F^i \) for \( 1 \leq i \leq k \) satisfies the three conditions of the corollary. For each \( 1 \leq i \leq k \), we will show that \( F^i \) admits an unsaturated Morse decomposition. Let \( \Lambda^i \) be the global attractor for \( F^i \). Condition 1 implies that either \( f^1_i(0) > 0 \) or \( f^2_i(0) > 0 \). Without loss of generality, assume that \( f^1_i(0) > 0 \). Define \( M_1 = \Lambda^i \cap \{(x_1,0) : x_1 > 0\} \) and \( M_2 = \Lambda^i \cap \{(0,x_2) : x_2 \geq 0\} \). Since \( f^1_i(0) > 0 \) and \( M_1 \) and \( M_2 \) are disjoint isolated invariant sets for \( \partial \mathbb{R}_+^2 \). Invariance of \( \{(0,x_2) : x_2 \geq 0\} \) implies that every point \( x = (0,x_2) \in \Lambda^i \) satisfies \( \alpha(F^i,x) \cup \omega(F^i,x) \subset M_2 \). Invariance of \( \{(x_1,0) : x_1 \geq 0\} \) and the fact that \( f^1_i(0) > 0 \) implies that every point \( x = (x_1,0) \in \mathbb{R}_+^2 \) with \( x_1 > 0 \) satisfies \( \omega(F^i,x) \subset M_1 \). Hence, \( \{M_1, M_2\} \) is a Morse decomposition for \( F^i \) restricted to \( \Lambda^i \cap \partial \mathbb{R}_+^2 \). Since all invariant measures for \( F^i \) restricted to \( \partial \mathbb{R}_+^2 \) are convex combinations of Dirac measures based at equilibria, conditions 1–3 imply that \( \{M_1, M_2\} \) is an unsaturated Morse decomposition for \( F^i \) restricted to \( \Lambda^i \cap \partial \mathbb{R}_+^2 \). Theorem 3.2 implies that \( F^1 \times \cdots \times F^k \) is \( C^r \) robustly permanent.
On the other hand, suppose that one of the conditions is not met for one of the vector fields $F^i$. We will show that for every $C^r$ neighborhood $N \subset \mathcal{P}^r(2)$ of $F^i$ contains a vector field that is not permanent. It follows that $F^1 \times \cdots \times F^k$ is not $C^r$ robustly permanent. If condition 1 is not met for $F^i$, then there is a $G \in N$ such that the origin is linearly stable for $G$. If condition 2 is not met for $F^i$, then there is an equilibrium $x^* = (x^*_1, 0)$ such that $f^*_2(x^*) \leq 0$. An appropriate perturbation of $F^i$ yields a $G \in \mathcal{P}^r(2)$ such that $x^*$ is an equilibrium for $G$ and $g_2(x^*) < 0$, where $(g_1, g_2)$ are the per capita growth rate functions for $G$. The stable manifold theorem implies there is a point $y \in \text{int} \mathbb{R}^2_+$ such that $\omega(y) = x^*$. Hence $G$ is not permanent. Similarly, if condition 3 is not met for $F^i$, then we can find $G \in N$ such that $G$ is not permanent.

4.2. Weakly coupled food chains. Using Theorem 3.2, we can prove our conjecture for food chain vector fields that represent a collection of populations where the $i$th population consumes the $(i-1)$st population and is consumed by the $(i+1)$st population [1]. Food chain models represent a fundamental ecological unit whose dynamics have been studied extensively [5, 6, 16, 17, 18, 20, 23].

**Definition 4.2.** Let $F \in \mathcal{P}^r(n)$ with $r \geq 1$ and $f = (f_1, \ldots, f_n)$ denote the per capita growth rate functions. $F$ is a food chain vector field provided that $F$ generates a dissipative flow and for all $2 \leq i \leq n$, $f_i(x) < 0$ whenever $x_{i-1} = 0$.

The definition of a food chain vector field asserts that in the absence of the $(i-1)$st population for $i \geq 2$, the $i$th population has a negative per capita growth rate and is doomed to extinction. Population 1 plays a special role under this assumption as $f_1(0)$ is permitted to be positive. Population 1 in food chain models typically represents an auto-trophic population (e.g., a population of plants) whose resources are not explicitly modeled.

Given a vector field $F$, recall a point $x \in \mathbb{R}^n_+$ is recurrent if $x \in \omega(F, x)$. The Birkhoff center for a compact invariant set $K$, denoted $BC(F, K)$, is the closure of the recurrent points of $K$. The following characterization of $C^r$ robust permanence for food chain models was proven by the author.

**Theorem 4.3** (Schreiber [26]). Let $F \in \mathcal{P}^r(n)$ with $r \geq 1$ be a food chain vector field with $r \geq 1$ that generates a dissipative flow $\phi$. Let $\Lambda$ be the maximal compact invariant set for $\phi|\partial \mathbb{R}^n_+$. Then the following are equivalent:

1. $F$ is $C^r$ robustly permanent.
2. There exist compact sets $A_0 = \{0\} = \mathbb{R}^n_+, A_1 \subset \text{int} \mathbb{R}^1_+, \ldots, A_{n-1} \subset \text{int} \mathbb{R}^{n-1}_+$ and $t > 0$ such that for each $m \in \{0, 1, \ldots, n-1\}$, $A_m$ is an attractor for $\phi|\mathbb{R}^n_+$ with basin of attraction $\text{int} \mathbb{R}^m_+$ and

$$\min_{x \in BC(F, A_m)} \int_0^t f_{m+1}(\phi_s x) ds > 0,$$

where $BC(F, A_m)$ is the Birkhoff center of $\phi|A_m$. In particular, $\{A_0, \ldots, A_{n-1}\}$ defines an unsaturated Morse decomposition for $\phi|\Lambda$.

With this characterization in hand, we immediately get the following corollary.

**Corollary 4.4.** If $F^1 \in \mathcal{P}^r(n_1), \ldots, F^k \in \mathcal{P}^r(n_k)$ are food chain vector fields with $r \geq 1$, then $F^1 \times \cdots \times F^k$ is $C^r$ robustly permanent if and only if $F^i$ is robustly permanent for each $1 \leq i \leq k$.

5. **Using the results.** Although the $C^r$ Whitney topology on $\mathcal{P}^r(n)$ is natural from a theoretical perspective, the perturbations considered in most models are not
This end, we need to make estimates for \( G \). Define \( \tilde{C} \)

\[ \tilde{C} \]

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of phase space). Instead we assume that the prey exhibits logistic dynamics in the predator-prey equations, but we choose not to use these equations as they exhibit some pathological properties (i.e., the equations are not continuous on the boundary of phase space). Instead we assume that the prey exhibits logistic dynamics in the

**Proposition 5.1.** Let \( F \in \mathcal{P}^r(n) \) with \( r \geq 1 \) be \( C^r \) robustly permanent. Let \( \Lambda \subset \mathbb{R}^n_+ \) be the maximal compact invariant set for \( F \). Let \( V_1 \) be a compact neighborhood of \( \Lambda \) and \( V_2 \) a compact neighborhood of \( V_1 \). Then there exists \( \epsilon > 0 \) such that if \( G \in \mathcal{P}^r(n) \) satisfies

1. \( G \) generates a dissipative flow,
2. the maximal compact invariant set for \( G \) is contained in \( V_1 \), and
3. \( \|G(x) - F(x)\| + \|DG(x) - DF(x)\| + \cdots + \|D^r G(x) - D^r F(x)\| \leq \epsilon \) for all \( x \in V_2 \),

then \( G \) is permanent.

**Proof.** Let \( F \) be \( C^r \) robustly permanent and have maximal compact invariant set \( \Lambda \). Since \( F \) is \( C^r \) robustly permanent, there exists a \( C^r \) neighborhood \( \mathcal{N} \subset \mathcal{P}^r(n) \) of \( F \) such that every \( G \in \mathcal{N} \) is permanent. Without loss of generality, we may assume that this neighborhood is given by

\[ \{ G \in \mathcal{P}^r(n) : \|G(x) - F(x)\|, < c(x) \text{ for all } x \in \mathbb{R}^n_+ \}, \]

where \( c : \mathbb{R}^n_+ \to (0, 1] \) is a continuous function and

\[ \|G(x) - F(x)\|_r = \|G(x) - F(x)\| + \|DG(x) - DF(x)\| + \cdots + \|D^r G(x) - D^r F(x)\|. \]

Let \( \rho : \mathbb{R}^n_+ \to [0, 1] \) be a smooth function such that \( \rho(x) = 1 \) for all \( x \in V_1 \) and \( \rho(x) = 0 \) for all \( x \in \mathbb{R}^n_+ \setminus V_2 \). Define

\[ \epsilon = \min_{x \in V_2} \frac{c(x)}{(r + 2)! (1 + \|\rho(x)\|_r^r)}. \]

Let \( G \in \mathcal{P}^r(n) \) be a vector field that satisfies conditions in the statement of the proposition. Define \( \tilde{G}(x) = F(x) + \rho(x)(G(x) - F(x)) \). We claim that \( \tilde{G} \) lies in \( \mathcal{N} \). To this end, we need to make estimates for \( \|D^i G(x) - D^i F(x)\| = \|D^i (\rho(x)(G(x) - F(x)))\| \) for all \( x \in \mathbb{R}^n_+ \) and \( 0 \leq i \leq r \). The product rule implies that for \( x \in V_2 \) and \( 0 \leq i \leq r \),

\[ \|D^i (\rho(x)(G(x) - F(x)))\| \leq i! \sum_{j=0}^{i} \|D^{i-j} \rho(x) D^j (G(x) - F(x))\| \]

\[ \leq (i + 1)! \|\rho(x)\|_r \epsilon. \]

Consequently, for \( x \in V_2 \),

\[ \|\tilde{G}(x) - F(x)\|_r \leq (r + 2)! \|\rho(x)\|_r \epsilon \leq c(x). \]

On the other hand, for \( x \in \mathbb{R}^n_+ \setminus V_2 \), \( \|F(x) - \tilde{G}(x)\|_r = 0 \). Hence \( \tilde{G} \) lies in \( \mathcal{N} \) and is permanent. Since \( \tilde{G} = G \) on the maximal compact invariant set for \( G \), it follows that \( G \) is permanent. \( \square \)

Now we illustrate how these results can be used for coupled predator-prey systems similar to those considered by Vandermeer [28]. Vandermeer used MacArthur predator-prey equations, but we choose not to use these equations as they exhibit some pathological properties (i.e., the equations are not continuous on the boundary of phase space). Instead we assume that the prey exhibits logistic dynamics in the
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abscense of the predator, and the predator has a Holling type II function response [1].

Coupling these equations only through the predators, we get

\[
\frac{dx_i}{dt} = r_i x_i \left( 1 - \frac{x_i}{K_i} \right) - \frac{a_i x_i y_i}{1 + b_i x_i + \epsilon c_i x_j} - \frac{\epsilon d_i y_j x_i}{1 + b_j x_j + \epsilon c_j x_i},
\]

\[
\frac{dy_i}{dt} = \frac{e_i x_i y_i}{1 + b_i x_i + \epsilon c_i x_j} - m_i y_i,
\]

where \( x_i \) and \( y_i \) are the densities of prey species \( i \) and predator species \( i \), respectively.

The parameters have the following interpretation: \( r_i \) is the intrinsic rate of growth of prey species \( i \); \( K_i \) is the carrying capacity of prey species \( i \); \( a_i \) and \( e_i \) correspond to the rates at which the predators encounter prey species; \( \frac{b_i}{a_i} \) and \( \frac{\epsilon c_i}{a_i} \) correspond to prey handling times for predator species \( i \); \( \frac{m_i}{a_i} \) correspond to the conversion rate of prey numbers to predator numbers; and \( m_i \) is the per capita mortality rate of predator species \( i \). The fact that this coupling is somewhat complex follows from the fact that the predators are handling both prey species when \( \epsilon > 0 \).

**Theorem 5.2.** Let \( r_i, K_i, a_i, b_i, c_i, d_i, e_i, f_i, \) and \( m_i \) be positive reals. There exists an \( \epsilon > 0 \) such that (5.1) is permanent for all \( 0 \leq \epsilon < \tilde{\epsilon} \) if and only if \( K_i > \frac{m_i}{e_i - b_im_i} > 0 \) for \( i = 1, 2 \).

**Proof.** Consider the uncoupled system (i.e., \( \epsilon = 0 \) in (5.1)) that is given by

\[
\frac{dx_i}{dt} = r_i x_i \left( 1 - \frac{x_i}{K_i} \right) - \frac{a_i x_i y_i}{1 + b_i x_i},
\]

\[
\frac{dy_i}{dt} = e_i x_i y_i - m_i y_i, \quad i = 1, 2.
\]

The only boundary equilibria for the predator-prey subsystem \( x_i - y_i \) of (5.2) are given by the origin \( (x_i, y_i) = (0, 0) \) and \( (x_i, y_i) = (K_i, 0) \). These equilibria satisfy the conditions of Corollary 4.1 if and only if \( K_i > \frac{m_i}{e_i - b_im_i} > 0 \). Alternatively, if \( K_i \leq \frac{m_i}{e_i - b_im_i} \) or \( \frac{m_i}{e_i - bim_i} \leq 0 \) for some \( i \in \{1, 2\} \), it can be shown [12, Lemma 3.2] that predator \( i \) is driven to extinction in the uncoupled system and (5.2) is not permanent. Hence (5.2) is \( C^1 \) robustly permanent if and only if \( K_i > \frac{m_i}{e_i - bim_i} > 0 \) for \( i = 1, 2 \).

To deduce that (5.1) is permanent for sufficiently small \( \epsilon \geq 0 \) when (5.2) is \( C^1 \) robustly permanent, we invoke Proposition 5.1. To this end, let \( \alpha = \min\{\frac{a_1}{e_1}, \frac{a_2}{e_2}, \frac{d_1}{f_1}, \frac{d_2}{f_2}\} \) and \( \beta = \min\{m_1, m_2\} \). Define \( S : \mathbb{R}_+^4 \to \mathbb{R} \) by \( S(x_1, y_1, x_2, y_2) = x_1 + \alpha y_1 + x_2 + \alpha y_2 \). Our choice of \( \alpha \) and \( \beta \) imply that any solution \( (x_1(t), y_1(t), x_2(t), y_2(t)) \) to (5.1) with \( x_i(0) \geq 0 \), \( y_i(0) \geq 0 \), and \( \epsilon \geq 0 \) satisfies

\[
\frac{d}{dt} S(x_1(t), y_1(t), x_2(t), y_2(t)) + \beta S(x_1(t), y_1(t), x_2(t), y_2(t)) \leq \alpha r_1 x_1(t) + \alpha r_2 x_2(t) + \beta (x_1(t) + x_2(t)) \leq C,
\]

where

\[
C = \frac{(r_1 + \beta \hat{\alpha})^2 K_1}{4r_1} + \frac{(r_2 + \beta \hat{\alpha})^2 K_2}{4r_2}.
\]

It follows that

\[
\limsup_{t \to \infty} S(x_1(t), y_1(t), x_2(t), y_2(t)) \leq \frac{C}{\beta}.
\]
Therefore, the maximal compact invariant set of (5.1) restricted to $\mathbb{R}^4_+$ for any $\epsilon \geq 0$ lies in the compact set
\[ V_1 = \left\{ (x_1, y_1, x_2, y_2) \in \mathbb{R}^4_+ : S(x_1, x_2, x_3, x_4) \leq \frac{C}{\beta} \right\}. \]
Choosing any compact neighborhood $V_2$ of $V_1$, Proposition 5.1 implies that whenever (5.2) is $C^1$ robustly permanent, there exists a $\tilde{\epsilon} > 0$ such that (5.1) is permanent for all $0 \leq \epsilon \leq \tilde{\epsilon}$.

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