Criteria for C^r Robust Permanence

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Let $\dot{x}_i = x_i f_i(x)$ $(i = 1, ..., n)$ be a C^r vector field that generates a dissipative flow ϕ on the positive cone of $\mathbf{R}^n$. ϕ is called *permanent* if the boundary of the positive cone is repelling. ϕ is called C^r *robustly permanent* if ϕ remains permanent for sufficiently small C^r perturbations of the vector field. A necessary condition and a sufficient condition for C^r robust permanence involving the average per-capita growth rates $\int f_i \, d\mu$ with respect to invariant measures μ are derived. The necessary condition requires that $\inf_\mu \max_i \int f_i \, d\mu > 0$, where the infimum is taken over ergodic measures with compact support in the boundary of the positive cone. The sufficient condition requires that the boundary flow admit a Morse decomposition $\{M_1, ..., M_k\}$ such that every M_j satisfies $\min_\mu \max_i \int f_i \, d\mu > 0$ where the minimum is taken over invariant measures with support in M_j. As applications, we provide a sufficient condition for C^r robust permanence of Lotka–Volterra models and a topological characterization of C^r robust permanence for food chain models. © 2000 Academic Press

1. INTRODUCTION

The equations governing the dynamics of n interacting populations in a closed environment often are given by a vector field $\dot{x} = F(x)$ on the positive cone of $\mathbf{R}^n$, where $x = (x_1, ..., x_n)$ represents the vector of population densities and $F = (F_1, ..., F_n)$ represents the vector of population growth rates. Our interest lies in vector fields F such that for any $1 \leqslant i \leqslant n$, $F_i(x) = 0$ whenever $x_i = 0$. This condition on F corresponds simply to the fact that if the density of population i is zero, then the growth rate of population i is zero. A fundamental biological issue is under what conditions (i.e., for what choices of F) are all of the populations able to coexist. Traditionally, theoretical ecologists have equated coexistence with the existence of an asymptotically stable equilibrium that lies in the interior of the positive cone [22, 30]. More recently, coexistence has been equated with the concept of permanence [11, 12, 33], also known as uniform persistence [1, 2, 5]. Stated roughly, permanence requires that there be a compact region in the interior of the positive cone such that all solutions

400

to $\dot{x} = F(x)$ with initial conditions in the interior of the positive cone eventually enter and never leave this region. Although both definitions of coexistence ensure that population densities are bounded away from extinction, permanence, unlike its traditional counterpart, permits more complex asymptotics which have been observed in relatively simple systems [20]. Reviews of mathematical progress in studying permanence and its applications can be found in [9, 13, 34].

While permanence ensures that populations persist despite large perturbations of the initial conditions, any sensible definition of coexistence implies that the populations persist despite small perturbations of the governing equations themselves. A natural step in this direction is to define the vector field F to be C^r robustly permanent if the vector field remains permanent following small C^r-perturbations (see [9, 13]). This concept is practical from a modeling standpoint, as most population dynamics models ignore weak interactions between populations. For instance, the modeler assumes that F_i is independent of x_j for $j \neq i$, when in fact there is a weak dependence on x_j. Hence it is desirable to know whether "nearby" models that include these interactions as well as the original model are permanent. Some progress in characterizing vector fields that are robustly permanent has been made in dimension 3 [32, Theorem 2]. In arbitrary dimensions, Hutson proved that all permanent systems exhibit a weaker type of robustness to perturbations [12, Definition 4.1 and Theorem 4.2]. This alternative notion of robustness is necessarily weaker since permanent systems need not be C^r robustly permanent (e.g., the one-dimensional system $\dot{x} = x^2(1-x)$).

In this article, we develop necessary and sufficient conditions for C^r robust permanence. To describe these conditions we begin by noting that if the vector field F is C^1 and satisfies $F_i(x) = 0$ whenever $x_i = 0$, then $\dot{x} = F(x)$ can be rewritten as

$$\dot{x}_i = x_i f_i(x) \qquad i = 1, ..., n,$$

where each $f_i(x)$, the per-capita growth rate of population i, is the continuous function defined by

$$f_i(x) = \begin{cases} \dfrac{F_i(x)}{x_i} & \text{if} \quad x_i \neq 0 \\ \dfrac{\partial F_i}{\partial x_i}(x) & \text{otherwise.} \end{cases} \tag{1}$$

The necessary condition and the sufficient condition for robust permanence involve the average per-capita growth rates $\int f_i \, d\mu$ with respect to invariant measures μ for the vector field F. In particular, we introduce the concepts

of an unsaturated invariant measure (i.e., an invariant measure μ that satisfies $\max_{1 \leqslant i \leqslant n} \int f_i \, d\mu > 0$), a weakly unsaturated invariant set (i.e., all the ergodic measures supported by the set are unsaturated), and an unsaturated invariant set (i.e., all the invariant measures supported by the set are unsaturated) which generalize the concept of an unsaturated equilibrium [8, 9, 16]. The necessary condition for C^r robust permanence requires that the boundary of the positive cone be weakly unsaturated. Therefore, this necessary condition generalizes the fact that each boundary equilibrium of a robustly permanent system must be unsaturated [9]. In the spirit of Garay [5] and Hofbauer and So [10] (see also Butler and Waltman [2]), we prove that a sufficient condition for C^r robust permanence is that boundary flow admits a Morse decomposition $\{M_1, ..., M_k\}$ such that every M_j is unsaturated.

The article is organized as follows. In Section 2, we introduce the basic notation and terminology. In Section 3, the concepts of unsaturated invariant measures and sets are introduced. Several examples and results of how to determine whether an invariant compact set is unsaturated are presented. In Section 4, we present our main results, giving their proofs in Sections 5 and 6. In Section 7, we provide two applications of the main results. We provide a sufficient condition for C^r robust permanence of Lotka–Volterra models and a topological characterization of C^r robust permanence for food chain models. Verifying the sufficient condition for the Lotka–Volterra models reduces to solving a finite number of linear equations and an associated linear-programming problem.

2. PRELIMINARIES

Let $\mathbf{R}^n_+$ denote the closed positive cone of $\mathbf{R}^n$. Given $x \in \mathbf{R}^n$, let x_i and $[x]_i$ denote the ith component of the vector x. For any subset $S \subseteq \{1, ..., n\}$ define $\mathbf{R}^S = \{(x_1, ..., x_n) \in \mathbf{R}^n : x_i = 0 \ \forall i \notin S\}$ and $\mathbf{R}^S_+ = \mathbf{R}^S \cap \mathbf{R}^n_+$. Note that $\mathbf{R}^\varnothing = \{0\}$. If $|S| = k$ then $\mathbf{R}^S_+$ is a *k-dimensional face* of $\mathbf{R}^n_+$. Given $S \subseteq \{1, ..., n\}$ and $A \subseteq \mathbf{R}^S$, let ∂A, $\overline{A}$, and int$A$ denote the boundary, closure, and interior of A relative to the topology of $\mathbf{R}^S$. Given a point $x \in \mathbf{R}^n_+$ and a compact set $A \subset \mathbf{R}^n_+$, let dist$(x, A) = \min_{a \in A} \|x - a\|$ denote the distance from x to A. Given a compact set $A \subset \mathbf{R}^n$ and $\delta > 0$, define $B(A, \delta) = \{x \in \mathbf{R}^n : \text{dist}(A, x) \leqslant \delta\}$.

We recall several definitions from dynamical systems theory. Assume that $F: \mathbf{R}^n_+ \to \mathbf{R}^n$ is C^1 and that $\dot{x} = F(x)$ generates a global flow $\phi: \mathbf{R} \times \mathbf{R}^n_+ \to \mathbf{R}^n_+$. Let $\phi_t x = \phi(t, x)$. Given sets $I \subseteq \mathbf{R}$ and $K \subseteq \mathbf{R}^n_+$, let $\phi_I K = \{\phi_t x : t \in I, x \in K\}$. A set $K \subseteq \mathbf{R}^n_+$ is called *invariant* if $\phi_t K = K$ for all $t \in \mathbf{R}$. The *omega limit set* of a set $K \subseteq \mathbf{R}^n_+$ equals $\omega(F, K) = \bigcap_{t \geqslant 0} \overline{\phi_{[t, \infty)} K}$. The

alpha limit set of a set $K \subseteq \mathbf{R}_+^n$ equals $\alpha(F, K) = \bigcap_{t \leqslant 0} \overline{\phi_{(-\infty, t]}K}$. Given an invariant set K, $A \subset K$ is called an *attractor* for $\phi \mid K$ provided there exists an open neighborhood $U \subseteq K$ of A such that $\omega(F, U) = A$. The *basin of attraction* of A for $\phi \mid K$ is the set of points $x \in K$ such that $\omega(F, x) \subseteq A$. The *stable set* of a compact invariant set K is defined by

$$W^s(F, K) = \{x \in \mathbf{R}_+^n : \omega(F, x) \neq \varnothing \text{ and } \omega(F, x) \subseteq K\}.$$

The flow ϕ is *dissipative* if there exists a compact attractor $A \subset \mathbf{R}_+^n$ for ϕ whose basin of attraction is $\mathbf{R}_+^n$.

DEFINITION 2.1. Let $\mathscr{P}_n^r$ be the space of C^r vector fields $F = (F_1, ..., F_n)$: $\mathbf{R}_+^n \to \mathbf{R}^n$ that satisfy $F_i(x) = 0$ whenever $x_i = 0$.

We view $\mathscr{P}_n^r$ as the space of all possible models of *n*-interacting species and endow $\mathscr{P}_n^r$ with the C^r Whitney topology [7, Chap. 2].

DEFINITION 2.2. $F \in \mathscr{P}_n^r$ is *permanent* provided that $\dot{x} = F(x)$ generates a dissipative flow ϕ and there exists a compact attractor $A \subset \text{int } \mathbf{R}_+^n$ for ϕ whose basin of attraction is int $\mathbf{R}_+^n$.

Permanence was originally introduced in [33] and is also known as uniform persistence [2]. A weaker but related concept is persistence.

DEFINITION 2.3. $F \in \mathscr{P}_n^r$ is *persistent* provided that $\dot{x} = F(x)$ generates a global flow ϕ and $\limsup_{t \to \infty} [\phi_t x]_i > 0$ for all $x \in \text{int } \mathbf{R}_+^n$ and $1 \leqslant i \leqslant n$.

Persistence was introduced in [4] and is also called weak persistence [2]. However, we retain the original definition so that our terminology is consistent with Hofbauer and Sigmund [9, Chap. 13].

DEFINITION 2.4. $F \in \mathscr{P}_n^r$ is C^r *robustly permanent* (respectively, C^r *robustly persistent*) if there exists a neighborhood $\mathscr{N} \subseteq \mathscr{P}_n^r$ of F such that every vector field $G \in \mathscr{N}$ is permanent (respectively, persistent).

3. UNSATURATED INVARIANT MEASURES AND SETS

Our main results require a measure-theoretic analog of the definition of an unsaturated equilibrium [8, 9, 16]. Hence, we review some definitions from ergodic theory. Given a Borel probability measure μ on $\mathbf{R}_+^n$, the *support of μ*, denoted supp(μ), is the smallest closed set whose complement has measure 0. Given a closed set $K \subseteq \mathbf{R}_+^n$, let $\mathscr{M}(K)$ denote the space of Borel probability measures with support in K. A Borel probability measure

μ is called *invariant* for the flow ϕ provided that $\mu(B) = \mu(\phi_t B)$ for all $t \in \mathbf{R}$ and for every Borel set $B \subseteq \mathbf{R}^n_+$. Given a closed invariant set K, let $\mathscr{M}_{\text{inv}}(F, K) \subseteq \mathscr{M}(K)$ be the subset of invariant Borel probability measures with $\text{supp}(\mu) \subseteq K$. An invariant measure $\mu \in \mathscr{M}_{\text{inv}}(F, K)$ is called *ergodic* provided that $\mu(B) = 0$ or 1 for any invariant Borel set B. Let $\mathscr{M}_{\text{erg}}(F, K) \subseteq \mathscr{M}_{\text{inv}}(F, K)$ denote the subset of ergodic measures.

DEFINITION 3.1.   Let $F \in \mathscr{P}^r_n$ be such that $\dot{x} = F(x)$ generates a global flow ϕ. Let $f = (f_1, ..., f_n)$ be the continuous map defined by (1). An invariant measure $\mu \in \mathscr{M}_{\text{inv}}(F, \mathbf{R}^n_+)$ with compact support is *unsaturated* if

$$\max_{1 \leqslant i \leqslant n} \int f_i \, d\mu > 0$$

else it is called *saturated*.

DEFINITION 3.2.   A compact invariant set K is *weakly unsaturated* if

$$\inf_{\mu \in \mathscr{M}_{\text{erg}}(F, K)} \max_{1 \leqslant i \leqslant n} \int f_i \, d\mu > 0.$$

DEFINITION 3.3.   A compact invariant set K is *unsaturated* if

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

Remark 3.1.   In the expression

$$\min_{\mu \in \mathscr{M}_{\text{inv}}(F, K)} \max_{1 \leqslant i \leqslant n} \int f_i \, d\mu \tag{2}$$

weak* compactness of $\mathscr{M}_{\text{inv}}(F, K)$ implies that the minimum is achieved.

Remark 3.2.   Equation (2) is the solution to the following measure-theoretic linear programming problem [17]: minimize z with respect to $\mu \in \mathscr{M}_{\text{inv}}(F, K)$ and $z \in \mathbf{R}$ subject to the constraints $\int f_i \, d\mu \leqslant z$ for all $1 \leqslant i \leqslant n$.

Remark 3.3.   While the union of weakly unsaturated invariant sets is weakly unsaturated, the union of unsaturated invariant sets need not be unsaturated.

For the following invariant sets there is no distinction between unsaturated and weakly unsaturated sets:

An equilibrium. If $x \in \mathbf{R}_+^n$ is an equilibrium for ϕ, then there is a unique invariant measure δ_x in $\mathscr{M}_{\text{inv}}(F, x)$. It is the Dirac measure based at the point x (i.e., the measure defined by $\int h \, d\delta_x = h(x)$ for all continuous functions $h: \mathbf{R}_+^n \to \mathbf{R}$). Hence, x is unsaturated if and only if $f_i(x) > 0$ for some i. Therefore, our definition of an unsaturated equilibrium coincides with the standard definition of an unsaturated equilibrium [8, 9, 16].

A periodic orbit. If $x \in \mathbf{R}_+^n$ defines a periodic orbit with period $T > 0$ for the flow ϕ, then there is a unique invariant measure μ in $\mathscr{M}_{\text{inv}}(F, \mathcal{O}(x))$, where $\mathcal{O}(x) = \overline{\{\phi_t x : t \in \mathbf{R}\}}$. It is given by a Dirac measure averaged along the orbit of x (i.e., $\int h \, d\mu = \frac{1}{T} \int_0^T h(\phi_s x) \, ds$ for any continuous function $h: \mathbf{R}_+^n \to \mathbf{R}$). μ and $\mathcal{O}(x)$ are unsaturated if and only if $\int_0^T f_i(\phi_s x) \, ds > 0$ for some i.

A quasi-periodic-set. Consider an invariant set $K \subset \mathbf{R}_+^n$ such that ϕ restricted to K is topologically conjugate to an irrational flow ψ on a k-dimensional torus T^k (i.e., $\psi_t(\theta_1, ..., \theta_k) = (\theta_1 + \alpha_1 t \pmod 1), ..., \theta_k + \alpha_k t \pmod 1)$, where $\alpha_1, ..., \alpha_k \in \mathbf{R}$ are linearly independent over the rationals). Let us assume the topological conjugacy is given by the homeomorphism $H: K \to T^k$. ϕ restricted to K admits a unique invariant measure μ given by $\mu = \lambda \circ H$ where λ is Lebesque measure on T^k. Therefore, K is unsaturated if and only if $\int f_i \, d\mu > 0$ for some i.

More generally, for any *uniquely ergodic* invariant set (i.e., an invariant set K such that $\mathscr{M}_{\text{inv}}(F, K)$ is a singleton) there is no distinction between weakly unsaturated and unsaturated. However, if $\mathscr{M}_{\text{inv}}(F, K)$ contains several ergodic measures, then the two concepts are distinct.

A particularly interesting case occurs when an invariant set supports only a finite number of ergodic measures. Examples of this type include heteroclinic cycles between a finite number of equilibria, periodic orbits, and quasi-periodic sets.

LEMMA 3.1. *Let* $K \subset \mathbf{R}_+^n$ *be a compact invariant set. Assume that* $\mathscr{M}_{\text{erg}}(F, K) = \{\mu_j\}_{j=1}^k$. *Then* K *is unsaturated if and only if*

$$\min_{a \in \Delta} \max_{1 \leq i \leq n} \sum_{j=1}^k a_j \int f_i \, d\mu_j > 0, \qquad (3)$$

where $\Delta = \{a \in \mathbf{R}_+^k : \sum_{j=1}^k a_j = 1\}$.

Remark 3.4. The left hand side of (3) is the solution to the following finite-dimensional linear programming problem: minimize z with respect to $a \in \Delta$ and $z \in \mathbf{R}$ subject to the constraints $\sum_{j=1}^k a_j \int f_i \, d\mu_j \leq z$ for all $1 \leq i \leq n$. Hence, whenever the ergodic averages $\int f_i \, d\mu_j$ are known, the left hand side of (3) is computable by standard linear programming methods.

Proof. Since $\mathcal{M}_{\mathrm{erg}}(F, K) = \{\mu_j\}_{j=1}^k$ the ergodic decomposition theorem (see, e.g., [21, Chap. II, Theorem 6.4.]) implies that every invariant measure $\mu \in \mathcal{M}_{\mathrm{inv}}(F, K)$ can be written in the form $\sum_{j=1}^k a_j \mu_j$ where the $a \in \Delta$. Therefore K is unsaturated if and only if (3) holds. ∎

Before ending this section, we mention a lemma that is useful for applications (e.g., the characterization of robust permanence for food chains in Section 7.2). Recall that the *Birkhoff center* $BC(F, K)$ for $F | K$ is the closure of the set $\{x \in K : x \in \omega(F, x)\}$. Theorem 1 of [31] and the ergodic decomposition theorem [21, Chap. II, Theorem 6.4.] imply

LEMMA 3.2. *Let* $K \subset \mathbf{R}_+^n$ *be a compact invariant set. Then*

$$\inf_{\mu \in \mathcal{M}_{\mathrm{erg}}(F, K)} \int f_i \, d\mu = \min_{\mu \in \mathcal{M}_{\mathrm{inv}}(F, K)} \int f_i \, d\mu = \sup_{t > 0} \frac{1}{t} \min_{x \in BC(F, K)} \int_0^t f_i(\phi_s x) \, ds$$

for all $1 \leqslant i \leqslant n$.

Consequently, if there exist an $i \in \{1, ..., n\}$ *and a* $t > 0$ *such that*

$$\min_{x \in BC(F, K)} \int_0^t f_i(\phi_s x) \, ds > 0,$$

then K *is unsaturated.*

4. MAIN RESULTS

Having introduced weakly unsaturated sets, we are able to state a necessary condition for C^r robust persistence which generalizes the fact that each boundary equilibrium of a robustly persistent system is unsaturated [9].

THEOREM 4.1. *Let* $F \in \mathcal{P}_n^r$ *with* $r \geqslant 1$ *be such that* $\dot{x} = F(x)$ *generates a dissipative flow* ϕ. *Let* Λ *be the maximal compact invariant set for* $\phi | \partial \mathbf{R}_+^n$. *If* F *is* C^r *robustly persistent, then* Λ *is weakly unsaturated.*

The proof of Theorem 4.1 appears in Section 5. The basic idea is to show that if there is a saturated measure $\mu \in \mathcal{M}_{\mathrm{erg}}(F, \Lambda)$, then one can C^r perturb F such that $W^s(F, \Lambda) \cap \mathrm{int}\, \mathbf{R}_+^n \neq \varnothing$. An interesting aspect of the proof is that the cases $r = 1$ and $r \geqslant 2$ require separate treatments as the tools employed in either case (the ergodic closing lemma for $r = 1$ and the Pesin stable manifold theorem for $r \geqslant 2$) do not apply to the complementary case.

It is not difficult to verify that the necessary condition in Theorem 4.1 is also sufficient for robust permanence in dimensions 1 and 2. However,

in higher dimensions, it may not suffice. A simple but nontrivial case arises with a three-dimensional Lotka–Volterra competitive system that admits a heteroclinic cycle on the boundary of the positive cone [23]. A one-parameter version of this system is given by

$$\frac{dx_1}{dt} = x_1(1 - x_1 - \alpha x_2)$$

$$\frac{dx_2}{dt} = x_2(1 - x_2 - \alpha x_3) \qquad (4)$$

$$\frac{dx_3}{dt} = x_3(1 - x_3 - \alpha x_1),$$

where we assume that $\alpha > 1$. This system exhibits a heteroclinic cycle on $\partial \mathbf{R}_+^3$ between the equilibria $(1, 0, 0)$, $(0, 1, 0)$, and $(0, 0, 1)$. For this system, the boundary $\partial \mathbf{R}_+^3$ is always weakly unsaturated. However, the system is permanent if and only if $1 < \alpha < 2$ (see, e.g., [9]). Lemma 3.1 implies that heteroclinic cycle formed by these three equilibria and their connecting orbits is unsaturated if and only if $1 < \alpha < 2$.

To state the sufficient condition for robust permanence, we follow the approach taken by Garay [5] who characterized permanence using Morse decompositions of the boundary flow. To this end, we recall several definitions due to Conley [3]. 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 $\{M_1, ..., M_k\}$ is a *Morse decomposition* for a compact invariant set K if $M_1, ..., M_k$ are pairwise disjoint, compact isolated invariant sets for $\phi \mid K$ with the property that for each $x \in K$ there are integers $l = l(x) \leqslant m = m(x)$ such that $\alpha(F, x) \subseteq M_m$ and $\omega(F, x) \subseteq M_l$ and if $l = m$ then $x \in M_l = M_m$. Garay [5] proved the following characterization of permanence (see, also, Hofbauer and So [10]).

THEOREM 4.2 (Garay 1989). *Let $F \in \mathscr{P}_n^1$ be such that $\dot{x} = F(x)$ generates a dissipative flow ϕ. Let $\{M_1, ..., M_k\}$ be a Morse decomposition for the maximal compact invariant set Λ of $\phi \mid \partial \mathbf{R}_+^n$. F is permanent if and only if each M_j satisfies*

1. *There exits $\gamma > 0$ such that such that the set*

$$\{x \in \text{int } \mathbf{R}_+^n : \text{dist}(x, M_j) < \gamma\}$$

contains no entire trajectories of ϕ, and

2. $W^s(F, M_j) \subseteq \partial \mathbf{R}_+^n$.

Remark 4.1. A similar theorem using acyclic covers of the boundary flow was proven by Butler and Waltman [2]. Garay [5] discusses the relationship between acyclic covers and Morse decompositions.

DEFINITION 4.1. Let K be a compact invariant set. We say that $\{M_1, ..., M_k\}$ is an *unsaturated Morse decomposition for K* if $\{M_1, ..., M_k\}$ is a Morse decomposition for K and each M_j is unsaturated (i.e., for each $1 \leq j \leq k$, $\min_{\mu \in \mathscr{M}_{\mathrm{inv}}(F, M_j)} \max_{1 \leq i \leq n} \int f_i \, d\mu > 0$).

With the assistance of Garay's theorem, we prove that the existence of an unsaturated Morse decomposition is sufficient for robust permanence.

THEOREM 4.3. *Let* $F \in \mathscr{P}_n^1$ *be such that* $\dot{x} = F(x)$ *generates a dissipative flow* ϕ. *Let* $\Lambda \subset \partial \mathbf{R}_+^n$ *be the maximal compact invariant set for* $\phi \mid \partial \mathbf{R}_+^n$. *If* Λ *admits an unsaturated Morse decomposition*, *then* F *is* C^1 *robustly permanent.*

We remark that if $F \in \mathscr{P}_n^r$ with $r \geq 1$, then C^1 robust permanence of F implies C^r robust permanence of F. A proof of Theorem 4.3 is given in Section 6. Since every dissipative flow admits a Morse decomposition, the difference between Theorem 4.1 and Theorem 4.3 concerns the difference between weakly unsaturated and unsaturated sets. This difference vanishes when there is a Morse decomposition consisting of uniquely ergodic pieces.

5. PROOF OF THE NECESSARY CRITERION FOR ROBUST PERSISTENCE

In order to prove Theorem 4.1, we use two major tools from smooth ergodic theory: the Pesin stable manifold theorem [28] and an ergodic closing lemma for flows [35]. The heart of the proof is given in Section 5.2. In order to use the Pesin stable manifold theorem, we need to be able to relate the average per-capita growth rates $\int f_i \, d\mu$ to the Lyapunov exponents of the flow. The relevant details are presented in Section 5.1. Since the usual formulation of the ergodic closing lemma for flows is too weak for our purposes, we show in Section 5.3 how to adapt Wen's proof of the ergodic closing lemma [35] to get our version of the ergodic closing lemma.

5.1. *Lyapunov Exponents and Average Per Capita Growth Rates*

Consider $F \in \mathscr{P}_n^r$ with $r \geq 1$ such that $\dot{x} = F(x)$ generates a dissipative flow ϕ. Let $f = (f_1, ..., f_n)$ be defined by (1). Let A be the maximal compact invariant set for ϕ and let $\mu \in \mathscr{M}_{\mathrm{erg}}(F, A)$. Since μ is ergodic, there exists a subset $S \subseteq \{1, ..., n\}$ such that $\mu(\mathrm{int}\, \mathbf{R}_+^S) = 1$.

LEMMA 5.1. $\int f_i \, d\mu = 0$ *for all* $i \in S$.

Remark 5.1.   When $\mu(\text{int } \mathbf{R}^n_+) = 1$, Lemma 5.1 implies that μ is saturated. In the special case where μ equals the Dirac measure at 0, we get $S = \varnothing$ and int $\mathbf{R}^S = \{0\}$.

Proof.   Let $i \in S$ be given. Since $\mu(\text{int } \mathbf{R}^S_+ \cap A) = 1$, the Birkhoff ergodic theorem implies that there exists an invariant Borel set $U \subseteq \text{int } \mathbf{R}^S_+ \cap A$ such that $\mu(U) = 1$ and

$$\lim_{t \to \infty} \frac{1}{t} \int_0^t f_i(\phi_s x) \, ds = \int f_i \, d\mu \qquad (5)$$

for all $x \in U$. Choose an open set $V \subset \text{int } \mathbf{R}^S_+$ such that $\bar{V} \subset \text{int } \mathbf{R}^S_+$ is compact and $\mu(V \cap U) > 0$. By the Poincaré recurrence theorem, we can choose $y \in V \cap U$ such that $\phi(t_k, y) \in V$ for all $k \geqslant 1$, where $t_k \in \mathbf{R}_+$ is an increasing sequence of positive reals satisfying $t_k \uparrow \infty$ as $k \to \infty$. Since $\bar{V} \subset \text{int } \mathbf{R}^S_+$ is compact, there exits a $\delta > 0$ such that

$$1/\delta \leqslant [\phi(t_k, y)]_i \leqslant \delta \qquad (6)$$

for all $k \geqslant 1$. As $\log([\phi(t, y)]_i / y_i) = \int_0^t f_i(\phi_s y) \, ds$, (5) and (6) imply that

$$\int f_i \, d\mu = \lim_{t \to \infty} \frac{1}{t} \int_0^t f_i(\phi_s y) \, ds = \lim_{k \to \infty} \frac{1}{t_k} \log \frac{[\phi(t_k, y)]_i}{y_i} = 0. \qquad \blacksquare$$

Let $D\phi_t(x)$ denote the derivative of $\phi_t(x)$ with respect to x and let $\bar{S} = \{1, ..., n\} \backslash S$. Oseledec's multiplicative ergodic theorem [15, 26] implies there exist a finite set of real numbers $\mathscr{L} \subset \mathbf{R}$ and a Borel set $O \subseteq \text{supp } \mu)$ with $\mu(O) = 1$ such that for each $x \in O$ there is a splitting $\mathbf{R}^n = \bigoplus_{\lambda \in \mathscr{L}} E^\lambda(x)$ satisfying $D\phi_t(x) \, E^\lambda(x) = E^\lambda(\phi_t x)$ for all $t \in \mathbf{R}$ and $\lim_{t \to \pm \infty} \frac{1}{t} \log \|D\phi_t(x) \, v\| = \lambda$ for all $v \in E^\lambda(x) \backslash \{0\}$. The set $\mathscr{L}$ is the set of *Lyapunov exponents* for (ϕ, μ) and the set O is called the *Oseledec regular points* for (ϕ, μ). When μ is supported on an equilibrium $x \in \mathbf{R}^S_+$, these exponents equal the real parts of the eigenvalues of $DF(x)$. When μ is supported on a periodic orbit, these exponents equal the real parts of the characteristic exponents of the periodic orbit. Since each face of $\mathbf{R}^n_+$ is ϕ-invariant, for each $i \in \bar{S}$ there is a Lyapunov exponent $\tau_i \in \mathscr{L}$ such that $E^{\tau_i}(x) \oplus \mathbf{R}^S$ spans $\mathbf{R}^{\{i\} \cup S}$. We call these exponents $\{\tau_i\}_{i \in \bar{S}}$ the *transverse Lyapunov exponents* for (ϕ, μ).

LEMMA 5.2. $\tau_i = \int f_i \, d\mu$ *for all* $i \in \bar{S}$.

Proof.   We prove the lemma under the assumption that $S \neq \varnothing$ and $S \neq \{1, ..., n\}$. The proof of the lemma when $S = \{1, ..., n\}$ is immediate and

the proof of the lemma when $S = \varnothing$ follows from similar arguments. By permuting coordinates if necessary, we may assume that $S = \{1, ..., m\}$ with $m < n$ and $i = m + 1$. Let $\phi^S = \phi \mid \mathbf{R}_+^m$ and $\psi = \phi \mid \mathbf{R}_+^{m+1}$. Since the faces of $\mathbf{R}_+^n$ are invariant, the Lyapunov exponents for (ϕ^S, μ) and (ψ, μ) correspond to Lyapunov exponents for (ϕ, μ). Oseledec's multiplicative ergodic theorem implies that $\lim_{t \to \infty} \frac{1}{t} \log |\det D\phi_t^S(x)|$ and $\lim_{t \to \infty} \frac{1}{t} \log |\det D\psi_t(x)|$ equal μ-almost surely the sum of the Lyapunov exponents for (ϕ^S, μ) and (ψ, μ) when counted with multiplicity (see, e.g., [15]). Hence,

$$\tau_{m+1} = \lim_{t \to \infty} \frac{1}{t} (\log |\det D\psi_t(x)| - \log |\det D\phi_t^S(x)|) \tag{7}$$

μ-almost surely. Invariance of $\mathbf{R}_+^m$ implies that $D\psi_t(x)$ has the upper-triangular block form

$$D\psi_t(x) = \begin{pmatrix} D\phi_t^S(x) & A(t, x) \\ 0 & \exp\left[\int_0^t f_{m+1}(\phi_s x) \, ds \right] \end{pmatrix} \tag{8}$$

for all $x \in \mathbf{R}_+^m$ and where $A(t, x)$ is an $m \times 1$ matrix. Equations (7) and (8) imply that

$$\tau_{m+1} = \lim_{t \to \infty} \frac{1}{t} \int_0^t f_{m+1}(\phi_s x) \, ds$$

μ-almost surely. The Birkhoff ergodic theorem implies that

$$\lim_{t \to \infty} \frac{1}{t} \int_0^t f_{m+1}(\phi_s x) \, ds = \int f_{m+1} \, d\mu$$

μ-almost surely. Hence, $\tau_{m+1} = \int f_{m+1} \, d\mu$. ∎

5.2. Proof of Theorem 4.1

Let $F \in \mathscr{P}_n^r$ with $r \geqslant 1$ be such that $\dot{x} = F(x)$ generates a dissipative flow ϕ. Let Λ be the maximal compact invariant set for $\phi \mid \partial \mathbf{R}_+^n$ and let $f = (f_1, ..., f_n)$ be defined by (1). Assume that

$$\inf_{\mu \in \mathscr{M}_{\mathrm{erg}}(F, \Lambda)} \max_{1 \leqslant i \leqslant n} \int f_i \, d\mu \leqslant 0. \tag{9}$$

We will show that F is not C^r robustly persistent by proving that every neighborhood $\mathscr{N} \subset \mathscr{P}_n^r$ of F contains a vector field that is not persistent.

Without loss of generality, we may assume that $\mathcal{N} \subset \mathcal{P}_n^r$ is a neighborhood of F given by

$$\{G \in \mathcal{P}_n^r : \|G(x) - F(x)\| + \|DG(x) - DF(x)\| + \cdots$$
$$+ \|D^r G(x) - D^r F(x)\| < c(x)\},$$

where $c : \mathbf{R}_+^n \to (0, 1]$ is a continuous function. Let $V \subset \mathbf{R}_+^n$ be a compact neighborhood of Λ and let $\rho : \mathbf{R}_+^n \to [0, 1]$ be a C^∞ function such that $\rho(x) = 1$ for all $x \in \Lambda$ and $\rho(x) = 0$ for all $x \in \mathbf{R}_+^n \setminus V$. Define $s(x) = x\rho(x)$ and

$$\eta = \min_{x \in V} \frac{c(x)}{1 + \|s(x)\| + \|Ds(x)\| + \cdots + \|D^r s(x)\|}.$$

Inequality (9) implies that there is a $\mu \in \mathcal{M}_{\mathrm{erg}}(F, \Lambda)$ such that $\max_{1 \leqslant i \leqslant n} \int f_i \, d\mu \leqslant \eta/4$. Ergodicity of μ implies there is a proper subset $S \subset \{1, ..., n\}$ such that $\mu(\mathrm{int}\, \mathbf{R}_+^S) = 1$. Let $\bar{S} = \{1, ..., n\} \setminus S$. Define $G = (G_1, ..., G_n)$: $\mathbf{R}_+^n \to \mathbf{R}^n$ by

$$G_i(x) = \begin{cases} F_i(x) & \text{if } i \in S \\ F_i(x) - \frac{3}{4}\eta\rho(x)\, x_i & \text{if } i \in \bar{S}. \end{cases}$$

Notice that $G \in \mathcal{N}$, $\mu \in \mathcal{M}_{\mathrm{erg}}(G, \mathbf{R}_+^S)$ and $\max_{i \in \bar{S}} \int g_i \, d\mu \leqslant -\eta/2$ where $g_i(x) = G_i(x)/x_i$ whenever $x_i \neq 0$ and $g_i(x) = \frac{\partial G_i}{\partial x_i}(x)$ otherwise. Let $\psi(t, x)$ be the flow generated by $\dot{x} = G(x)$.

At this point we break up the proof of Theorem 4.1 into two cases: $r \geqslant 2$ and $r = 1$.

Consider the case $r \geqslant 2$. Let $\mathscr{L}$ and O be the Lyapunov exponents and Oseledec regular points for (ψ, μ). At each point $x \in O$, the splitting of $\mathbf{R}^n$ determines three subspaces: the stable subspace $E^s(x) = \bigoplus_{\lambda < 0} E^\lambda(x)$, the center subspace $E^c(x) = \bigoplus_{\lambda = 0} E^\lambda(x)$, and the unstable subspace $E^u(x) = \bigoplus_{\lambda > 0} E^\lambda(x)$. The Pesin stable manifold theorem [28, Corollaries 3.17 and 3.18] implies that tangent to $E^s(x)$, $E^c(x)$ and $E^u(x)$ are locally ψ-invariant families of C^1 discs $\mathscr{W}_x^s$, $\mathscr{W}_x^c$, and $\mathscr{W}_x^u$ corresponding to the stable, center and unstable manifolds. The family of stable manifolds $\mathscr{W}_x^s$ is contained in $W^s(G, \mathrm{supp}(\mu))$. Lemma 5.2 and our choice of G imply that all of the transverse Lyapunov exponents of (ψ, μ) are less than $-\eta/2$. Therefore, $\mathbf{R}^S \oplus E^s(x)$ spans $\mathbf{R}^n$ and $\mathscr{W}_x^s \cap \mathrm{int}\, \mathbf{R}_+^n \neq \varnothing$ for all $x \in O$. Consequently, G is not persistent.

Consider the case $r = 1$. We claim that there are an $H \in \mathcal{N}$ and a point $z \in \mathrm{int}\, \mathbf{R}_+^S$ such that z is either an equilibrium or periodic for the flow of $\dot{x} = H(x)$ and such that the transverse Lyapunov exponents for the orbit $\mathcal{O}(z)$ of z are strictly negative. Before proving this claim, let us see how it

completes the proof of theorem. If such an $H \in \mathcal{N}$ and $z \in$ int $\mathbf{R}_+^S$ exist, then the stable manifold theorem for periodic orbits and equilibria (see, e.g., [29]) implies that $W^s(H, \mathcal{O}(z)) \cap$ int $\mathbf{R}_+^n \neq \varnothing$. Therefore, we have shown there is an H in $\mathcal{N}$ that is not persistent.

Now, let us prove the claim. Suppose μ is supported on an equilibrium or periodic orbit for ψ. Then by choosing $H = G$ and $z \in \operatorname{supp}(\mu)$ we are done. Next, suppose that μ is *not* supported on an equilibrium point or periodic orbit for ψ. We will show that we can C^1 perturb G to get the desired periodic orbit. The necessary tool for this perturbation is an ergodic closing lemma which is proven in Section 5.3. To formulate this lemma, let $G^S = G \mid \mathbf{R}_+^S$ and let $K \subset \mathbf{R}_+^S$ be a compact neighborhood of $\operatorname{supp}(\mu)$. Define $\operatorname{Sing}(G)$ to be the equilibria of ψ. We define the set $\Sigma = \Sigma(G^S, K, \mu)$ of *strongly closable points* to be the set of points $y \in \operatorname{supp}(\mu) \backslash \operatorname{Sing}(G)$ such that for every $\varepsilon > 0$, there exist a C^1 vector field $H^S: \mathbf{R}_+^S \to \mathbf{R}^S$, a point $z \in \mathbf{R}_+^S$, and a real number $\tau > 0$ satisfying

(C1) For all $i \in S$, $H_i^S(x) = 0$ whenever $x_i = 0$.

(C2) $\|H^S(x) - G^S(x)\| + \|DH^S(x) - DG^S(x)\| < \varepsilon$ for all $x \in K$.

(C3) $H^S(x) = G^S(x)$ for all $x \in \mathbf{R}_+^S \backslash K$

(C4) $\xi_\tau z = z$, where ξ_t is the flow of $\dot{x} = H^S(x)$.

(C5) $\|\psi_t y - \xi_t z\| < \varepsilon$ for all $0 \leqslant t \leqslant \tau$.

Using Wen's proof of the ergodic closing lemma for flows [35, Theorem 3.9], we prove the following result in Section 5.3:

THEOREM 5.4 (An ergodic closing lemma). $\mu(\Sigma \cup \operatorname{Sing}(G)) = 1$.

Since we have assumed that μ is not supported on an equilibrium, we have $\mu(\Sigma) = 1$. The Birkhoff ergodic theorem implies that there exists a Borel set $U \subseteq$ int $\mathbf{R}_+^S$ with $\mu(U) = 1$ such that

$$\lim_{t \to \infty} \frac{1}{t} \int_0^t g_i(\psi_s x)\, ds = \int g_i\, d\mu$$

for all $1 \leqslant i \leqslant n$ and $x \in U$. Let y be a point in $\Sigma \cap U$. Since $\max_{i \in \bar{S}} \int g_i\, d\mu \leqslant -\eta/2$, we can choose $T > 0$ sufficiently large such that

$$\max_{i \in \bar{S}} \frac{1}{t} \int_0^t g_i(\psi_s y)\, ds \leqslant -\eta/3 \tag{10}$$

for all $t \geqslant T$. Since $y \in \Sigma$, for every $\varepsilon > 0$ there are a C^1 map $H^S: \mathbf{R}_+^S \to \mathbf{R}^S$, a point $z \in \mathbf{R}_+^S$, and a real number $\tau > 0$ such that (C1)–(C5) hold. Let $\tilde{\rho}: \mathbf{R}_+^n \to [0, 1]$ be a C^∞ function such that $\tilde{\rho}(x) = 1$ for all $x \in K$ and $\rho(x) = 0$ for all $x \in \mathbf{R}_+^n \backslash W$, where $W \subset \mathbf{R}_+^n$ is a compact neighborhood of K.

Let $\pi: \mathbf{R}^n \to \mathbf{R}^S$ be the orthogonal projection of $\mathbf{R}^n$ onto $\mathbf{R}^S$. We extend H^S to $H: \mathbf{R}^n_+ \to \mathbf{R}^n$ by

$$H_i(x) = \begin{cases} G_i(x) + \tilde{\rho}(x)(H_i^S(\pi x) - G_i(\pi x)) & \text{for} \quad i \in S \\ G_i(x) & \text{for} \quad i \in \bar{S}. \end{cases} \tag{11}$$

Notice that $H_i(x) = H_i^S(x)$ for $x \in \mathbf{R}^S_+$ and $i \in S$. (C1)–(C3) imply that for $\varepsilon > 0$ sufficiently small H as defined in (11) lies in $\mathcal{N}$. Furthermore, since y is not periodic for ψ, (C5) implies that the period τ of the H-orbit of z goes to infinity as ε goes to zero. Therefore, (C2)–(C5) and (10) imply that if $\varepsilon > 0$ is sufficiently small, then the period τ is greater than T and

$$\max_{i \in \bar{S}} \frac{1}{\tau} \int_0^\tau g_i(\xi_s z) \, ds \leqslant -\eta/4. \tag{12}$$

Hence for $\varepsilon > 0$ sufficiently small H lies in $\mathcal{N}$ and the flow of $\dot{x} = H(x)$ has a periodic orbit whose transverse Lyapunov exponents are strictly negative.

5.3. *An Ergodic Closing Lemma*

In this section, we discuss how the proof of the ergodic closing lemma for flows given by Wen [35, Sect. 4] can be adapted to prove Theorem 5.1. To this end, we prove a more general result for flows on $\mathbf{R}^n$ and use this result to prove Theorem 5.1. The need for this generalization stems from the fact that the perturbations required in Theorem 5.1 need to leave the faces of $\mathbf{R}^n_+$ invariant.

Let $G: \mathbf{R}^n \to \mathbf{R}^n$ be a C^1 function that generates a flow ψ. Let μ be an ergodic measure for ψ with compact support. Let $K \subset \mathbf{R}^n$ be a compact neighborhood of $\text{supp}(\mu)$. Let $\varepsilon > 0$, $\delta > 0$, and $L \geqslant 1$ be given. We say a point $y \in \text{supp}(\mu) \backslash \text{Sing}(G)$ is $(G, K, \varepsilon, L, \delta)$-*strongly closable* if there are a C^1 vector field $H: \mathbf{R}^n \to \mathbf{R}^n$, a point $z \in \mathbf{R}^n$, and a real number $\tau > 0$ such that

1. $\|H(x) - G(x)\| + \|DH(x) - DG(x)\| < \varepsilon$ for all $x \in K$.

2. $\xi_\tau z = z$, where ξ_t is the flow of $\dot{x} = H(x)$.

3. $\|\xi_t z - \psi_t y\| < \delta$ for all $0 \leqslant t \leqslant \tau$.

4. $H = G$ for all $x \in \mathbf{R}^n \backslash B(\psi_{[-L, 0]} y, \delta)$.

Using the proof of Wen's ergodic closing lemma for flows [35], we prove the following result.

THEOREM 5.2. *There exists a Borel set $U \subset \text{supp}(\mu)$ satisfying $\mu(U \cup \text{Sing}(G)) = 1$ such that for every $\varepsilon > 0$ and $x \in U$, there is a $L \geqslant 1$ such that x is $(G, K, \varepsilon, L, \delta)$-strongly closable for all $\delta > 0$.*

This statement of the ergodic closing lemma is more complicated than the usual statement of the ergodic closing lemma as it describes more explicitly on what set the perturbation takes place. Prior to proving this theorem, we show how Theorem 5.2 can be used to prove Theorem 5.1.

Proof (Theorem 5.1). Let $G: \mathbf{R}_+^n \to \mathbf{R}^n$ be a C^1 function such that $G_i(x) = 0$ whenever $x_i = 0$. Since G is C^1 on $\mathbf{R}_+^n$ it can be extended to a C^1 function of $\mathbf{R}^n$ to $\mathbf{R}^n$. Let ψ be the flow generated by G. Let μ be an ergodic measure for ψ with compact support such that $\mathrm{supp}(\mu) \subset \mathbf{R}_+^n$. Ergodicity of μ implies there is a set $S \subseteq \{1, ..., n\}$ such that $\mu(\mathrm{int}\ \mathbf{R}_+^S) = 1$. If $S = \varnothing$, then the proof reduces to noting that $\mu(\{0\}) = 1$ and $0 \in \mathrm{Sing}(G)$. Assume that $S \neq \varnothing$. Let $K \subset \mathbf{R}^S$ be a compact neighborhood of $\mathrm{supp}(\mu)$. Theorem 5.2 applied to $G^S = G \mid \mathbf{R}^S$ implies that there exists a set $U \subset \mathrm{int}\ \mathbf{R}_+^S$ satisfying $\mu(U) = \mu(\mathbf{R}^S \backslash \mathrm{Sing}(G))$ such that for every $\varepsilon > 0$ and $x \in U$, there exists an $L \geq 1$ such that x is $(G^S, K, \varepsilon, L, \delta)$-strongly closable for all $\delta > 0$. Since $\psi_{[-L, 0]} x \subset \mathrm{int}\ \mathbf{R}_+^S$ and L does not depend on δ for a given $x \in U$, we can choose $\delta > 0$ sufficiently small so that $B(\psi_{[-L, 0]} x, \delta) \subset \mathrm{int}\ \mathbf{R}_+^S$. Hence, for sufficiently small $\delta > 0$ the perturbation H^S that closes the orbit of x satisfies (C1)–(C5). ∎

Proof (Theorem 5.2). Let $G: \mathbf{R}^n \to \mathbf{R}^n$ be a C^1 vector field that generates the flow ψ. Let μ be an ergodic measure with compact support and let $K \subset \mathbf{R}^n$ be a compact neighborhood of $\mathrm{supp}(\mu)$. To prove this version of the ergodic closing lemma, we go through a series of reductions that differs slightly from the series of reductions used by Wen [35].

Let $\Sigma(\varepsilon, L, \delta)$ denote the set of $(G, K, \varepsilon, L, \delta)$-strongly closable points. Let $U \subseteq \mathrm{supp}(\mu)$ be the set of points such that for every $x \in U$ and $\varepsilon > 0$, there exists an $L \geq 1$ such that x is $(G, K, \varepsilon, L, \delta)$-stongly closable for all $\delta > 0$. Let $\varepsilon_k \downarrow 0$, $\delta_k \downarrow 0$ and $L_k \uparrow \infty$ be monotonic sequences of positive reals. Notice that $U = \bigcap_i \bigcup_j \bigcap_k \Sigma(\varepsilon_i, L_j, \delta_k)$. Since $\bigcup_j \bigcap_k \Sigma(\varepsilon_{i+1}, L_j, \delta_k) \subseteq \bigcup_j \bigcap_k \Sigma(\varepsilon_i, L_j, \delta_k)$ for any positive integer i, proving that $\mu(U \cup \mathrm{Sing}(G)) = 1$ reduces to proving that

$$\mu\left(\bigcup_i \bigcap_j \Sigma(\varepsilon, L_i, \delta_j)\right) = \mu(\mathbf{R}^n \backslash \mathrm{Sing}(G)) \tag{13}$$

for any $\varepsilon > 0$.

The key to the proof of (13) is a ratio version of the C^1 closing lemma. To state this version of the closing lemma, we make the following definitions. Given any $x \in \mathbf{R}^n \backslash \mathrm{Sing}(G)$ and small $a > 0$, let $\Pi(x, a)$ denote a local cross section to the flow at the point x with radius a. Given $r > 0$, $\rho > 2$, $L \geq 1$, and $\delta > 0$, define a point $x \in \mathbf{R}^n \backslash \mathrm{Sing}(G)$ to be $(G, K, \varepsilon, L, \delta, r, \rho)$-*responsible* if whenever y and $\psi_T y$ are both in $\Pi(x, b)$ for some $0 < b \leq r$

and some $T > 2b$, there is a C^1 function $H: \mathbf{R}^n \to \mathbf{R}^n$ and there are $0 \leqslant T_1 < T_2 \leqslant T$ such that $\|H(x) - G(x)\| + \|DH(x) - DG(x)\| < \varepsilon$ for all $x \in K$, $\psi_{T_1} y$ and $\psi_{T_2} y$ are both in $\Pi(x, \rho b)$, and for any $z \in \psi_{[T_1 - b, T_1 + b]} y$, we have

1. $\xi_{T_2 - T_1} z = z$ where ξ_t is the flow generated by $\dot{x} = H(x)$.
2. $\|\psi_t z - \xi_t z\| < \delta$ for all $0 \leqslant t \leqslant T_2 - T_1$.
3. $G = H$ on $\mathbf{R}^n \backslash B(\psi_{[-L, 0]} x, \delta)$.

Let $R(\varepsilon, L, \delta, r, \rho)$ denote the set of $(G, K, \varepsilon, L, \delta, r, \rho)$-responsible points.

As noted by Wen (see Theorems 4.1 and 4.2 and the remark following Theorem 4.2 in [35]), the C^1 closing lemma can be formulated in the following manner.

THEOREM 5.3 (The C^1 Closing Lemma, Ratio Version).   *Given $\varepsilon > 0$ and $x \in \text{supp}(\mu) \backslash \text{Sing}(G)$, there exists $L \geqslant 1$ (usually large) such that for every $\delta > 0$, there are an $r > 0$ (usually small) and $\rho > 2$ (usually large) such that x is $(G, K, \varepsilon, L, \delta, r, \rho)$-responsible.*

This statement of the C^1 closing lemma is more complex than the usual statement as it specifies how the closing of an orbit is accomplished. In particular, it says if an orbit hits a sufficiently small b-box of a $(G, K, \varepsilon, L, \delta, r, \rho)$-responsible point x twice, then there will be a $(G, K, \varepsilon, L, \delta)$-strongly closable segment that hits the ρb-box of x at some time in between.

The C^1 closing lemma implies that if we have monotonic sequences of positive reals $r_k \downarrow 0$ and $\rho_k \uparrow \infty$, then

$$\mu(\mathbf{R}^n \backslash \text{Sing}(G)) = \mu\left(\bigcup_i \bigcap_j \bigcup_{k, l} R(\varepsilon, L_i, \delta_j, r_k, \rho_l)\right) \tag{14}$$

for any $\varepsilon > 0$. Lemma 4.3, Lemma 4.4, and the proof of (E4) in [35] imply that

$$\mu(R(\varepsilon, L, \delta, r, \rho) \backslash \Sigma(\varepsilon, L, \delta)) = 0 \tag{15}$$

for any choice of $L \geqslant 1$, $r > 0$, $\rho > 2$, $\varepsilon > 0$ and $\delta > 0$. Since

$$R(\varepsilon, L, \delta, r_k, \rho) \subseteq R(\varepsilon, L, \delta, r_{k+1}, \rho) \quad \text{and}$$

$$R(\varepsilon, L, \delta, r, \rho_k) \subseteq R(\varepsilon, \delta, L, r, \rho_{k+1})$$

for any positive integer k, (15) implies that

$$\mu(R(\varepsilon, L, \delta)) \leqslant \mu(\Sigma(\varepsilon, L, \delta)), \tag{16}$$

where we define

$$R(\varepsilon, L, \delta) = \bigcup_{i, j} R(\varepsilon, L, \delta, L, r_i, \rho_j)$$

for any $\varepsilon > 0$, $L \geqslant 1$, and $\delta > 0$. Since $\Sigma(\varepsilon, L, \delta_{k+1}) \subseteq \Sigma(\varepsilon, L, \delta_k)$ and $R(\varepsilon, L, \delta_{k+1}) \subseteq R(\varepsilon, L, \delta_k)$ for any positive integer k, inequality (16) implies that

$$\mu \left(\bigcap_i R(\varepsilon, L, \delta_i) \right) \leqslant \mu \left(\bigcap_i \Sigma(\varepsilon, L, \delta_i) \right) \tag{17}$$

for any choice of $L \geqslant 1$ and $\varepsilon > 0$. Since $\bigcap_i \Sigma(\varepsilon, L_k, \delta_i) \subseteq \bigcap_i \Sigma(\varepsilon, L_{k+1}, \delta_i)$ and $\bigcap_i R(\varepsilon, L_k, \delta_i) \subseteq \bigcap_i R(\varepsilon, L_{k+1}, \delta_i)$ for any positive integer k, (14) and (17) imply that

$$\mu(\mathbf{R}^n \backslash \mathrm{Sing}(G)) = \mu \left(\bigcup_i \bigcap_j R(\varepsilon, L_i, \delta_j) \right) \leqslant \mu \left(\bigcup_i \bigcap_j \Sigma(\varepsilon, L_i, \delta_j) \right),$$

which completes the proof of (13). ∎

6. PROOF OF THEOREM 4.3

Let $F \in \mathscr{P}_n^r$ be such that $\dot{x} = F(x)$ generates a dissipative flow ϕ. Let Λ be the maximal compact invariant set for $\phi \mid \partial \mathbf{R}_+^n$. Let $M_1, ..., M_k$ be a Morse decomposition of Λ. The proof of Theorem 4.3 consists of two parts. First, we prove that if F is not permanent, then there exists a $j \in \{1, ..., k\}$ such that $\mathscr{M}_{\mathrm{inv}}(F, M_j)$ contains a saturated invariant measure. Hence, it follows contrapositively that if each M_j is unsaturated, then F is permanent. Second, we prove that if each M_j is unsaturated, then there exists a C^1 neighborhood $\mathscr{N} \subset \mathscr{P}_n^1$ of F such that every $G \in \mathscr{N}$ has an unsaturated Morse decomposition. From these two facts it follows that if each M_j is unsaturated, then F is robustly permanent.

6.1. *Not Permanent Implies Existence of a Saturated Measure*

Assume that F is not permanent. We will show that there exists a saturated invariant measure $\mu \in \mathscr{M}_{\mathrm{inv}}(F, M_j)$ for some $j \in \{1, ..., k\}$. As F is not permanent, either condition 1 or condition 2 of Theorem 4.2 is not satisfied. In either case, there are a $j \in \{1, ..., k\}$ and a sequence $\{x(m)\}_{m=1}^{\infty}$ in int $\mathbf{R}_+^n$ such that

$$\mathrm{dist}(\phi_t x(m), M_j) < \frac{1}{m} \qquad \text{for all} \quad t \geqslant 0 \quad \text{and} \quad m \geqslant 1. \tag{18}$$

Let $f = (f_1, ..., f_n)$ be defined as in (1). Since $\ln([\phi_t x(m)]_i/[x(m)]_i) = \int_0^t f_i(\phi_s x(m)) \, ds$ for all $1 \leqslant i \leqslant n$, $t \in \mathbf{R}$ and $m \geqslant 1$, inequality (18) implies that

$$\limsup_{t \to \infty} \frac{1}{t} \int_0^t f_i(\phi_s x(m)) \, ds \leqslant 0 \qquad \text{for all} \quad m \geqslant 1 \quad \text{and} \quad 1 \leqslant i \leqslant n.$$

Choose a sequence $t(m)$ of positive reals such that $\lim_{m \to \infty} t(m) = \infty$ and

$$\frac{1}{t(m)} \int_0^{t(m)} f_i(\phi_s x(m)) \, ds \leqslant \frac{1}{m} \qquad \text{for all} \quad m \geqslant 1 \quad \text{and} \quad 1 \leqslant i \leqslant n. \quad (19)$$

Define a sequence of Borel probability measures μ_m on $\mathbf{R}_+^n$ by

$$\int h \, d\mu_m = \frac{1}{t(m)} \int_0^{t(m)} h(\phi_s x(m)) \, ds$$

for any continuous function $h: \mathbf{R}_+^n \to \mathbf{R}$. Inequality (18) implies that μ_m lies in the space $\mathscr{M}(C)$ of Borel probability measures with support in the compact set $C = \{x \in \mathbf{R}_+^n : \operatorname{dist}(x, M_j) \leqslant 1\}$. Weak* compactness of $\mathscr{M}(C)$ implies that by passing to a subsequence if necessary there exists a Borel probability measure $\mu \in \mathscr{M}(C)$ such that μ_m converges in the weak* topology to μ as $m \to \infty$. To show that μ is an invariant measure for ϕ, it suffices to verify that $\int h \circ \phi_T \, d\mu = \int h \, d\mu$ for any continuous function $h: \mathbf{R}_+^n \to \mathbf{R}$ and $T \in \mathbf{R}$. If we write $\|h\|_C = \sup_{x \in C} |h(x)|$, then

$$\left| \int (h \circ \phi_T - h) \, d\mu \right| = \lim_{m \to \infty} \frac{1}{t(m)} \left| \int_0^{t(m)} h(\phi_{T+s} x(m)) - h(\phi_s x(m)) \, ds \right|$$

$$= \lim_{m \to \infty} \frac{1}{t(m)} \left| \int_0^T h(\phi_{t(m)+s} x(m)) - h(\phi_s x(m)) \, ds \right|$$

$$\leqslant \lim_{m \to \infty} \frac{2T \|h\|_C}{t(m)} = 0.$$

Hence μ is an invariant measure. Inequality (18) and weak* convergence imply that $\mu \in \mathscr{M}_{\text{inv}}(F, M_j)$. Inequality (19) and weak* convergence imply that μ is saturated.

6.2. Openness of Unsaturated Morse Decompositions

In the second part of the proof, we prove that if the Morse decomposition $\{M_1, ..., M_k\}$ for $F \mid \Lambda$ is unsaturated, then there exists a C^1 neighborhood $\mathscr{N} \subset \mathscr{P}_n^1$ of F such that each $G \in \mathscr{N}$ admits an unsaturated Morse decomposition on its boundary. The proof of this fact breaks down into two steps. First, let $V_1, ..., V_k$ be pairwise disjoint compact subsets of

$\partial \mathbf{R}_+^n$ that are isolating neighborhoods of $M_1, ..., M_k$ for $\phi \mid \partial \mathbf{R}_+^n$. We prove that there is a C^1 neighborhood $\mathcal{N} \subset \mathcal{P}_n^1$ of F such that every $G \in \mathcal{N}$ generates a dissipative flow ϕ^G and such that the maximal compact invariant set $\Lambda(G)$ of $\phi^G \mid \partial \mathbf{R}_+^n$ admits a Morse decomposition $\{M_1(G), ..., M_k(G)\}$ satisfying $M_j(G) \subset V_j$ for all $1 \leq j \leq k$. Second, we prove that if there exist a sequence $F^m \in \mathcal{N}$ that converges in the C^1 topology to F and a $j \in \{1, ..., k\}$ such that $\mathcal{M}_{\mathrm{inv}}(F^m, M_j(F^m))$ contains a saturated measure for each m, then $\mathcal{M}_{\mathrm{inv}}(F, M_j)$ contains a saturated measure. The first fact and the contrapositive of the second fact imply that if the M_j are unsaturated, then there exists a neighborhood of F such that every element of this neighborhood admits an unsaturated Morse decomposition for $\partial \mathbf{R}_+^n$.

The first step is accomplished by the following proposition.

PROPOSITION 6.1. *Let $F \in \mathcal{P}_n^1$ be such that $\dot{x} = F(x)$ generates a dissipative flow ϕ. Let Λ be the maximal compact invariant set of $\phi \mid \partial \mathbf{R}_+^n$, let $\{M_1, ..., M_k\}$ be a Morse decomposition of Λ, and let $\{V_j\}_{j=1}^k$ be a collection of compact pairwise disjoint sets in $\partial \mathbf{R}_+^n$ such that each V_j is an isolating neighborhood for M_j. Then there exists a C^1 neighborhood $\mathcal{N} \subset \mathcal{P}_n^1$ of F such that for every $G \in \mathcal{N}$*

  1. *$\dot{x} = G(x)$ generates a dissipative flow ϕ^G.*

  2. *The maximal compact invariant set $\Lambda(G)$ for $\phi^G \mid \partial \mathbf{R}_+^n$ admits a Morse decomposition $\{M_j(G)\}_{j=1}^k$.*

  3. *$M_j(G) \subset V_j$ for each $j \in \{1, ..., k\}$.*

Proof. We need two lemmas. The proof of the first lemma follows from the proof of [36, Theorem 3.2] adapted to manifolds with corners.

LEMMA 6.1. *Let $X = \mathbf{R}_+^n$ or $\partial \mathbf{R}_+^n$. Let $A \subset X$ be a compact attractor for $\phi \mid X$ with basin of attraction $U \subseteq X$. Then there exists a C^∞ function $W: U \to [0, \infty)$ such that*

  (i)   *$W^{-1}(0) = A$.*

  (ii) *$W^{-1}([0, c])$ is compact for all $c \geq 0$.*

  (iii) *$DW(x) F(x) < 0$ for all $x \in U \backslash A$.*

  (iv) *$W(x) \to \infty$ as $x \to \partial U$ or $|x| \to \infty$.*

LEMMA 6.2. *There exists a C^∞ function $L: \partial \mathbf{R}_+^n \to [1, \infty)$ such that*

  (i)   *$L^{-1}(j) = M_j$ for all $1 \leq j \leq k$.*

  (ii) *$DL(x) F(x) < 0$ for all $x \in \partial \mathbf{R}_+^n \backslash \bigcup_{j=1}^k M_j$.*

  (iii) *$L^{-1}([1, c])$ is compact for all $c \geq 1$.*

Proof. Since ϕ is dissipative, the maximal compact invariant set Λ for $\phi \mid \partial \mathbf{R}_+^n$ is a global attractor for $\phi \mid \partial \mathbf{R}_+^n$. Lemma 6.1 implies there exists a C^∞ function $W: \partial \mathbf{R}_+^n \to \mathbf{R}_+$ that satisfies (i)–(iv) of Lemma 6.1 with $A = \Lambda$. Let $\rho: \partial \mathbf{R}_+^n \to [0, 1]$ be a C^∞ function such that $\rho^{-1}(1) = W^{-1}([0, 1])$ and $\rho^{-1}(0) = W^{-1}([2, \infty))$. Let ψ be the flow on $\partial \mathbf{R}_+^n$ generated by $\dot{x} = \rho(x) F(x)$. Let $Y = W^{-1}([0, 3])$. Y is a compact manifold with corners. The set $M_{k+1} = W^{-1}([2, 3])$ consists of equilibria for ψ and is a repellor for $\psi \mid Y$. Therefore, $\{M_1, ..., M_{k+1}\}$ is a Morse decomposition for $\psi \mid Y$. A result of Nitecki and Shub [25, Proposition 6] implies there exists a C^∞ function $\tilde{L}: Y \to [1, k+1]$ such that $\tilde{L}^{-1}(j) = M_j$ for $1 \leqslant j \leqslant k+1$ and $D\tilde{L}(x) F(x) < 0$ for all $x \in Y \backslash \bigcup_{j=1}^{k+1} M_j$. Since $\tilde{L}^{-1}(k+1) = M_{k+1}$ we can extend $\tilde{L}$ smoothly to $\partial \mathbf{R}_+^n$ by setting $\tilde{L}(x) = k+1$ for all $x \in \partial \mathbf{R}_+^n \backslash Y$. Defining $L(x) = \tilde{L}(x) + W(x)$ completes the proof of the lemma. ∎

Returning to the proof of Proposition 6.1, let $A \subset \mathbf{R}_+^n$ be a compact global attractor for ϕ. Lemma 6.1 implies that there exists a C^∞ function $W: \mathbf{R}_+^n \to \mathbf{R}_+$ satisfying (i)–(iv) of Lemma 6.1 with $X = \mathbf{R}_+^n$. Since $\{M_1, ..., M_k\}$ is a Morse decomposition for Λ, Lemma 6.2 implies that there is a C^∞ function $L: \partial \mathbf{R}_+^n \to [1, \infty)$ satisfying (i)–(iii) of Lemma 6.2. Choose $0 < \delta < 1/2$ sufficiently small so that $L^{-1}([j-\delta, j+\delta]) \subset V_j$ for all $1 \leqslant j \leqslant k$. Let $\mathscr{N} \subset \mathscr{P}_n^1$ be a neighborhood of F such that every $G \in \mathscr{N}$ satisfies

(P1) $DW(x) G(x) < 0$ for all $x \in \mathbf{R}_+^n \backslash W^{-1}([0, 1])$.

(P2) $DL(x) G(x) < 0$ for all $x \in \partial \mathbf{R}_+^n \backslash \bigcup_{j=1}^k L^{-1}([j-\delta, j+\delta])$.

(P1) implies that $\dot{x} = G(x)$ generates a dissipative flow ϕ^G on $\mathbf{R}_+^n$ for every $G \in \mathscr{N}$. Let $\Lambda(G) \subset \partial \mathbf{R}_+^n$ denote the maximal compact set for $\phi^G \mid \partial \mathbf{R}_+^n$. (P2) implies that for each $G \in \mathscr{N}$, the maximal compact invariant sets $M_j(G)$ of $\phi^G \mid L^{-1}((j-\delta, j+\delta))$ define a Morse decomposition for $\Lambda(G)$. ∎

Let $\mathscr{N} \subset \mathscr{P}_n^1$ be the neighborhood of F given by Proposition 6.1. Now assume that there exists a sequence $\{F^m\}_{m=1}^\infty$ in $\mathscr{N}$ such that F^m converges in the C^1 topology to F and an integer $j \in \{1, ..., k\}$ such that for each $m \geqslant 1$ there is a F^m-saturated invariant measure $\mu_m \in \mathscr{M}_{\mathrm{inv}}(F^m, M_j(F^m))$. We will show that there exists a F-saturated invariant measure $\mu \in \mathscr{M}_{\mathrm{inv}}(F, M_j)$.

Let ϕ^m denote the flow generated by $\dot{x} = F^m(x)$. Since the support of each μ_m is contained in the compact set V_j, weak* compactness implies that by passing to a subsequence if necessary μ_m converges to a Borel probability measure μ with support in V_j. To see that μ is ϕ invariant, it

suffices to show that $\int h \circ \phi_T \, d\mu = \int h \, d\mu$ for all continuous functions
$h: \mathbf{R}^n_+ \to \mathbf{R}$ and $T \in \mathbf{R}$. Notice that

$$\left| \int (h \circ \phi_T - h) \, d\mu \right| = \limsup_{m \to \infty} \left| \int (h \circ \phi_T - h) \, d\mu_m \right|$$

$$\leqslant \limsup_{m \to \infty} \int |h \circ \phi_T - h \circ \phi^m_T| \, d\mu_m + \left| \int (h \circ \phi^m_T - h) \, d\mu_m \right|$$

$$= 0,$$

where the last line follows from uniform convergence of F^m to F on V_j and
ϕ^m-invariance of μ_m. Hence μ is ϕ-invariant. Since the maximal compact
invariant set for ϕ restricted to V_j is M_j, it follows that $\mu \in \mathcal{M}_{\mathrm{inv}}(F, M_j)$.

Let $f^m = (f^m_1, ..., f^m_n)$ be defined by

$$f^m_i(x) = \begin{cases} \dfrac{F^m_i(x)}{x_i} & \text{if} \quad x_i \neq 0 \\[2ex] \dfrac{\partial F^m_i}{\partial x_i}(x) & \text{else.} \end{cases}$$

As noted earlier, the f^m_i are continuous functions. C^1 convergence of F^m to
F implies that

$$\lim_{m \to \infty} \sup_{x \in V_j} \| f^m(x) - f(x) \| = 0. \tag{20}$$

Weak* convergence of μ_m to μ implies that for all $1 \leqslant i \leqslant n$

$$\int f_i \, d\mu = \lim_{m \to \infty} \int f_i - f^m_i \, d\mu_m + \int f^m_i \, d\mu_m \leqslant 0,$$

where the last inequality follows from (20) and the fact that μ_m is
F^m-saturated for all m. Hence $\mu \in \mathcal{M}_{\mathrm{inv}}(F, M_j)$ is an F-saturated invariant
measure.

7. APPLICATIONS

7.1. *Lotka–Volterra Systems*

Consider the special case when $F(x) = \mathrm{diag}(x)(Ax + b)$, where A is an
$n \times n$ matrix, $b \in \mathbf{R}^n$, and $\mathrm{diag}(x)$ is an $n \times n$ diagonal matrix whose ith
diagonal entry equals x_i. In this case, $\dot{x} = F(x)$ is a Lotka–Volterra equa-
tion. Permanence of Lotka–Volterra equations has been studied extensively

with great success [9]. The key observation for Lotka–Volterra systems is the following lemma.

LEMMA 7.1.   *Assume that $F(x) = \mathrm{diag}(x)(Ax + b)$ with A an $n \times n$ matrix and $b \in \mathbf{R}^n$ is such that $\dot{x} = F(x)$ generates a dissipative flow ϕ. Let μ be an ergodic measure for ϕ with compact support. Then there exist $S \subseteq \{1, ..., n\}$ and an equilibrium $\bar{x} \in \mathrm{int}\ \mathbf{R}_+^S$ for ϕ such that $\mu(\mathrm{int}\ \mathbf{R}_+^S) = 1$ and*

$$\int (Ax + b)\, d\mu(x) = A\bar{x} + b.$$

Proof.   Ergodicity of μ implies that there exists a subset $S \subseteq \{1, ..., n\}$ such that $\mu(\mathrm{int}\ \mathbf{R}_+^S) = 1$. Define

$$\bar{x} = \int x\, d\mu(x).$$

Linearity implies that $\int (Ax + b)\, d\mu(x) = A\bar{x} + b$. Lemma 5.1 implies that $[A\bar{x}]_i + b_i = 0$ for all $i \in S$. Since $\bar{x}_i = 0$ for all $i \notin S$, it follows that $\bar{x}$ is an equilibrium for ϕ.   ∎

Lemma 7.1 implies that verifying whether a compact invariant set for a Lotka–Volterra system is unsaturated reduces to verifying whether a set of equilibria form an unsaturated invariant set. To illustrate the utility of this fact, we derive a sufficient condition for robust permanence under the assumption that there are only a finite number of equilibria on the boundary. This additional assumption holds for an open and dense set of A and b.

THEOREM 7.2.   *Assume that $F(x) = \mathrm{diag}(x)(Ax + b)$ with A an $n \times n$ matrix and $b \in \mathbf{R}^n$ is such that $\dot{x} = F(x)$ generates a dissipative flow ϕ. Let $f(x) = Ax + b$. If ϕ only has a finite number of equilibria $\{p_1, ..., p_k\}$ that lie in $\partial \mathbf{R}_+^n$ and*

$$\min_{a \in \varDelta}\ \max_{1 \leqslant i \leqslant n}\ \sum_{j=1}^{k} a_j f_i(p_j) > 0,$$

where $\varDelta = \{a \in \mathbf{R}_+^k : \sum_{j=1}^{k} a_j = 1\}$, then f is C^1 robustly permanent.

The condition in Theorem 7.1 is similar to other linear-programming problems associated with permanence [14]. However, unlike these permanence results, the condition in Theorem 7.1 ensures that the system remains permanent following small nonlinear perturbations of the linear per-capita growth function.

SEBASTIAN J. SCHREIBER

Proof. Let $\Lambda \subset \partial \mathbf{R}_+^n$ be the maximal compact invariant set of $\phi \mid \partial \mathbf{R}_+^n$. The ergodic decomposition theorem [21, Chap. II, Theorem 6.4] implies that every invariant probability measure $\mu \in \mathscr{M}_{\text{inv}}(F, \Lambda)$ with compact support in $\partial \mathbf{R}_+^n$ satisfies

$$\int h \, d\mu = \int \left(\int h \, d\eta_x \right) d\mu(x)$$

for any continuous function $h: \mathbf{R}_+^n \to \mathbf{R}$ where $\eta_x \in \mathscr{M}_{\text{erg}}(F, \Lambda)$ μ-almost surely. Lemma 7.1 implies that for every ergodic measure η_x there exists $J(x) \in \{1, ..., k\}$ such that $\int f \, d\eta_x = f(p_{J(x)})$. If $a_j = \mu(\{x : J(x) = j\})$ for $1 \leqslant j \leqslant k$, then

$$\int f \, d\mu = \int f(p_{J(x)}) \, d\mu(x) = \sum_{j=1}^k a_j f(p_j).$$

Hence,

$$\min_{a \in \Delta} \max_{1 \leqslant i \leqslant n} \sum_{j=1}^k a_j f_i(p_j) \leqslant \min_{\mu \in \mathscr{M}_{\text{inv}}(F, \Lambda)} \max_{1 \leqslant i \leqslant n} \int f_i \, d\mu.$$

On the other hand, given $a \in \Delta$, the probability measure $\mu = \sum_{j=1}^k a_j \delta_{p_j}$ lies in $\mathscr{M}_{\text{inv}}(F, \Lambda)$. Hence,

$$\min_{a \in \Delta} \max_{1 \leqslant i \leqslant n} \sum_{j=1}^k a_j f_i(p_j) = \min_{\mu \in \mathscr{M}_{\text{inv}}(F, \Lambda)} \max_{1 \leqslant i \leqslant n} \int f_i \, d\mu.$$

Applying Theorem 4.3 with the trivial Morse decomposition $\{M_1 = \Lambda\}$ of Λ completes the proof. ∎

7.2. *Food Chain Models*

As an application of our main results, we consider models of *food chains*, a collection of populations where the ith population consumes the $(i-1)$th population and is consumed by the $(i+1)$th population [20]. Food chain models represent a fundamental ecological unit whose dynamics has been studied extensively [4, 6, 18, 19, 22, 24, 27]. We consider a general model, $F \in \mathscr{P}_n^r$ that is based on two assumptions where $f = (f_1, ..., f_n)$ is defined in (1).

    (A1)   For any $i \geqslant 2$, $f_i(x) < 0$ whenever $x_{i-1} = 0$.

    (A2) $\dot{x} = F(x)$ generates a dissipative flow ϕ.

Assumption (A1) asserts that in the absence of the $(i-1)$th population for $i \geqslant 2$, the ith 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 autotrophic population (e.g., a population of plants) whose resources are not explicitly modeled. Models that satisfy (A1) and (A2) include the standard food chain models in which each predator only feeds on the trophic level below.

For food chain models, we can use Theorems 4.1 and 4.3 to characterize C^r robust permanence. By an abuse of notation, for any $1 \leqslant m \leqslant n$ we let $\mathbf{R}_+^m$ denote either the positive cone of m-dimensional Euclidean space or the m-dimensional face $\mathbf{R}_+^{\{1, \dots, m\}}$ of $\mathbf{R}_+^n$ depending on the context. In this vein, we let $\mathbf{R}_+^0$ denote $\{0\} = \mathbf{R}_+^\varnothing$.

THEOREM 7.2. *Let $F \in \mathscr{P}_n^r$ with $r \geqslant 1$ be such that F satisfies* (A1)–(A2). *Let ϕ be the flow generated by $\dot{x} = F(x)$ and Λ be the maximal compact invariant set for $\phi \mid \partial \mathbf{R}_+^n$. Then the following are equivalent*

1. *F is C^r robustly permanent.*

2. *Λ is weakly unsaturated.*

3. *There exist compact sets $A_0 = \{0\} = \mathbf{R}_+^0$, $A_1 \subset \operatorname{int} \mathbf{R}_+^1$, ..., $A_{n-1} \subset \operatorname{int} \mathbf{R}_+^{n-1}$, and $t > 0$ such that for each $m \in \{0, 1, \dots, n-1\}$, A_m is an attractor for $\phi \mid \mathbf{R}_+^m$ with basin of attraction $\operatorname{int} \mathbf{R}_+^m$ and*

$$\min_{x \in BC(F, A_m)} \int_0^t f_{m+1}(\phi_s x) \, ds > 0 \tag{21}$$

where $BC(F, A_m)$ is the Birkhoff center of $\phi \mid A_m$.

Remark 7.1. Three-species food chain models can exhibit "chaotic" behavior [18, 24]. Hence, four-species food chain models can have an infinite number of periodic orbits in the boundary and, consequently, can support an infinite number of ergodic measures.

Proof. Let $F \in \mathscr{P}_n^r$ with $r \geqslant 1$ be such that F satisfies (A1) and (A2). By Theorem 4.1, assertion 1 implies assertion 2.

To prove that assertion 3 implies assertion 1 and that assertion 2 implies assertion 3, we prove the following key lemma.

LEMMA 7.2. *Let $F \in \mathscr{P}_n^r$ with $r \geqslant 1$ be such that F satisfies* (A1) *and* (A2). *Assume that Λ is the maximal compact invariant set for $\phi \mid \partial \mathbf{R}_+^n$ and $\mu \in \mathscr{M}_{\mathrm{erg}}(F, \Lambda)$. Then*

(i) $\varLambda \subset \bigcup_{0 \leqslant m \leqslant n-1}$ int $\mathbf{R}_+^m$, *where* int $\mathbf{R}_+^0 = \{0\}$.

(ii) *There exists an* $m \in \{0, 1, ..., n-1\}$ *such that* $\mu(\text{int } \mathbf{R}_+^m) = 1$.

(iii) *If* $\max_{1 \leqslant i \leqslant n} \int f_i \, d\mu > 0$, *then* $\max_{1 \leqslant i \leqslant n} \int f_i \, d\mu = \int f_{m+1} \, d\mu$.

Proof. To prove (i), notice that for any $x \in \partial \mathbf{R}_+^n \setminus \bigcup_{0 \leqslant m \leqslant n-1}$ int $\mathbf{R}_+^m$, there is an $i \in \{2, ..., n\}$ such that $x_i > 0$ and $x_{i-1} = 0$. Assumption (A1) implies that for such an x and i, $f_i(\phi_t x) < 0$ for all $t \geqslant 0$. It follows for such an x that $\lim_{t \to \infty} \|\phi_{-t} x\| = \infty$ and, consequently, $x \notin \varLambda$.

Let $\mu \in \mathscr{M}_{\text{erg}}(F, \partial \mathbf{R}_+^n)$. Since μ is ergodic and $\text{supp}(\mu) \subseteq \varLambda \subset \bigcup_{0 \leqslant m \leqslant n-1}$ int $\mathbf{R}_+^m$, there exists an $m \in \{0, ..., n-1\}$ such that $\mu(\text{int } \mathbf{R}_+^m) = 1$. Lemma 5.1 implies that $\int f_i \, d\mu = 0$ for all $1 \leqslant i \leqslant m$. Assumption (A1) implies that $\int f_i \, d\mu < 0$ for all $i \geqslant m+2$. Hence, if $\max_{1 \leqslant i \leqslant n} \int f_i \, d\mu > 0$, then $\max_{1 \leqslant i \leqslant n} \int f_i \, d\mu = \int f_{m+1} \, d\mu$. ∎

Now, we prove that assertion 3 implies assertion 1. Assume that assertion 3 holds. Since the A_m are global attractors for $\phi \,|\, \text{int } \mathbf{R}_+^m$ for every $0 \leqslant m \leqslant n-1$, assertion (i) of Lemma 7.2 implies that $\{M_1 = A_{n-1}, M_2 = A_{n-2}, ..., M_n = A_0\}$ defines a Morse decomposition for the maximal compact invariant set $\varLambda$ for $\phi \,|\, \partial \mathbf{R}_+^n$. Lemma 3.2 and (21) imply that this Morse decomposition is unsaturated. Therefore, F is C^r robustly permanent by Theorem 4.3.

Finally, we prove that assertion 2 implies assertion 3 by proceeding inductively on the dimension n. When $n = 1$, it is clear that assertion 2 implies assertion 3. Let $k \geqslant 1$ be given. Assume that for any vector field in $\mathscr{P}_n^r$ with $n \leqslant k$ satisfying (A1) and (A2), assertion 2 implies assertion 3. Let $F \in \mathscr{P}_{k+1}^r$ be such that (A1) and (A2) are satisfied. Let ϕ be the flow of $\dot{x} = F(x)$ for this F and $\varLambda$ be the maximal compact invariant set for $\phi \,|\, \partial \mathbf{R}_+^{k+1}$. Let $f = (f_1, ..., f_{k+1})$ be defined as in (1). Assume that $\varLambda$ is weakly unsaturated. We need to prove that assertion 3 holds for this choice of F. Given any $m \in \{1, ..., k\}$, define the embedding $e^m: \mathbf{R}^m \to \mathbf{R}^{k+1}$ by $(x_1, ..., x_m) \mapsto (x_1, ..., x_m, 0, ..., 0)$ and the projection $\pi^m: \mathbf{R}^{k+1} \to \mathbf{R}^m$ by $(x_1, ..., x_{k+1}) \mapsto (x_1, ..., x_m)$. For any $1 \leqslant m \leqslant k$, $F^m = \pi^m \circ F \circ e^m$ lies in $\mathscr{P}_m^r$ and the flow of $\dot{x} = F^m(x)$ is given by $\phi \,|\, \mathbf{R}_+^m$. Therefore, F^m satisfies (A1) and (A2), where $f^m = \pi^m \circ f \circ e^m$. Our assumption that $\varLambda$ is weakly unsaturated for F and Lemma 7.2 imply that

$$\inf_{\mu \in \mathscr{M}_{\text{erg}}(F^m, \varLambda \cap \partial \mathbf{R}_+^m)} \max_{1 \leqslant i \leqslant m} \int f_i^m \, d\mu > 0$$

whenever $1 \leqslant m \leqslant k$. Hence $\varLambda \cap \partial \mathbf{R}_+^m$ is weakly unsaturated for F^m whenever $1 \leqslant m \leqslant k$, and our inductive assumption implies that assertion 3 of the theorem holds for F^m with $1 \leqslant m \leqslant k$. We have proven that assertion 3 implies assertion 1. Hence, F^m is robustly permanent for all $1 \leqslant m \leqslant k$.

Permanence of F^m with $1 \leqslant m \leqslant k$ implies there is an compact attractor $A_m \subset \text{int } \mathbf{R}_+^m$ for $\phi \mid \mathbf{R}_+^m$ whose basin of attraction equals $\text{int } \mathbf{R}_+^m$. Set $A_0 = \{0\}$. Assertion (iii) of Lemma 7.2 and our assumption that $\varLambda$ is weakly unsaturated imply

$$\inf_{\mu \in \mathscr{M}_{\text{erg}}(F, A_m)} \int f_{m+1} \, d\mu = \inf_{\mu \in \mathscr{M}_{\text{erg}}(F, A_m)} \max_{1 \leqslant i \leqslant k+1} \int f_i \, d\mu > 0$$

for every $0 \leqslant m \leqslant k$. Lemma 3.3 implies that there exists $t > 0$ such that

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

for all $0 \leqslant m \leqslant k$. Hence we have shown that assertion 3 is satisfied for F. ∎

ACKNOWLEDGMENTS

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