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Kolmogorov Vector Fields with Robustly Permanent Subsystems

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The following results are proven. All subsystems of a dissipative Kolmogorov vector field $\dot{x}_i = x_i f_i(x)$ are robustly permanent if and only if the external Lyapunov exponents are positive for every ergodic probability measure μ with support in the boundary of the nonnegative orthant. If the vector field is also totally competitive, its carrying simplex is C^1. Applying these results to dissipative Lotka–Volterra systems, robust permanence of all subsystems is equivalent to every equilibrium x^* satisfying $f_i(x^*) > 0$ whenever $x_i^* = 0$. If in addition the Lotka–Volterra system is totally competitive, then its carrying simplex is C^1. © 2002 Elsevier Science (USA)

1. INTRODUCTION

A basic issue in community ecology is to understand how communities assemble from a fixed pool of species. In the framework of dynamical systems, this issue can be tackled as follows [8, 9]. Consider a pool of n species

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with densities given by the vector $x = (x_1, \ldots, x_n)$, with per-capita growth rates given by the function $f(x) = (f_1(x), \ldots, f_n(x))$ and whose dynamics are described by a system of ordinary differential equations of the form

$$\dot{x}_i = x_i f_i(x) \qquad 1 \le i \le n \tag{K}$$

on the nonnegative orthant $C := \{x \in \mathbb{R}^n : x_i \ge 0 \text{ for } 1 \le i \le n\}$. Using these Kolmogorov equations, theoretical ecologists study the community assembly process by identifying collections of species (i.e., subsets of $\{1, \ldots, n\}$) that can coexist and how transitions between communities occur due to the introduction of other species from the species pool. A precise mathematical formulation of this approach was developed in [14] when coexistence is equated with permanence or robust permanence. Permanence corresponds to the recovery of populations from large short-term perturbations of their densities. Recognizing that all models are approximations, robust permanence requires (K) to remain permanent following small structural perturbations of (K) [15]. The simplest possibility for community assembly occurs when the introduction of any new species from the species pool augments the existing community. Such species pools are in some sense the restoration an ecologist's dream as they are easy to reassemble [7]. In the framework of [14], these easily assembled species pools correspond to a system (K) such that every subsystem of (K) is robustly permanent. In this paper, we characterize such systems and show that when the system is also totally competitive, the associated carrying simplex is C^1. Applying these results to Lotka–Volterra systems, we show that our conditions reduce to algebraically verifiable conditions.

2. PRELIMINARIES

Given a Kolmogorov system (K) with $F(x) := (x_1 f_1(x), \ldots, x_n f_n(x))$ of class C^1, let $DF(x)$ denote the derivative of F. The local flow generated by (K) on C will be denoted by $\phi = \{\phi_t\}$. A subset $B \subseteq C$ is *invariant* if $\phi_t x \in B$ for all $(t, x) \in \mathbb{R} \times B$ for which $\phi_t x$ is defined. For $x \in C$ and $B \subseteq C$ the symbols $\omega(x)$, $\alpha(x)$, $\omega(B)$, $\alpha(B)$ have their usual meanings. An invariant subset B of a compact invariant set S is called an *attractor* (resp. a *repellor*) *relative to* S if there is a relative neighborhood U of B in S such that $\omega(U) = B$ (resp. $\alpha(U) = B$). For an attractor B relative to a compact invariant set S, its *dual repellor* is the (compact invariant) set $D = \{x \in S : \omega(x) \cap B = \emptyset\}$. The attractor *dual* to a repellor is defined in an analogous way. System (K) is *dissipative* if there is a compact set $B \subseteq C$ such that for each bounded $D \subseteq C$ its ω-limit set $\omega(D)$ is a nonempty subset of B. By standard results on global attractors, for a dissipative system (K) there exists a unique compact invariant set $\Gamma \subseteq C$ (the *global attractor* for (K)) such that $\omega(D) \subseteq \Gamma$ for each bounded $D \subseteq C$. A *Morse decomposition* of a compact invariant set B is a collection $\{M_1, \ldots, M_k\}$ of compact, pairwise disjoint, invariant sets in B such that for each $x \in B \setminus \bigcup_{i=1}^k M_i$ there are $l = l(x) > m = m(x)$ satisfying $\alpha(x) \subseteq M_l$ and $\omega(x) \subseteq M_m$.

For $I \subseteq \{1, \ldots, n\}$, let

$$\begin{aligned} C_I &:= \{x \in C : x_i = 0 \text{ for } i \in I\}, \\ C_I^\circ &:= \{x \in C_I : x_j > 0 \text{ for } j \notin I\}, \\ \partial C_I &:= C_I \setminus C_I^\circ. \end{aligned}$$

From the form of (K) it follows readily that C_I, ∂C_I, and C_I° are invariant. We denote by $(\mathrm{K})_I$ the restriction of (K) to C_I. Instead of $C_\emptyset^\circ$ and $\partial C_\emptyset$, we write C° and ∂C.

3. MAIN RESULTS

(K) is *permanent* if (K) is dissipative and there is an attractor $B \subseteq C^\circ$ such that $\omega(x) \subseteq B$ for all $x \in C^\circ$. (K) is *robustly permanent* if all C^1 vector fields $G(x) = (x_1 g_1(x), \ldots, x_n g_n(x))$ sufficiently close to F in the C^1 Whitney topology are permanent. We say (K) satisfies *property* (P) provided that $(\mathrm{K})_I$ is robustly permanent for all $I \subseteq \{1, \ldots, n\}$. Given an ergodic probability measure μ, let $S(\mu)$ denote the subset of $\{1, \ldots, n\}$ such that $\mu(C_{S(\mu)}^\circ) = 1$.

3.1. *A Characterization of* (P) *Systems*

In [15], the following necessary and sufficient criteria for robust permanence were described in terms of the average per-capita growth rates f_i with respect to ergodic probability measures μ supported in ∂C.

THEOREM 3.1 [15, Theorem 4.1]. *If* (K) *is* C^1 *and robustly permanent, then*

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

where the infimum is taken over all ergodic probability measures with support in ∂C.

THEOREM 3.2 [15, Theorem 4.3]. *If* (K) *is* C^1, *dissipative with global attractor* Γ, *and* $\Gamma \cap \partial C$ *admits a Morse decomposition* $\{M_1, \ldots, M_k\}$ *such that for each* M_j

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

where the minimum is taken over invariant probability measures with support in M_j, *then* (K) *is robustly permanent.*

Remark 3.1. Recently, Hirsch *et al.* [3] proved that when the conditions of Theorem 3.2 hold, (K) remains permanent following sufficiently small C^0-Lipschitz perturbations of (K).

The average per-capita growth rates are related to Lyapunov exponents as follows. Recall that Oseledec's multiplicative ergodic theorem [6, 13] implies that there exists a finite set of real numbers $\mathscr{L} \subset \mathbb{R}$ and a Borel set $O \subset C$ with $\mu(O) = 1$ such that for each $x \in O$ there is a splitting $\mathbb{R}^n = \bigoplus_{\lambda \in \mathscr{L}} E^\lambda(x)$ satisfying $D\phi_t(x)E^\lambda(x) = E^\lambda(\phi_t x)$ for all $t \in \mathbb{R}$ and $\lim_{t\to\pm\infty} \frac{1}{t} \log \|D\phi_t(x)v\| = \lambda$ for all $v \in E^\lambda(x)\setminus\{0\}$. 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). Since each face of C is ϕ-invariant, for each $i \in S(\mu)$ there is a Lyapunov exponent $\tau_i \in \mathscr{L}$ such that $E^{\tau_i}(x) \oplus C_{S(\mu)}$ spans $C_{S(\mu)\setminus\{i\}}$. Following Hofbauer [4], we call these exponents $\{\tau_i\}_{i\in S(\mu)}$ the *external Lyapunov exponents* for (ϕ, μ). The τ_i are called the transverse Lyapunov exponents in [15].

LEMMA 3.1 [15, Lemmas 5.1 and 5.2]. *For each ergodic probability measure μ with compact support in C,*

$$\tau_i = \int f_i \, d\mu \qquad \text{for all } i \in S(\mu)$$

and

$$\int f_i \, d\mu = 0 \qquad \text{for all } i \notin S(\mu).$$

Before stating our main result we state an important consequence of property (P). Let M_I denote the global attractor for ϕ restricted to C_I° whenever $(\mathrm{K})_I$ is permanent with $I \subseteq \{1, \ldots, n\}$.

PROPOSITION 3.1. *Let* (K) *be such that* $(\mathrm{K})_I$ *is permanent for all* $I \subseteq \{1, \ldots, n\}$. *Then the family* $\{M_I\}_{I\subseteq\{1,\ldots,n\}}$ *is a Morse decomposition for the global attractor* Γ.

Proof. Define the *k-skeleton*, $\partial_k C$, of C as the union of all k-dimensional faces of C, $\partial_k C = \bigcup_{\operatorname{card} I = n-k} C_I$. We prove that the collection $\{M_I\}_{\operatorname{card} I \geq n-k}$ is a Morse decomposition for $\partial_k C \cap \Gamma$ by induction on k. Clearly $M_{\{1,\ldots,n\}} = \{0\}$ is a Morse decomposition for $\partial_0 C \cap \Gamma = \{0\}$. Suppose that $\{M_I\}_{\operatorname{card} I \geq n-k+1}$ is a Morse decomposition of $\partial_{k-1} C \cap \Gamma$. We will show that $\{M_I\}_{\operatorname{card} I\geq n-k}$ is a Morse decomposition of $\partial_k C \cap \Gamma$. Given $J \subseteq \{1, \ldots, n\}$ with $\operatorname{card} J = n - k$, consider $x \in C_J^\circ \cap \Gamma\setminus M_J$. Since M_J is a global attractor for ϕ restricted to C_J°, $\omega(x) \subseteq M_J$. Since the dual repellor of $\bigcup_{\operatorname{card} I = n-k} M_I$ relative to $\partial_k C \cap \Gamma$ is $\partial_{k-1} C \cap \Gamma$, $\alpha(x) \subseteq \partial_{k-1} C \cap \Gamma$. Theorem 3.1 in [1] implies that $\alpha(x)$ is connected and ϕ restricted to $\alpha(x)$ is chain recurrent. Since $\{M_I\}_{\operatorname{card} I \geq n-k+1}$ is a Morse decomposition for $\partial_{k-1} C \cap \Gamma$, $\bigcup_{\operatorname{card} I\geq n-k+1} M_I$ contains the chain recurrent set of

ϕ restricted to $\partial_{k-1}C \cap \Gamma$. Hence, there is a $J' \subseteq \{1, \dots, n\}$ such that card $J' \geq n-k+1$ and $\alpha(x) \subseteq M_{J'}$. It follows that $\{M_I\}_{\mathrm{card}\, I \geq n-k}$ is a Morse decomposition of $\partial_k C$. ∎

Using these results, we are able to characterize Kolmogorov vector fields satisfying property (P).

THEOREM 3.3. *If* (K) *is dissipative, then the following are equivalent*

(1) (K) *satisfies property* (P).

(2) *For every ergodic probability measure μ with support in ∂C,*

$$\int f_i \, d\mu > 0 \quad \textit{for all } i \in S(\mu).$$

(3) *For every nonempty $I \subseteq \{1, \dots, n\}$ and $x \in C_I^o$,*

$$\liminf_{t\to\infty} \frac{1}{t}\int_0^t f_i(\phi_s x)\, ds > 0 \quad \textit{for all } i \in I.$$

An ecological interpretation of Theorem 3.3 is that if every population trajectory of the system can be eventually invaded by the missing species, then every subset of the species pool forms a viable community.

Proof. We prove the following implications: $1 \Leftrightarrow 2$, 1 and $2 \Rightarrow 3$, and $3 \Rightarrow 1$. Let Γ be the global attractor for ϕ.

To prove that $1 \Rightarrow 2$, assume that (K) satisfies (P). Let μ be an ergodic probability measure with support in ∂C. Fix $j \in S(\mu)$. Since $(\mathrm{K})_{S(\mu)\setminus\{j\}}$ is robustly permanent and the support of μ is in $\partial C_{S(\mu)\setminus\{j\}}$, Theorem 3.1 implies that

$$\max_{i \notin S(\mu) \text{ or } i=j} \int f_i \, d\mu > 0.$$

By Lemma 3.1 $\int f_i \, d\mu = 0$ for all $i \notin S(\mu)$. Therefore, $\int f_j \, d\mu > 0$.

To prove that $2 \Rightarrow 1$, we proceed inductively on the dimension n. The case $n = 1$ is immediate. Now, suppose that $2 \Rightarrow 1$ for all dimensions strictly less than n and that (K) is an n-dimensional dissipative vector field for which 2 holds. Our inductive hypothesis implies that $(\mathrm{K})_I$ is robustly permanent for every nonempty subset I of $\{1, \dots, n\}$. From Proposition 3.1 it follows that the family $\{M_I\}_{\mathrm{card}\, I>0}$ is a Morse decomposition for $\partial C \cap \Gamma$. Consider any nonempty $I \subseteq \{1, \dots, n\}$ and $i \in I$. Since 2 holds, $\int f_i \, d\mu > 0$ for any ergodic probability measure μ with support in M_I. The ergodic decomposition theorem implies that $\int f_i \, d\mu > 0$ for any invariant probability measure μ with support in M_I. Weak* compactness of the space of invariant probability measures with support in M_I implies that $\min \int f_i \, d\mu > 0$, where the minimum is taken over all invariant probability measures with support in M_I. Theorem 3.2 implies that (K) is robustly permanent.

To prove that 1 and 2 $\Rightarrow$ 3, suppose (K) satisfies (P) and 2 holds. Let $I \subseteq \{1, \ldots, n\}$ be nonempty. Since $(\mathrm{K})_I$ is permanent, there is a compact global attractor M_I for ϕ restricted to C_I^o. Let $x \in C_I^o$. We will show that

$$\liminf_{t\to\infty} \frac{1}{t} \int_0^t f_i(\phi_s x)\, ds \geq \min_{\mu} \int f_i \, d\mu \quad \text{for all } i \in \{1, \ldots, n\}, \tag{1}$$

where the minimum is taken over invariant probability measures with support in M_I. To this end, let t_k be an increasing sequence of positive reals such that $\lim_{k\to\infty} t_k = \infty$ and

$$\lim_{k\to\infty} \frac{1}{t_k} \int_0^{t_k} f_i(\phi_s x)\, ds = \liminf_{t\to\infty} \frac{1}{t} \int_0^t f_i(\phi_s x)\, ds.$$

Define a sequence of Borel probability measures by

$$\nu_k = \frac{1}{t_k} \int_0^{t_k} \delta_{\phi_s x} ds,$$

where δ_y denotes the Dirac measure at the point y. Since (K) is dissipative, $\mathscr{O} = \overline{\{\phi_s x : s \geq 0\}}$ is compact. As each of the ν_k is supported on $\mathscr{O}$, weak* compactness of the Borel probability measures supported on $\mathscr{O}$ implies that by passing to a subsequence if necessary ν_k converges to a Borel probability measure ν. To see that ν is ϕ-invariant, it suffices to show that $\int (h \circ \phi_T)\, d\nu = \int h\, d\nu$ for every continuous function $h: \Gamma \to \mathbb{R}$ and real number T. Let $\|h\| = \sup_{y\in\mathscr{O}} |h(y)|$. Weak* convergence and the definition of the ν_k imply that

$$\begin{aligned} \left| \int (h \circ \phi_T - h)\, d\nu \right| &= \left| \lim_{k\to\infty} \frac{1}{t_k} \int_0^{t_k} (h(\phi_{T+s} x) - h(\phi_s x))\, ds \right| \\ &= \left| \lim_{k\to\infty} \frac{1}{t_k} \int_0^{T} (h(\phi_{t_k+s} x) - h(\phi_s x))\, ds \right| \\ &\leq \limsup_{k\to\infty} \frac{2|T|\|h\|}{t_k} = 0. \end{aligned}$$

Hence, ν is ϕ-invariant. Since $x \in C_I^\circ$ and M_I is a global attractor for ϕ restricted to C_I°, the support of ν is contained in M_I. By weak* convergence of ν_k to ν,

$$\liminf_{t\to\infty} \frac{1}{t} \int_0^t f_i(\phi_s x)\, ds = \int f_i \, d\nu \quad \text{for all } i \in \{1, \ldots, n\}$$

completing the proof of (1). Since $\int f_i \, d\mu > 0$ for all ergodic probability measures with support in M_I and $i \in I$, the ergodic decomposition theorem implies that the right-hand side of (1) is positive whenever $i \in I$. Hence, 1 and 2 $\Rightarrow$ 3.

Finally, assume that 3 holds. Let μ be any ergodic probability measure with support in ∂C. By the Birkhoff ergodic theorem, there exists $x \in C^\circ_{S(\mu)}$ such that

$$\lim_{t\to\infty} \frac{1}{t} \int_0^t f_i(\phi_s x)\, ds = \int f_i\, d\mu \quad \text{for all } i \in \{1, \ldots, n\}.$$

Since 3 holds, it follows that $\int f_i\, d\mu > 0$ for all $i \in S(\mu)$. ∎

As a corollary of Theorem 3.3, we get an algebraically verifiable classification of Lotka–Volterra systems satisfying property (P). In particular, all subsystems of these Lotka–Volterra systems remain permanent even after small *nonlinear* perturbations of the linear per-capita growth rates.

COROLLARY 3.1. *Assume that $f(x) = Ax + b$, where A is an $n \times n$ real-valued matrix and $b \in \mathbb{R}^n$. If* (K) *is dissipative, then* (K) *satisfies* (P) *if and only if for every nonempty $I \subseteq \{1, \ldots, n\}$ there is a unique equilibrium $x_I^* \in C_I^\circ$ and $f_i(x_I^*) > 0$ for all $i \in I$.*

Remark 3.2. A sufficient condition for (K) with $f(x) = Ax + b$ to be dissipative is given by the following condition due to Hofbauer and Sigmund [5, Theorem 15.2.4]: for every $x \in C$ with $x \neq 0$ there is an $i \in \{1, \ldots, n\}$ such that $x_i > 0$ and $(Ax)_i < 0$.

Proof. Suppose for every nonempty $I \subseteq \{1, \ldots, n\}$ there is a unique equilibrium $x_I^* \in C_I^\circ$ and $f_i(x_I^*) > 0$ for all $i \in I$. Let μ be any ergodic probability measure with support in ∂C. Define $x^* = \int x\, d\mu(x)$. x^* lies in $C^\circ_{S(\mu)}$ and $\int f\, d\mu = \int (Ax + b)\, d\mu(x) = Ax^* + b = f(x^*)$. Lemma 3.1 implies that $(Ax^* + b)_i = 0$ for all $i \notin S(\mu)$. Since x^* lies in $C^\circ_{S(\mu)}$, $x_i^* = 0$ for all $i \in S(\mu)$. Hence, x^* is an equilibrium for (K) and must equal $x^*_{S(\mu)}$. Therefore, $\int f_i\, d\mu = f_i(x^*_{S(\mu)}) > 0$ for all $i \in S(\mu)$. Since μ was any ergodic probability measure with support in ∂C, Theorem 3.3 implies that (K) satisfies (P).

On the other hand, suppose that (K) with $f(x) = Ax + b$ satisfies (P). Let $I \subseteq \{1, \ldots, n\}$ be nonempty. Since $(K)_I$ is permanent, Theorem 13.3.1 in [5] implies that there is an equilibrium $x^* \in C_I^\circ$. Suppose to the contrary that x^* is not the only equilibrium in C_I°. Say $y^* \in C_I^\circ$ with $y^* \neq x^*$ is also an equilibrium. It follows that $(Ax^* + b)_i = (Ay^* + b)_i = 0$ for all $i \notin I$. Since $(A(x^* + t(y^* - x^*)) + b)_i = 0$ for all $i \notin I$ and $t \in \mathbb{R}$, dissipativeness of (K) implies that there are real numbers $a < b$ such that $x^* + t(y^* - x^*) \in C_I$ is an equilibrium for every $t \in [a, b]$ and $x^* + a(y^* - x^*), x^* + b(y^* - x^*) \in \partial C_I$. It follows that at least one of the external Lyapunov exponents of the equilibrium $x^* + a(y^* - x^*)$ is zero. But this contradicts Assertion 2 of Theorem 3.3. Hence, C_I° contains exactly one equilibrium x^*. Assertion 2 of Theorem 3.3 applied to δ_{x^*} implies that $f_i(x^*) > 0$ for all $i \in I$. ∎

3.2. *Smoothness of Carrying Simplices for Competitive* (P) *Systems*

System (K) is called *totally competitive* if $(\partial f_i/\partial x_j)(x) < 0$ for each $1 \le i, j \le n, x \in C$. The following important result was established by M. W. Hirsch.

THEOREM 3.4 [2, Theorem 1.7]. *Assume* (K) *is dissipative and totally competitive, and* $\{0\}$ *is a repellor relative to* Γ. *Then the attractor* $\Sigma \subseteq \Gamma$ *dual to the repellor* $\{0\}$ *relative to* Γ *is homeomorphic via radial projection to the standard* $(n-1)$*-simplex* $\Delta := \{x \in C : x_1 + \cdots + x_n = 1\}$. *Moreover, the global attractor* Γ *equals the set* $\{\alpha x : 0 \le \alpha \le 1, x \in \Sigma\}$.

The invariant compact set Σ is referred to as the *carrying simplex* for (K). We write $\partial\Sigma$ instead of $\Sigma \cap \partial C$.

THEOREM 3.5. *If* (K) *satisfies* (P) *and is totally competitive, then the carrying simplex* Σ *is a* C^1 *submanifold-with-corners, neatly embedded in* C.

Remark 3.3. The proof of this result when F is C^2 follows from [11].

Proof. Theorem 3.3 implies that $f_i(0) = \int f_i \, d\delta_0 > 0$ for all i. Consequently, $\{0\}$ is a repellor. By Theorem 3.4 there is a Lipschitz carrying simplex Σ. By Lemma 3.1 and Theorem 3.3 for each ergodic probability measure μ on $\partial\Sigma$ its external Lyapunov exponents are positive. Now Theorem 3.2 in [12] gives the desired result. ∎

As a corollary, we get an algebraically verifiable class of totally competitive Lotka–Volterra systems with a C^1 carrying simplex.

COROLLARY 3.2. *Assume that* $f(x) = Ax + b$, *where* A *is an* $n \times n$ *real-valued matrix* A *and* $b \in \mathbb{R}^n$. *If*

(1) $A_{ij} < 0$ *for all* $i, j \in \{1, \dots, n\}$, *and*

(2) *for every nonempty* $I \subseteq \{1, \dots, n\}$ *there is a unique equilibrium* $x_I^* \in C_I^\circ$ *and* $f_i(x_I^*) > 0$ *for all* $i \in I$, *then* (K) *satisfies property* (P) *and the carrying simplex* Σ *is a* C^1 *submanifold-with-corners, neatly embedded in* C.

Proof. When $A_{ij} < 0$ for all $i, j \in \{1, \dots, n\}$, Remark 3.2 implies that (K) with $f(x) = Ax + b$ is dissipative. Corollary 3.1 implies that (K) satisfies (P). Applying Theorem 3.5 completes the proof. ∎

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