ON PERSISTENCE AND EXTINCTION FOR RANDOMLY PERTURBED DYNAMICAL SYSTEMS

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ABSTRACT. Let $f : M \to M$ be a continuous map of a locally compact metric space. Models of interacting populations often have a closed invariant set ∂M that corresponds to the loss or extinction of one or more populations. The dynamics of f subject to bounded random perturbations for which ∂M is absorbing are studied. When these random perturbations are sufficiently small, almost sure absorbtion (i.e. extinction) for all initial conditions is shown to occur if and only if $M \setminus \partial M$ contains no attractors for f. Applications to evolutionary bimatrix games and uniform persistence are given. In particular, it shown that random perturbations of evolutionary bimatrix game dynamics result in almost sure extinction of one or more strategies.

1. **Introduction.** Often the dynamics of interacting populations in ecological, evolutionary, epidemiological, etc. systems are modeled by iterating a continuous map with an invariant set that corresponds to the extinction or loss of one or more species, genotypes, pathogens, etc. Understanding the conditions under which extinction is or is not inevitable has been the focus of much research. On one hand, coexistence in these models has been equated with a range of mathematical definitions including existence of attractors disjoint from the extinction set, uniform persistence or permanence, and robust permanence [1, 2, 10, 11, 12, 16, 17]. On the other hand, extinction has been typically equated with all initial conditions resulting in the demise of one or more of the interacting populations [6, 9, 15, 18]. Since interacting populations are always subject to random perturbations (e.g. demographic or environmental stochasticity) and numerical simulations of iterated maps are subject to computer roundoff errors, the purpose of this paper is to take into account these small perturbations when defining coexistence and extinction. In the remainder of this section, the main result of this paper is introduced. Section 2 provides a proof of the main result. Section 3 gives applications to evolutionary bimatrix games and uniform persistence.

Let $f : M \to M$ be a continuous map of a locally compact metric space M with metric d. Let ∂M be a closed *invariant* set, i.e. $f(\partial M) = \partial M$, and define $M^\circ = M \setminus \partial M$. For models of interacting populations, ∂M corresponds to the absence or extinction of one or more populations. Given $A, B \subset M$, let $\mathrm{dist}(A, B) =$

$\inf\{d(x,y) : x \in A, y \in B\}$, and for $\delta \geq 0$, let $N(A,\delta) = \{y \in M : \mathrm{dist}(y,A) \leq \delta\}$. For notational convenience, when $A = \{x\}$, we write $N(x,\delta)$ and $\mathrm{dist}(x,B)$ instead of $N(\{x\},\delta)$ and $\mathrm{dist}(\{x\},B)$, respectively. For a set $A \subset M$, let $\omega(A) = \cap_{n\geq 1}\overline{\cup_{m\geq n}f^m(A)}$ denote the ω-limit set of A. A compact set $A \subset M$ is an attractor if there exists an open neighborhood U of A such that $\omega(U) = A$. The basin of attraction of an attractor A is given by $\mathcal{B}(A) = \{x \in M : \omega(x) \subset A\}$.

To account for small random perturbations of f, for every $\epsilon > 0$, let $\{X_n^\epsilon\}_{n\geq 0}$ be a Markov chain with transition kernel $P_x^\epsilon(U) = P(X_1^\epsilon \in U|X_0^\epsilon = x)$ for $x \in M$ and Borel sets $U \subset M$. Let $\mathrm{supp}P_x^\epsilon$ denote the support of the transition kernel. Throughout this article, we assume that the transition kernel satisfies the following hypotheses.

H1: $P_x^\epsilon(N(f(x),\epsilon)) = 1$ for all $x \in M$.

H2: $P_x^\epsilon(\partial M) = 1$ for all $x \in \partial M$.

H3: There exists $\delta = \delta(\epsilon) \in (0,\epsilon)$ such that $N(f(x),\delta) \subset \mathrm{supp}P_x^\epsilon$ for any $x \in M^\circ$ and $P_x^\epsilon(\partial M) > 0$ whenever $f(x) \in N(\partial M,\delta)$.

H4: If $P_x^\epsilon(K) > 0$ for a closed set $K \subset M$, then there exists a neighborhood U (depending on x and ϵ) of x such that $\inf_{y\in U} P_y^\epsilon(K) > 0$.

H1 corresponds to assuming that the random perturbations of f are small with probability one. **H2** ensures that ∂M is absorbing for the Markov chain. **H3** ensures that the random perturbations locally go in all directions. In particular, there is a positive probability of absorbtion when the Markov chain gets close to the absorbing set. For ecological or evolutionary models, this assumption corresponds to a species or a genotype going extinct with positive probability when their density or frequency is to low. **H4** is a mild regularity assumption about the transition kernel of the Markov chain. When $\partial M = \emptyset$, X_n^ϵ satisfying **H1**-**H4** corresponds to a small random perturbation of f in the sense of Ruelle [13].

We introduce the following definition.

Definition 1. ∂M is almost surely absorbing for f if for all $x \in M$

$$P_x^\epsilon(X_n^\epsilon \in \partial M \text{ for all } n \text{ sufficiently large}) = 1$$

whenever $\epsilon > 0$ is sufficiently small.

For models of interacting populations, almost surely absorbing corresponds to one or more populations going to extinct with probability one. The following theorem characterizes almost sure absorbtion via attractors of f.

Theorem 1. Assume f is dissipative, ∂M is a closed invariant set, and X_n^ϵ satisfies **H1**–**H4**. Then ∂M is almost surely absorbing if and only if f has no attractors contained in M°. Moreover, if $A \subset M^\circ$ is an attractor and $K \subset \mathcal{B}(A)$ is compact, then there exists $\epsilon_0 > 0$ and $\eta > 0$ such that

$$P(\liminf_{n\to\infty} \mathrm{dist}(X_n^\epsilon, \partial M) \geq \eta|X_0^\epsilon = x) = 1$$

for all $x \in K$ and $\epsilon \in [0,\epsilon_0)$.

For models of population processes, Theorem 1 implies that coexistence requires, at the very least, the existence of an attractor bounded away from extinction. Further implications for coexistence are discussed in Section 3.

2. **Proof of Theorem 1.** The proof consists of combining two deterministic ingredients with one probabilistic ingredient. For the deterministic ingredients of the proof, two results about chain recurrence are needed. Recall, an ϵ *chain from x to y of length n* is a set of points $x_1 = x, x_2, \ldots, x_n = y$ such that $d(f(x_i), x_{i+1}) < \epsilon$ for $i = 1, 2, \ldots, n-1$. x *chains to y* if there exists an ϵ chain from x to y for all $\epsilon > 0$. A standard result about attractors and ϵ-chains is the following (for a proof, see for example, [14, Proposition 1]).

Proposition 1. *Let A be an attractor with basin of attraction $\mathcal{B}(A)$ and $U \subset V$ be neighborhoods of A such that the closure $\overline{V}$ of V is compact and contained in $\mathcal{B}(A)$. Then there exists $N \geq 0$ and $\epsilon > 0$ such that every ϵ chain of length $n \geq N$ starting in V ends in U.*

For $x \in M$, define $\Omega(x)$ to be the collection of points $y \in M$ such that for all $\epsilon > 0$ and $n \geq 0$ there exists an ϵ chain from x to y of length at least n. The following proposition is the key deterministic ingredient for the proof of Theorem 1.

Proposition 2. *Let f be dissipative. If f has no attractors contained in M°, then $\Omega(x) \cap \partial M \neq \emptyset$ for all $x \in M$.*

While a proof of this proposition can be found in [14], it is included here for the convenience of the reader.

Proof. Let $x \in M$ be given. Since f is dissipative, there exists a global attractor Γ such that $\mathcal{B}(\Gamma) = M$. Let K be the intersection of all attractors that contain $\Omega(x)$. We begin by proving that $\Omega(x) = K$. The proof follows Conley [3] who proved the analogous statement for continuous flows. The proof is included for the reader's convenience. By definition, $\Omega(x) \subset K$. To see that $K \subset \Omega(x)$, define $\Omega(x, \epsilon, n)$ to be the set of points y such that there exists an ϵ chain of length at least n from x to y. $\Omega(x, \epsilon, n)$ is an open set. Moreover, since Γ is a global attractor, Proposition 1 implies that $\overline{\Omega(x, \epsilon, n)}$ is compact for $\epsilon > 0$ sufficiently small. Moreover, we claim that $f(\overline{\Omega(x, \epsilon, n)}) \subset \Omega(x, \epsilon, n)$. Indeed, given $z \in \overline{\Omega(x, \epsilon, n)}$, continuity of f implies that there exists $y \in \Omega(x, \epsilon, n)$ such that $d(f(z), f(y)) < \epsilon$. Since $y \in \Omega(x, \epsilon, n)$, there exists an ϵ chain, $x_1 = x, x_2, \ldots, x_m = y$, with $m \geq n$. Since $d(f(z), f(y)) < \epsilon$, we get that $x_1 = x, x_2, \ldots, x_m = y, x_{m+1} = f(z)$ is an ϵ chain from x to $f(z)$ of length $m + 1$. Hence, $f(z) \in \Omega(x, \epsilon, n)$ and $f(\overline{\Omega(x, \epsilon, n)}) \subset \Omega(x, \epsilon, n)$. Since $f^m(\Omega(x)) = \Omega(x) \subset \Omega(x, \epsilon, n)$ for all m, $A(\epsilon, n) = \cap_{m \geq 1} f^m(\Omega(x, \epsilon, n))$ is an attractor containing $\Omega(x)$ whenever $\epsilon > 0$ is sufficiently small. Hence, $K \subset A(\epsilon, n)$. Since $\Omega(x) = \cap_{n \geq 1, \epsilon > 0} \Omega(x, \epsilon, n)$ and $\Omega(x) \subset K \subset A(\epsilon, n) \subset \Omega(x, \epsilon, n)$, we get $\Omega(x) = K = \cap_{n \geq 1, \epsilon > 0} A(\epsilon, n)$.

Suppose that f has no attractors in M°. Let $\mathcal{F}$ be the collection of sets

$$\{A \cap \partial M : A \text{ is an attractor containing } \Omega(x)\}$$

Since finite intersections of attractors are attractors and f has no attractors in M° (i.e. every attractor intersects ∂M), $\mathcal{F}$ satisfies the finite intersection property. Compactness of Γ implies that intersection of all sets in $\mathcal{F}$ is non-empty. Since the intersection of all sets in $\mathcal{F}$ is $\Omega(x) \cap \partial M$, $\Omega(x) \cap \partial M \neq \emptyset$. $\qquad \square$

The probabilistic ingredient of the proof is given by the following proposition.

Proposition 3. *Let $x \in M$ chain to a point $y \in \partial M$. Then for any $\epsilon > 0$ there exists a neighborhood U of x and $\beta > 0$ such that*

$$P(X_n^\epsilon \in \partial M \text{ for all } n \text{ sufficiently large} | X_0^\epsilon = z) \geq \beta$$

for all $z \in U$.

Proof. Let $\delta = \delta(\epsilon) > 0$ be as given by **H3**. Let $x_0 = x$, x_1, ..., $x_n = y$ be a δ chain from x to a point $y \in \partial M$. **H3** implies that there exists $\gamma_n > 0$ such that $P_{x_{n-1}}^\epsilon(N(x_n, \gamma_n) \cap \partial M) > 0$. **H4** implies that there exist $\gamma_{n-1} > 0$ and $\alpha_n > 0$ such that $P_z^\epsilon(N(x_n, \gamma_n) \cap \partial M) \geq \alpha_n$ for all $z \in N(x_{n-1}, \gamma_{n-1})$. **H3** and **H4** imply that there exist $\gamma_{n-2} > 0$ and $\alpha_{n-1} > 0$ such that $P_z^\epsilon(N(x_{n-1}, \gamma_{n-1})) \geq \alpha_{n-1}$ for all $z \in N(x_{n-2}, \gamma_{n-2})$. Continuing in this manner, we get for $i = 1, \ldots, n-2$ there exist $\gamma_{i-1} > 0$ and $\alpha_i > 0$ such that $P_z^\epsilon(N(x_i, \gamma_i)) \geq \alpha_i$ for all $z \in N(x_{i-1}, \gamma_{i-1})$. Define $U(i) = N(x_i, \gamma_i)$ for $i = 0, 1, \ldots, n-1$, $U(n) = N(y, \gamma_n) \cap \partial M$, and $\alpha = \min_i \alpha_i$. We claim that

$$P(X_n^\epsilon \in U(n) | X_0^\epsilon = z) \geq \alpha^n \quad \text{for all } z \in U(1). \tag{1}$$

Choosing $U = U(1)$ and $\beta = \alpha^n$ implies the main statement of the proposition. To prove (1) notice that

$$P(X_n^\epsilon \in U(n) | X_0^\epsilon = z) = \int \ldots \int P_{z_{n-1}}^\epsilon(U(n)) \, dP_{z_{n-2}}^\epsilon(z_{n-1}) \ldots dP_z^\epsilon(z_1).$$

Since $P_z^\epsilon(U(n)) \geq \alpha 1_{U(n-1)}(z)$ for all $z \in M$, we get that

$$P(X_n^\epsilon \in U(n) | X_0^\epsilon = z) \geq \alpha \int \ldots \int 1_{U(n-1)}(z_{n-1}) \, dP_{z_{n-2}}^\epsilon(z_{n-1}) \ldots dP_z^\epsilon(z_1)$$

$$= \alpha \int \ldots \int P_{z_{n-2}}^\epsilon(U(n-1)) \, dP_{z_{n-3}}^\epsilon(z_{n-2}) \ldots dP_z^\epsilon(z_1).$$

Similarly, applying the estimates $P_z^\epsilon(U(n-i)) \geq \alpha 1_{U(n-i-1)}(z)$ for $i = 1, 2, \ldots, n-1$ yields (1). $\square$

With these propositions in hand, we are ready to prove Theorem 1. First, let us assume that there are no attractors in M° for f. We will show that ∂M is almost surely absorbing. Let $x \in M$. Since f is dissipative, there exists an attractor A such that $\mathcal{B}(A) = M$. Choose neighborhoods $U \subset V$ of A with compact closure such that $x \in V$. Choose $N \geq 1$ and $\epsilon > 0$ as given by Proposition 1. **H1** and Proposition 1 imply that $X_n^\epsilon \in U$ for all $n \geq N$ with probability one. Without loss of generality, we assume that $N = 1$. Proposition 2 implies that all points in M chain to points in ∂M. Hence, by Proposition 3 for all $y \in M$ there exists a neighborhood U_y of y and $\beta_y > 0$ such that

$$P(X_n^\epsilon \in \partial M \text{ for all } n \text{ sufficiently large} | X_0^\epsilon = z) \geq \beta_y$$

for all $z \in U_y$. Compactness of $\overline{U}$ implies there exists $\beta > 0$ such that

$$P(X_n^\epsilon \in \partial M \text{ for all } n \text{ sufficiently large} | X_0^\epsilon = z) \geq \beta$$

for all $z \in \overline{U}$. Next we apply the following standard result in Markov chain theory (see e.g. Theorem 2.3 in Chapter 5 in [4]) to $X_n = X_n^\epsilon$, $B = \partial M$ and $C = U \cap M^\circ$

Proposition 4. *Let X be a Markov chain and suppose that*

$$P\left(\bigcup_{m=n+1}^\infty \{X_m \in B\} \Big| X_n \right) \geq \beta > 0 \ on \ \{X_n \in C\}.$$

Then

$$P(\{X_n \text{ enters } C \text{ infinitely often}\} \setminus \{X_n \text{ enters } B \text{ infinitely often}\}) = 0.$$

It follows that

$$P(X_n^\epsilon \text{ enters } U \cap M^\circ \text{ infinitely often}|X_0^\epsilon = x) = 0$$

and, consequently, **H2** implies

$$P(X_n^\epsilon \in \partial M \text{ for all } n \text{ sufficiently large}|X_0^\epsilon = x) = 1$$

Since $x \in M$ was arbitrary, we have shown that ∂M is almost-surely absorbing for f.

To prove the other direction of Theorem 1, let us assume that there exists an attractor $A \subset M^\circ$. Let $x \in \mathcal{B}(A)$ and $X_0^\epsilon = x$. Since $A \subset M^\circ$ and $f(\partial M) \subset \partial M$, $\mathcal{B}(A) \subset M^\circ$. Let $U \subset V$ be neighborhoods of A with compact closure such that $x \in V$ and $\overline{V} \subset \mathcal{B}(A)$. Let N and $\epsilon > 0$ be as given by Proposition 1. For any $n \geq 1$, **H1** implies that $X_0^\epsilon, \ldots X_n^\epsilon$ with probability one defines an ϵ chain of length $n + 1$ starting at x. Hence, Proposition 1 implies that $X_n^\epsilon \in U \subset M^\circ$ for all $n \geq N$ with probability one. In particular, there exists $\eta > 0$ (e.g. $\eta = \text{dist}(\overline{U}, \partial M)$) such that

$$P(\text{dist}(X_n^\epsilon, \partial M) \geq \eta \text{ for } n \geq N|X_0^\epsilon = x) = 1$$

for all $x \in \overline{U}$.

3. Applications.

3.1. Evolutionary bimatrix games.

As an application of Theorem 1, consider an evolutionary game consisting of two populations engaging in asymmetric contests. In the first population (respectively second population), individuals can play one of n (respectively m) strategies and the frequency of individuals playing strategy i is x_i (respectively y_i). After a contest between an individual playing strategy i in the first population and an individual playing strategy j in the second population, the payoff for strategy i (respectively j) is a_{ij} (respectively b_{ji}). If $A = (a_{ij})$ and $B = (b_{ij})$, then the evolutionary dynamics are given by (see, e.g., [9])

$$\begin{align}
\frac{dx_i}{dt} &= x_i((Ay)_i - x \cdot Ay) & i = 1, \ldots, n \tag{2}\\
\frac{dy_j}{dt} &= y_j((Bx)_j - y \cdot Bx) & j = 1, \ldots, m.
\end{align}$$

Let

$$M = \{(x, y) : x \in \mathbf{R}^n, y \in \mathbf{R}^m, x_i \geq 0, y_i \geq 0, \sum_i x_i = 1, \sum_j y_j = 1\} \tag{3}$$

Points in M correspond to pairs of distributions of strategies for the two populations. Extinction of one or more strategies in either population corresponds to the set

$$\partial M = \{x \in M : \prod_i x_i \prod_j y_j = 0\} \tag{4}$$

To apply Theorem 1, let ϕ_t denote the flow of (2) and $f = \phi_h$ for some $h > 0$. Eshel and Akin [5, page 133] (see, also, Hofbauer [8]) have shown that ϕ_t is volume preserving. Hence, there can be no attractors for f in M° and Theorem 1 implies the following corollary.

Corollary 1. *Let ϕ_t be the flow of (2), $f = \phi_h$ for some $h > 0$, M be given by (3), and ∂M be given by (4). Then ∂M is almost surely absorbing.*

Hence for these bimatrix games, the inclusion of small random perturbations results in the eventual demise of one or more strategies. In fact, applying this argument inductively on the skeleton of ∂M implies the inclusion of small random perturbations preserving strategy extinction results in the eventual demise of all but one strategy in each population. Hofbauer [7, 8] has also introduced a 'canonical' discrete-time analog of (2) with the map $f = (g, h) : M \to M$ given by

$$
\begin{aligned}
g_i(x, y) &= x_i \frac{(Ay)_i}{x \cdot Ay} & i = 1, \ldots, n \\
h_j(x, y) &= y_j \frac{(Bg(x, y))_j}{y \cdot Bg(x, y)} & j = 1, \ldots, m
\end{aligned}
\tag{5}
$$

and has shown that this map preserves volume. Hence, for this map, ∂M is also almost surely absorbing.

3.2. **Uniform persistence and random perturbations.** Assume that f is dissipative. f is *uniformly persistent* or *permanent* [12] if there exists an attractor $A \subset M^\circ$ such that $\mathcal{B}(A) = M^\circ$. Equivalently, there exists a $\eta > 0$ such that $\liminf_{n\to\infty} \operatorname{dist}(f^n x, \partial M) \geq \eta$ for all $x \in M^\circ$. Recall an invariant set $A \subset M$ is *isolated* if there is a closed neighborhood U of A such that A is the largest invariant set in U. Hofbauer and So [10, Theorem 2.1] have shown that a dissipative map f is uniformly persistent if and only if ∂M is isolated and $W^s(\partial M) \subset \partial M$ where $W^s(\partial M) = \{x \in M : \omega(x) \subset \partial M\}$. Using this characterization of uniform persistence and Theorem 1, we get the following corollary.

Corollary 2. *Assume f is dissipative, ∂M is a closed isolated set, and X_n^ϵ satisfies **H1**–**H4**. If f is uniformly persistent, then there exists $\eta > 0$ such that for all $x \in M^\circ$*

$$
P(\liminf_{n\to\infty} \operatorname{dist}(X_n^\epsilon, \partial M) \geq \eta | X_0^\epsilon = x) = 1
$$

whenever $\epsilon > 0$ is sufficiently small. If f is not uniformly persistent, then for all $\epsilon > 0$ there exist an open set $U \subset M^\circ$ and $\beta > 0$ such that

$$
P(X_n^\epsilon \in \partial M \text{ for all } n \text{ sufficiently large} | X_0^\epsilon = x) \geq \beta
$$

for all $x \in U$.

Proof. Assume f is uniformly persistent. Then applying the second statement of Theorem 1 to $K = \{x\}$ for $x \in M^\circ$ implies the first statement of the corollary.

Assume f is not uniformly persistent. Since ∂M is isolated, Theorem 2.1 of Hofbauer and So [10] implies there exists $x \in M^\circ$ such that $\omega(x) \subset \partial M$. In particular x chains to a point $y \in \partial M$. Applying Proposition 3 completes the proof of the corollary. $\square$

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