Persistence despite perturbations for interacting populations

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Abstract

Two definitions of persistence despite perturbations in deterministic models are presented. The first definition, persistence despite frequent small perturbations, is shown to be equivalent to the existence of a positive attractor i.e. an attractor bounded away from extinction. The second definition, persistence despite rare large perturbations, is shown to be equivalent to permanence i.e. a positive attractor whose basin of attraction includes all positive states. Both definitions set up a natural dichotomy for classifying models of interacting populations. Namely, a model is either persistent despite perturbations or not. When it is not persistent, it follows that all initial conditions are prone to extinction due to perturbations of the appropriate type. For frequent small perturbations, this method of classification is shown to be generically robust: there is a dense set of models for which persistent (respectively, extinction prone) models lies within an open set of persistent (resp. extinction prone) models. For rare large perturbations, this method of classification is shown not to be generically robust. Namely, work of Josef Hofbauer and the author have shown there are open sets of ecological models containing a dense sets of permanent models and a dense set of extinction prone models. The merits and drawbacks of these different definitions are discussed.
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1. Introduction

"the concept of 'persistence despite perturbations' is currently too vague to be useful"—Stuart Pimm (1982, p. 8).

A fundamental issue in population biology is what are the minimal conditions to ensure the long-term survivorship for all of the interacting components whether they be viral particles, bio-chemicals, plants, or animals. When these conditions are meet the interacting populations are said to persist or coexist. One method to identify mechanisms promoting persistence is the development and analysis of mathematical models. Models provide a deductive framework in which to simplify and unravel the complexities of biological systems such as ecological communities or immune systems. The first step in this simplification often involves making a decision whether to focus on deterministic or stochastic processes underlying the system

dynamics. For models emphasizing demographic stochasticity, the extinction of all components in finite time is inevitable due to finite population sizes and mortality events occurring with positive probability. Persistence or coexistence for these stochastic models is measured in terms of probabilities of survival for specified time intervals and, consequently, is a relative notion depending on the intent of the analysis. For systems with large number of individuals or particles, the effects of demographic stochasticity tend to average out and the stochastic dynamics are well approximated on long time intervals by the (conditionally) expected dynamics (Freidlin and Wentzell, 1998). Hence, modelers often study the deterministic counterparts of stochastic models to hone their expectations about the dynamical consequences of nonlinear interactions between populations. In contrast to the aforementioned stochastic models, these deterministic models may have population trajectories that persist indefinitely. While this persistence for infinite time cannot occur in reality, one can view these persistent trajectories as implying long-term survival for populations experiencing weak demographic noise.

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For deterministic models, mathematical and theoretical biologists have over the past century introduced various definitions of persistence or coexistence including a positive equilibrium attractor, a positive quasi-attractor, a positive attractor, and permanence (Grimm and Wissel, 1997; Jacobs and Metz, 2003; Jansen and Sigmund, 1998; Pimm, 1982; Schuster et al., 1979). While each of the existing notions of persistence provides different insights into a model's dynamics, the purpose of this note is to introduce a framework for classifying ecological dynamics as persistent or as extinction prone and evaluating the aforementioned definitions of persistence within this framework. The proposed framework is motivated by three principles. First, persistence of a population should be equated with the existence of population trajectories that remain bounded away from extinction in the presence of perturbations. This principle tips its hat to the stochastic origins of the deterministic models and captures the notion of what Pimm (1982, p. 8) called "persistence despite perturbations." Persistent despite perturbations can mean lots of different things as real world perturbations come in all shapes and sizes. Since frequent large perturbations can obliterate the deterministic signature of the dynamics, we focus on two types of perturbations: "frequent small perturbations" and "rare large perturbations." The second principle is that non-persistent systems should be viewed as "prone to extinction". Hence, every model can be classified as "persistent" or as "extinction prone." Third, since models are mere approximations to reality, generically a persistence system or an extinction prone system should remain persistent or extinction prone, respectively, under small structural perturbations of the model. This framework is described in further detail in Section 2. In Section 3, three classical definitions of persistence are evaluated within this context. This evaluation reveals that persistence despite frequent small perturbations is equivalent to the existence of a positive attractor (i.e. an attractor bounded away from extinction), while persistence despite rare large perturbations is equivalent to permanence. Moreover, while classifying systems as persistent or not persistent despite frequent small perturbations is generically robust, classifying systems as persistent or not persistent despite rare large perturbations is not generically robust. In Section 4, the merits and drawbacks of these different definitions are discussed.

2. Classification of ecological dynamics

Let S denote the population state space which we assume is a locally compact metric space with metric d. Let $f: S \to S$ be a continuous map. Given an initial state x, $f^n(x)$ defines the state of the system at time n. Let S_0 denote the closed set of states for which one or more populations are not present and $S_1 = S \backslash S_0$. For a closed system, the "no cats no kittens" principle implies that $f(S_0) \subset S_0$. For example, for models of n interacting species, S can be the nonnegative orthant $\mathbf{R}_+^n$ of $\mathbf{R}^n$ where $x \in \mathbf{R}_+^n$ corresponds to the vector of species densities. The continuous map f can be the time one map of an ecological differential equation $\mathrm{d}x_i/\mathrm{d}t = x_i g_i(x)$ where $g_i(x)$ denotes the per-capita growth rate of species i. The extinction set S_0 is given by the boundary of the nonnegative orthant, $\partial \mathbf{R}_+^n = \{x \in \mathbf{R}_+^n : \prod_{i=1}^n x_i = 0\}$. Alternatively, for replicator dynamics of n interacting strategies (see, e.g. Hofbauer and Sigmund, 1998), S can be the simplex $\{x \in \mathbf{R}_+^n : \sum_{i=1}^n x_i = 1\}$ where $x \in S$ is the distribution of strategies in the population. The map f can be given by $f_i(x) = (x_i g_i(x))/(\sum_{j=1}^n x_j g_j(x))$ where g_i is the fitness of strategy i. The extinction set is the boundary of the simplex $S_0 = \{x \in S : \prod_{i=1}^n x_i = 0\}$. More generally, f can correspond to matrix models, integrodifference equations, time one maps of partial differential equations, etc.

Before describing the properties, lets recall a few definitions from dynamical systems. A point $x \in S$ is an *equilibrium* if $f(x) = x$. A set $K \subset S$ is *invariant* if $f(K) = K$. For a set $A \subset S$, let $\overline{A}$ denote the *closure of A*. A non-empty compact set $A \subset S$ is an *attractor* if there exists an open neighborhood U of A such that $f(\overline{U}) \subset U$ and $\cap_{n \geqslant 1} f^n(\overline{U}) = A$. For a point $x \in S$, define the *ω-limit set of x* as $\omega(x) = \{y : \lim_{k \to \infty} f^{n_k}(x) = y \text{ for some } n_k \to \infty\}$. The *basin of attraction* of an attractor A, denoted $\mathscr{B}(A)$, is the set of points x such that $\omega(x) \subset A$. f is called *dissipative* if there exists an attractor whose basin of attraction is S. Since any biologically realistic model has bounded dynamics, we assume throughout this article that f is dissipative.

2.1. Persistence despite perturbations

Since populations that reach low densities or frequencies are susceptible to extinction, any definition of persistence requires the existence of states $x \in S$ such that $f^n(x)$ remains bounded away from extinction for all time. In other words, there exists $x \in S$ and $\varepsilon > 0$ such that the distance between $f^n(x)$ and S_0 is greater than ε for all n. When such an x exists, there exists a compact invariant set K disjoint from the extinction set S_0. Indeed, one can choose K to be $\omega(x)$. The existence of an x bounded away from extinction is in itself not sufficient for persistence. Consider, for example, a population genetics model with two alleles at a single locus. Let x denote the frequency of the first allele. If the fitness of homozygotes is a and the fitness of heterozygotes is b, then the dynamics on $S = [0, 1]$ with $S_0 = \{0, 1\}$ is given by $f(x) = (x^2 a + x(1-x)b)/(x^2 a + 2x(1-x)b + (1-x)^2 a)$. For all parameter values, $x = \frac{1}{2}$ is an equilibrium for this system. If $b > a$ (i.e. the homozygotes have an advantage over heterozygotes), then the system exhibits disruptive selection in which $f^n(x)$ converges to 0 if $x < \frac{1}{2}$ and $f^n(x)$ converges to 1 if $x > \frac{1}{2}$ (Fig. 1). Hence, even if the populations started at $x = \frac{1}{2}$, the slightest perturbation of the population would result in the extinction of one allele.

Since biological systems are "constantly confronted by the unexpected" (Holling, 1973), persistence should be
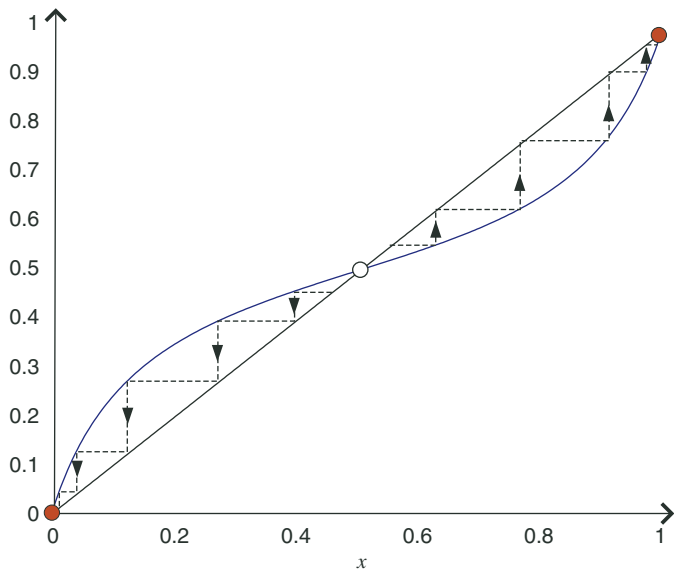
Fig. 1. $f(x) = (x^2 a + x(1-x)b)/(x^2 a + 2x(1-x)b + (1-x)^2 a)$ when $b > a$. Solid circle indicates a stable equilibrium and open circle indicates an unstable equilibrium. Cobwebbing for states initially near $x = \frac{1}{2}$ are shown as dashed lines.

equated with the existence of population trajectories that remain bounded away from extinction despite perturbations. To formalize this statement, the type of perturbation needs to be specified. Two types of perturbations, frequent small perturbations or rare large perturbations, are natural to consider. For frequent small perturbations, Conley (1978) provides the key concept, ε chains. A set of points $x = x_0, x_1, \ldots, x_n = y$ is an ε *chain from* x *to* y if $d(f(x_i), x_{i+1}) < \varepsilon$ for $i = 0, 1, \ldots, n-1$ (Fig. 2). Roughly, an ε chain is a population trajectory that gets an ε sized perturbation at every time step. With this concept in hand, the following definition arises:

Definition 1. f is *persistent despite frequent small perturbations* if there exists a state $x \in S_1$ and $\varepsilon > 0$ such that there are no ε-chains from x to any point in S_0.

The use of ε chains to represent frequent small perturbations for biological models has been suggested previously (Hofbauer et al., 1980; Jacobs and Metz, 2003). For instance, Hofbauer et al. (1980, p. 286) call states that persist despite frequent small perturbations *cooperative*. For a state x that persists despite frequent small perturbations, there is an $\varepsilon > 0$ such that the distance between $f^n(x)$ and S_0 is always greater than ε. Indeed, let $\varepsilon > 0$ be such that are no ε-chains from x to any point in S_0. Suppose to the contrary that there is an n and $y \in S_0$ such that $d(f^n(x), y) < \varepsilon$. Then $x = x_0, x_1 = f(x), x_2 = f^2(x), \ldots, x_n = f^n(x), x_{n+1} = y$ is an ε chain from x to a point in S_0 which contradicts the assumption that there is no ε chain from x to S_0. Therefore, states x that persist despite frequent small perturbations ensure that there is an invariant set (e.g. $\omega(x)$) bounded away from extinction.

In contrast to frequent small perturbations, population may experience occasional large perturbations. If these
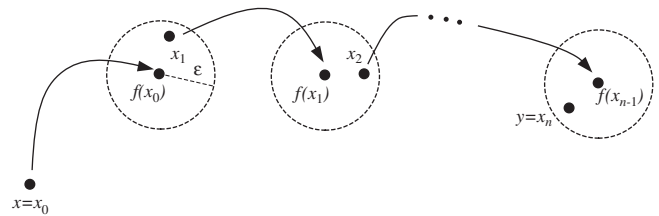

Fig. 2. An ε-chain from x to y.

large environmental perturbations never result in the immediate extinction of the population and initially the population lies in S_1, then after each perturbation the population state continues to lie in S_1. For example if $S = \mathbf{R}_+^k$, then a large shake up can correspond to multiplying the population state by an arbitrarily small $\varepsilon > 0$. If the environmental perturbations are sufficiently rare, then a population in state x will have sufficient time to approach its ω-limit set before experiencing another perturbation. Hence, we can view rare large perturbations as repeatedly jumping between ω-limit sets for population states in S_1. This description motivates the following definition:

Definition 2. f is *persistent despite rare large perturbations* if the closure of $\cup_{x \in S_1} \omega(x)$ does not intersect S_0 i.e. there exist no sequences $x_n \in S_1$ and $y_n \in \omega(x_n)$ such that y_n converges to a point in S_0 as $n \to \infty$.

2.2. Non-persistence implies prone to extinction

While it is tautological to state that all systems should either be persistent or not be persistent, we need to ask what does "not persistent" mean? Certainly "not persistent" should mean in some sense that the system is prone to extinction. The complement of both definitions of persistence despite perturbations naturally satisfy this statement. For a system not persistent despite frequent small perturbations, every initial population state can be driven to extinction by arbitrarily small repeated perturbations. More precisely,

Definition 3. f is *prone to extinction due to frequent small perturbations*[1] if there are ε chains from x to S_0 for all $\varepsilon > 0$ and all $x \in S_1$.

For a system not persistent despite rare large perturbations, there are sequence of rare large perturbations that asymptotically drive one or more components of the population to extinction. More precisely,

Definition 4. f is *prone to extinction due to rare large perturbations* if the closure of $\cup_{x \in S_1} \omega(x)$ intersects S_0 i.e. there exist sequences $x_n \in S_1$ and $y_n \in \omega(x_n)$ such that y_n converges to a point in S_0 as $n \to \infty$.

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[1] Hofbauer et al. (1980, p. 286) say that a state $x \in S_1$ which ε chains to S_0 for all $\varepsilon > 0$ is a state that *leads to exclusion* (or *extinction*).

2.3. Generic robustness to structural perturbations

Since it is impossible (and in fact not even desirable) to account for all the features of a real system, all models are approximations to reality. In the words of Hall and DeAngelis (1985, p. 340) (cf. Grimm and Wissel, 1997) "every situation in nature can be described in an infinite number of ways. An observer can choose any arbitrary set of variables and parameters to define an abstract system, which then can be the object of study by empirical and theoretical methods." For instance, a modeler may assume that dynamics of one species is independent of another when in fact there is a weak interdependence or that the per-capita growth rates are linear when in fact they are weakly nonlinear. While these assumptions may simplify the analysis of determining whether a model is persistent or extinction prone, they necessitate knowing whether nearby models (e.g. the possibly more realistic models) are persistent or extinction prone, respectively. If nearby models exhibit a different type of behavior (e.g. nearby models are not persistent despite the focal model being persistent), then one can draw few (if any!) conclusions about the persistence of the biological system being approximated by the model.

Ideally a model classified as persistent remains so following small structural perturbations of the model. Consequently, we make the following definitions. A map f is *robustly persistent despite frequent small perturbations* (*respectively, despite rare large perturbations*) if all dissipative maps g sufficiently near f are persistent to frequent small perturbations (resp. rare large perturbations). Similarly, a map f is *robustly extinction prone due to frequent small perturbations (respectively, to rare large perturbations)* if all dissipative maps g sufficiently near f are extinction prone due to frequent small perturbations (resp. rare large perturbations). As any interesting collection of models has persistent as well as extinction prone systems, models lying at the boundary of persistence are neither robustly persistent nor robustly extinction prone. Consequently, it is unreasonable to expect all models to be robustly persistent or robustly extinction prone. However, we might hope that maps robustly persistent despite frequent small (resp. rare large) perturbations or robustly extinction prone due to frequent small (resp. rare large) perturbations are dense in the set of dissipative continuous maps $f : S \to S$ satisfying $f(S_0) \subset S_0$.

3. Three candidates

With the two classification schemes (i.e. persistence despite frequent small versus rare large perturbations) in hand, how well do various definitions of persistence fare?

3.1. Stable positive equilibrium

Throughout the first half of the 20th century, persistence was equated with the existence of a positive equilibrium

attractor $\hat{x}$ i.e. $\hat{x} \in S_1$, $f(\hat{x}) = \hat{x}$, and $\hat{x}$ is an attractor. This definition is relatively straightforward to verify for many models using linearization.[2] Since $\hat{x}$ is a positive attractor (i.e. an attractor that lies in S_1), a standard argument (Proposition 1 in the Appendix) implies that for any neighborhood U of $\hat{x}$ and $\varepsilon > 0$ sufficiently small, all ε chains starting at $\hat{x}$ remain in U. Choosing U such that it is compact and disjoint from S_0 implies that f is persistent despite frequent small perturbations. Moreover, if $\hat{x}$ is globally stable (i.e. the basin of attraction of $\hat{x}$ is S_1), then $\cup_{x \in S_1} \omega(x) = \hat{x}$ and f is persistent despite rare large perturbations. However, when f has no positive equilibrium attractor, f need not be extinction prone due to frequent small perturbations or rare large perturbations. Consider the classical Lotka–Holling model of predator–prey interactions:

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = rx_1(1 - x_1/K) - \frac{ax_1x_2}{1 + bax_1}$$
$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \frac{cax_1x_2}{1 + bax_1} - dx_2 \tag{1}$$

where x_1 and x_2 denote prey and predator densities, respectively, r and K are the intrinsic rate of growth and carrying capacity of the prey, and a, b, c, and d are the searching efficiency, mean handling time, conversion efficiency, and per-capita mortality rate of the predator. For certain parameter values, this model has an unstable positive equilibrium and all non-equilibrium positive initial conditions converge to a positive periodic orbit (Fig. 3). Since this positive periodic orbit is an attractor, Proposition 1 in the Appendix implies that for every positive x and sufficiently small ε, there are no ε-chains from x to $\partial \mathbf{R}^2_+$. Hence, despite not having a positive equilibrium attractor, this system is not extinction prone due to frequent small perturbations. Alternatively, since $\cup_{x \in S_1} \omega(x)$ consists of the positive unstable equilibrium and the stable periodic orbit, both of which are bounded away from extinction, this system is also not extinction prone due to rare large perturbations.

3.2. Positive attractor

An attractor A is *positive* if $A \subset S_1$. A standard argument implies that for any neighborhood U of A and $\varepsilon > 0$ sufficiently small, all ε chains starting at A remain in U. Choosing U such that it is compact and disjoint from S_0 implies that any map f with a positive attractor is persistent despite frequent small perturbations. Proposition 2 in the Appendix proves that if f has no positive attractors, then every point $x \in S$ ε-chains to a point in S_0 for every $\varepsilon > 0$. In other words, if there are no positive attractors, then f is extinction prone due to frequent small perturbations. Hence, *existence of a positive attractor is equivalent to*

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[2]Linearization characterizes stability only generically. Consider, for example $\mathrm{d}x/\mathrm{d}t = x(1 - x)^3$. The equilibrium $x = 1$ is stable, but linearization is inclusive.
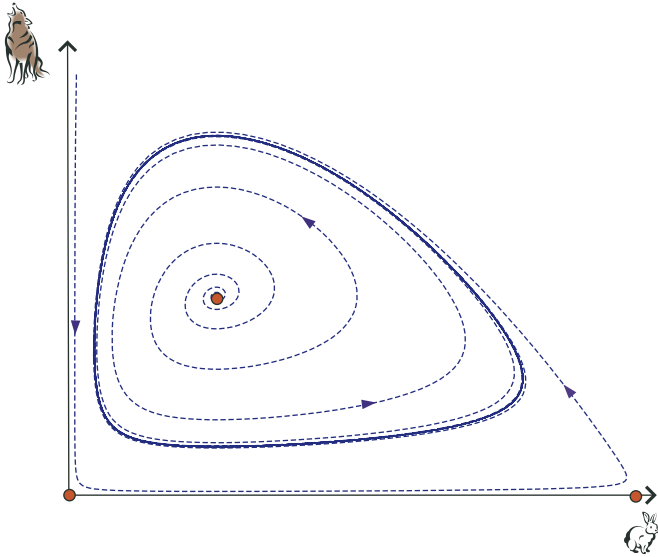
Fig. 3. Dynamics of (1) with $r = a = b = c = 1$, $K = 4$, and $d = 0.5$. Filled circles correspond to (unstable) equilibria. Dashed curves correspond to population trajectories that converge to the periodic orbit which is shown as a solid curve.

persistence despite small perturbations. Moreover, the author has proven (Schreiber, 2005) that when there are no positive attractors, small random perturbations result in extinction with probability one.

To determine whether or not generically a map is robustly persistent or extinction prone for frequent small perturbations, recall that continuity implies that if f has a positive attractor, then continuous maps near f (in the appropriate C^0 topology) have a positive attractor (see, e.g. Easton, 1998, Theorem 4.A.7). Hence, positive attractors are robust to perturbations of f. Alternatively, if f does not have positive attractors, then either f can be approximated by maps that have a positive attractor or f lies in a open set of maps with no positive attractors. In either case, f can be approximated by maps that are robustly persistent despite frequent small perturbations (i.e. has a positive attractor) or by maps that are robustly extinction prone due to frequent small perturbations (i.e. has no positive attractors).

Systems with positive attractors need not be persistent despite rare large perturbations. For example, population models that account for mate limitation, cooperative behavior, or other forms of positive density dependence may exhibit a strong Allee effect: a positive attractor coexists with an attractor corresponding to the extinction of one or more biological components (Allee, 1931; Dennis, 1989; Schreiber, 2003). This Allee effect can be phenomenologically modeled by the difference equation $f(x) = rx^b/(1 + ax^b)$ where r is proportional to the maximal fitness of the population, a accounts for intraspecific competition, and b accounts for positive density dependence. When $b > 1$ and the maximal fitness is greater than one (i.e. $r(b/a)^{1-1/b}/(1 + b) > 1$), there are three equilibria, $0 < x^* < x^{**}$. When $x < x^*$, $f^n(x)$ converges to the stable equilibrium 0. When $x > x^*$, $f^n(x)$ converges to the stable

equilibrium x^{**}. While f admits a positive attractor, f is extinction prone due to rare large perturbations as $\omega(x) = \{0\}$ for all $x < x^*$.

3.3. Permanence

f is called *permanent* (or *uniformly persistent*) if there exists $\varepsilon > 0$ such that distance between $f^n(x)$ and S_0 is greater than ε for all $x \in S_1$ and n sufficiently large. Equivalently, f is permanent if there is a positive attractor whose basin of attraction is S_1. Permanence was initially formulated by Schuster et al. (1979) in the context of hypercycles. It was independently formulated and called *uniform persistence* by Butler et al. (1986). Since permanence implies the existence of a positive attractor, permanence implies persistence despite frequent small perturbations. Moreover, since $\cup_{x \in S_1} \omega(x)$ is contained in the positive attractor of a permanent system, permanence implies persistence despite rare large perturbations. Conversely, we can prove that if f is not permanent, then f is extinction prone due to rare large perturbations. To this end, recall two definitions. An invariant set K is *isolated* if there is closed neighborhood U of K such that K is the largest invariant set in U. For an invariant set K, the *stable set of K* is the set of points attracted to K under iterations i.e. $W^s(K) = \{x : \omega(x) \subset K\}$. The Ura–Kimura theorem for maps (see, e.g. Hofbauer and So, 1989) implies that f is permanent if and only if S_0 is isolated and $W^s(S_0) \subset S_0$. Hence, if f is not permanent, then either $W^s(S_0)$ contains points in S_1 or S_0 is not isolated. If $W^s(S_0)$ contains points in S_1, then there exists $x \in S_1$ such that $\omega(x)$ intersects S_0. Alternatively, if S_0 is not isolated, then for every neighborhood U of S_0 there is an $x \in U \cap S_1$ such that $\omega(x) \subset U$. Consequently, in either case the closure of $\cup_{x \in S_1} \omega(x)$ intersects S_0. Hence, *permanence is equivalent to persistence despite rare large perturbations*.

While a non-permanent system is extinction prone due to rare large perturbations, it need not be extinction prone due to frequent small perturbations. For instance, when the map $f(x) = rx^b/(1 + ax^b)$ with $S = \mathbf{R}_+$ and $S_0 = \{0\}$ admits a positive stable equilibrium and $b > 1$, f is not permanent as 0 is stable and is not extinction prone due to frequent small perturbations. Alternatively, consider $S = \mathbf{R}_+$, $S_0 = \{0\}$ and f be the time one map for $dx/dt = g(x)$ where $g(0) = 0$ and $g(x) = x(\sin(1/x) - x)$ for $x > 0$ (Fig. 4). This map has a sequence of positive equilibria that converge to 0. Hence, f is not permanent. Alternatively, because of this sequence of equilibria, for every $x > 0$ there exists $\varepsilon > 0$ such that $f^n(x) \geqslant \varepsilon$ for all $n \geqslant 0$. Hence, aside from populations of low densities remaining at low densities, this system has no positive states prone to extinction due to frequent small perturbations.

Several people have developed criteria for robust persistence despite rare large perturbations (Garay and Hofbauer, 2003; Hirsch et al., 2001; Schreiber, 2000; Thieme, 2000). For instance, the author provided necessary and sufficient criteria for ecological equations of the form
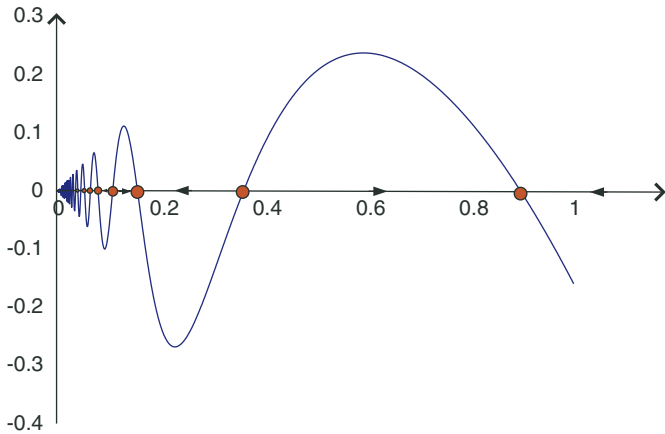
Fig. 4. Graph of $g(x) = x(\sin(1/x) - x)$ and dynamics of $dx/dt = g(x)$. Filled circles correspond to equilibria.

$dx_i/dt = x_i g_i(x)$ where $S = \mathbf{R}_+^n$ and $S_0 = \{x \in S : \prod_{i=1}^n x_i = 0\}$. The sufficient criteria requires that S_0 admits a Morse decomposition such that $\max_{1 \leqslant i \leqslant n} \int g_i \, d\mu > 0$ for any invariant measure μ supported by a component of the Morse decomposition (for definitions of Morse decompositions and invariant measures, see Schreiber, 2000). Since $\int g_i \, d\mu = 0$ for any species supported by μ, this criterion requires that on average there is a missing species that can "invade" i.e. have a positive growth rate. Garay and Hofbauer (2003) have shown that the condition, $\max_{1 \leqslant i \leqslant n} \int g_i \, d\mu > 0$ for all invariant measures μ supported by a compact invariant set K, is equivalent to the existence of nonnegative weights $p_1, \ldots, p_n$ such that $\sum_{i=1}^n p_i \frac{1}{T} \int_0^T g_i (x.t) \, dt > 0$[3] for all $x \in K$ and T sufficiently large. In other words, a weighted sum of the average per-capita growth rates has to be positive for all initial conditions in K. Using a more topologically based approach, Hirsch et al. (2001) have developed related criteria for more general state spaces.

Unfortunately, none of the aforementioned results provide a definitive characterization of robust persistence despite rare large perturbations. The underlying reason for this failure may be due to the fact that generically a system need not be robustly persistent or robustly extinction prone in the presence of rare large perturbations. In particular, Hofbauer and Schreiber (2004) have shown that for $S = \mathbf{R}_+^n$ and $S_0 = \partial \mathbf{R}_+^n$, there is an open (in the C^1 topology) set of ecological differential equations for which a dense subset are permanent and for which a dense subset are extinction prone due to rare large perturbations. Ecological differential equations in this set cannot be approximated by robustly permanent equations or be approximated by robustly non-permanent equations. This indeterminacy of permanence can occur whenever the system has a collection of subsystems with chaotic attractors that are connected by population trajectories in a cyclic fashion. For example, consider a tritrophic community consisting of a prey species, two predator species, and two top predator species. Imagine that at least one of the prey–predator–top

predator food chains promotes chaotic dynamics e.g. the tea-cup attractor of Hastings and Powell (1991) as illustrated in Fig. 5. Moreover, imagine that each top-predator while consuming both predator species specializes mainly on one of the two species. Then the ecological community can cycle between the four prey–predator–top predator food chains of this community. Top predator and predator invasions alternatively lead to predator displacement via apparent competition and top predator displacement via exploitative competition (Schreiber and Rittenhouse, 2004) as illustrated in Fig. 6. For this setup, one might expect the existence of an open set of ecological
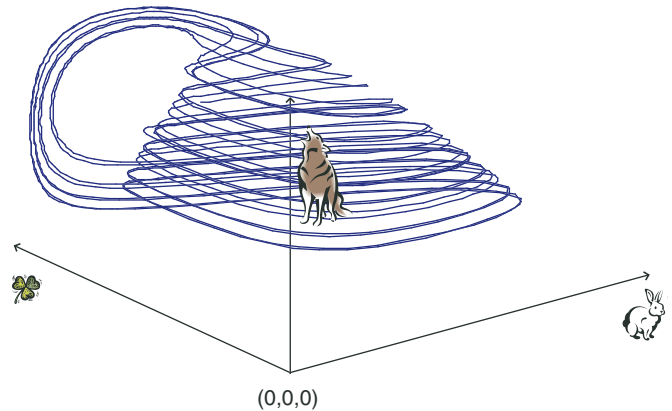

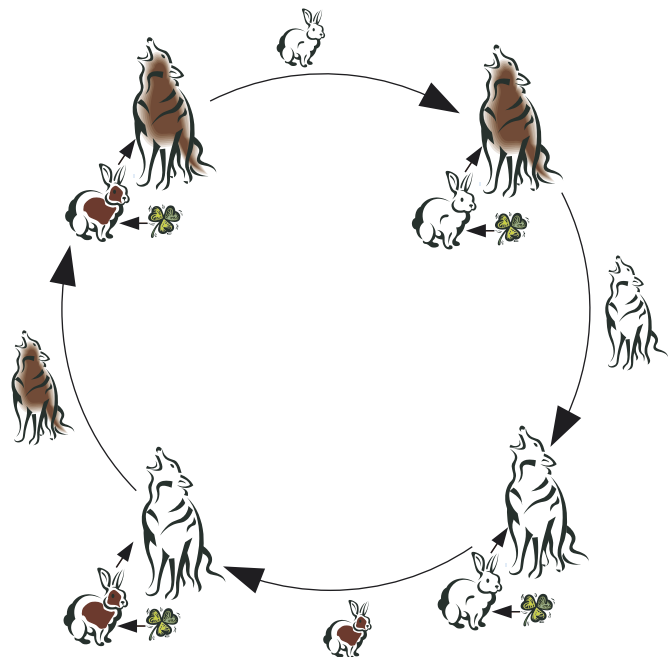Fig. 5. The Hastings–Powell "tea-cup" attractor for a three species food chain.

Fig. 6. Community cycling in a five species system consisting of one prey (e.g. a plant), two predators (e.g. herbivores) and two top predators (e.g. carnivores). One species invasions can lead to a never ending cycle of displacements due to apparent competition (i.e. two prey sharing a common predator) or due to exploitative competition (i.e. two predators sharing a common prey).

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[3] $x.t$ denotes the solution of $dx_i/dt = x_i g_i(x)$ with the initial condition x.

models that cannot be approximated by robustly permanent or by robustly non-permanent models.

4. Discussion

Since the pioneering work in the early 20th century of Lotka and Volterra on competitive and predator–prey interactions (Lotka, 1925; Volterra, 1926), Thompson, Nicholson, and Bailey on host–parasite interactions (Nicholson and Bailey, 1935; Thompson, 1924), and Kermack and McKendrick (1927) on disease outbreaks, nonlinear difference and differential equations have been used to unravel the complexities of biological systems. Each of these pioneering pieces investigated the persistence or the long-term survival of the interacting components. During these formative years, persistence was typically equated with the existence of a positive stable equilibrium (Hastings, 1988; May, 1975). While this notion of persistence is mathematically tractable, is robust to repeated small perturbations of the state, is generically robust to structural perturbations of the model, and, in the words of Jansen and Sigmund (1998, p. 195), "serves perfectly well to describe the stability of a control mechanism or a mixture of chemicals, [it] is not really appropriate for ecologists brought up on lynx–hare cycles and the antics of budworm populations." Indeed, since this definition of persistence only encodes one type of population behavior, systems without stable positive equilibria such as the Holling predator–prey model need not be prone to extinction. In fact, persistent trajectories despite frequent small perturbations are possible without the presence of a positive equilibrium. For instance, in their classic paper, Armstrong and McGehee (Armstrong and McGehee, 1980; McGehee and Armstrong, 1977) proved that two species competing for a limiting resource support a positive attractor and no positive equilibria. The author proved a similar phenomena occurs for species sharing a predator (Schreiber, 2004).

In the mid 20th century, theoretical biologists and mathematical biologists recognized the diversity of dynamical behaviors that allow long-term survival of all biological components. In additional to the periodic antics of predator–prey interactions (Rosenzweig, 1971) and nerve conduction (Hodgkin and Huxley, 1952), populations can exhibit quasi-periodic and chaotic dynamics (Costantino et al., 1997; Hastings et al., 1993; Hastings and Powell, 1991; May, 1976; Schaffer and Kot, 1986; Turchin

and Taylor, 1992). Hence, it became natural to equate persistence or coexistence with the existence of a positive attractor. This definition is graced by three properties (see Table 1). First, it assures that there are population trajectories that remain bounded away from extinction even in the presence of small repeated perturbations. Second, if a model has no positive attractors, then all population trajectories subject to arbitrarily small perturbations are doomed to extinction. Hence, existence of a positive attractor is equivalent to persistence despite frequent small perturbations. In particular, this means that the more general concept of the existence of a positive chain-transitive attractor or positive quasi-attractor (see, e.g. Jacobs and Metz (2003)) is unnecessary. Third, positive attractors persist under small structural perturbations of the model. Consequently, the generic model is robustly persistent despite frequent small perturbations or is robustly extinction prone due to frequent small perturbations. On the negative side, this definition of persistence places no constraints on the size of the basins of attraction. If the basin of a positive attractor is extremely small, then only the smallest perturbations ensure persistence. Moreover, unlike stability of an equilibrium there are no sure fire methods for verifying that a model supports a positive attractor. Three approaches to finding attractors are unfolding bifurcations of equilibria, singular perturbation analysis of systems that admit a fast–slow decomposition, and checking for permanence.

Permanence corresponds to the existence of a positive attractor that attracts all positive population trajectories. Permanence implies that positive population trajectories can recover from large perturbations of the state variable. Hence, permanent populations are more likely to survive "vigorous shake ups" Jansen and Sigmund (1998). Moreover, as permanence implies the existence of a positive attractor, permanent systems also persist despite frequent small perturbations. Permanence can be verified by studying the stable sets of boundary dynamics (Butler and Waltman, 1986; Garay, 1989; Hofbauer and So, 1989) or using average Lyapunov functions (Hofbauer, 1981; Hutson, 1984, 1988). On the other hand, despite recent progress in understanding robustly permanent systems (Garay and Hofbauer, 2003; Hirsch et al., 2001; Schreiber, 2000; Smith and Zhao, 2001; Thieme, 2000), a complete topological or Lyapunov-style characterization remains to be discovered. The difficulty in finding this characterization is highlighted by the fact that some permanent systems

Table 1
Properties satisfied by different definitions of persistence

	Persistence despite FSP	Compliment ⇓ extinction prone with FSP	Persistence despite RLP	Compliment ⇓ extinction prone with FSP	Generically robust classification
Permanent	Yes	No	Yes	Yes	No
Positive attractor	Yes	Yes	No	Yes	Yes

cannot be approximated by robustly permanent systems or robustly non-permanent systems (Hofbauer and Schreiber, 2004). Consequently, classifying systems as persistent or extinction prone in the presence of rare large perturbations does not provide a generically robust method for classifying biological models (Hofbauer and Schreiber, 2004).

In conclusion, all definitions of persistence have their merits and drawbacks. Moreover, the appropriateness of any particular definition is context dependent. In the words of Stuart Pimm "models that withstand severe perturbations might be expected to have features of some real world systems... so might many of the models that cannot withstand such severe shocks" (Pimm, 1982, p. 7). However, as all real world systems are subject to frequent small perturbations, a persistent model should support, at the very least, a positive attractor. If we take this minimalist view of persistence, we gain a generically robust classification of biological models. In which case, we can view permanence or existence of a positive stable equilibria as particular shades of persistence that refine our understanding of the population dynamics.

Acknowledgments

Appendix

In this Appendix, we prove two of the results stated in the main text. Throughout the Appendix, $f : S \to S$ is a continuous dissipative map of a locally compact metric space S, $S = S_0 \cup S_1$ where S_0 is a closed set, and $f(S_0) \subset S_0$. 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 $d(f(x_i), x_{i+1}) < \varepsilon$ for $i = 1, 2, \ldots, n-1$. The first proposition (a standard argument provided for the reader's convenience) implies that maps f with a positive attractor is persistent despite frequent small perturbations. The second proposition proves that no positive attractors implies extinction prone due to frequent small perturbations.

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

Proof. Since A is an attractor, there exists an open neighborhood $W \subset U$ of A such that $f(\overline{W}) \subset W$ and an $N \geqslant 1$ such that $f^N(\overline{V}) \subset W$. Continuity of f and compactness of $\overline{V}$ implies that there exists an $\varepsilon_1 > 0$ such that every ε_1 chain of length N starting in $\overline{V}$ ends in W. Let $\varepsilon_2 = \mathrm{dist}(\partial W, f(\overline{W}))$ where ∂W is the boundary of W. Since $f(\overline{W}) \subset W$, every ε_2 chain starting in W must remain in W. Let $\varepsilon = \min\{\varepsilon_1, \varepsilon_2\}$. Since every ε chain of length $n \geqslant N$ starting in V is a concatenation of an ε chain of length N starting in V with an ε chain of length $n - N$ starting in W, all ε chains of length $n \geqslant N$ starting in V must end in $W \subset U$. $\quad\square$

For $x \in S$, define $\Omega(x)$ to be the collection of points $y \in S$ such that for all $\varepsilon > 0$ and $n \geqslant 0$ there exists an ε chain from x to y of length at least n.

Proposition 2. *If f has no attractors contained in S_1, then $\Omega(x) \cap S_0 \neq \emptyset$ for all $x \in S$.*

Proof. Let $x \in S$ be given. Since f is dissipative, there exists a global attractor Γ such that $\mathscr{B}(\Gamma) = S$. Let K be the intersection of all attractors that contain $\Omega(x)$. We begin by proving that $\Omega(x) = K$. The proof follows Conley (1978) 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 $\Omega(x, \varepsilon, n)$ to be the set of points y such that there exists an ε chain of length at least n from x to y. $\Omega(x, \varepsilon, n)$ is an open set. Moreover, since Γ is a global attractor, Proposition 1 implies that $\overline{\Omega(x, \varepsilon, n)}$ is compact for $\varepsilon > 0$ sufficiently small and n sufficiently large. Moreover, we claim that $f(\overline{\Omega(x, \varepsilon, n)}) \subset \Omega(x, \varepsilon, n)$. Indeed, given $z \in \overline{\Omega(x, \varepsilon, n)}$, continuity of f implies that there exists $y \in \Omega(x, \varepsilon, n)$ such that $d(f(z), f(y)) < \varepsilon$. Since $y \in \Omega(x, \varepsilon, n)$, there exists an ε chain, $x_1 = x, x_2, \ldots, x_m = y$, with $m \geqslant n$. Since $d(f(z), f(y)) < \varepsilon$, 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, $f(z) \in \Omega(x, \varepsilon, n)$ and $f(\overline{\Omega(x, \varepsilon, n)}) \subset \Omega(x, \varepsilon, n)$. Since $f^m(\Omega(x)) = \Omega(x) \subset \Omega(x, \varepsilon, n)$ for all m, $A(\varepsilon, n) = \cap_{m \geqslant 1} f^m(\overline{\Omega(x, \varepsilon, n)})$ is an attractor containing $\Omega(x)$ whenever $\varepsilon > 0$ is sufficiently small and n is sufficiently large. Hence, $K \subset A(\varepsilon, n)$. Since $\Omega(x) = \cap_{n \geqslant 1, \varepsilon > 0} \Omega(x, \varepsilon, n)$ and $\Omega(x) \subset K \subset A(\varepsilon, n) \subset \Omega(x, \varepsilon, n)$, we get $\Omega(x) = K = \cap_{n \geqslant 1, \varepsilon > 0} A(\varepsilon, n)$.

Suppose that f has no attractors in S_1. Let $\mathscr{F}$ be the collection of sets

$$\{A \cap S_0 : A \text{ is an attractor containing } \Omega(x)\}.$$

Since finite intersections of attractors are attractors and f has no attractors in S_1 (i.e. every attractor intersects S_0), $\mathscr{F}$ satisfies the finite intersection property. Compactness of Γ implies that intersection of all sets in $\mathscr{F}$ is non-empty. Since the intersection of all sets in $\mathscr{F}$ is $\Omega(x) \cap S_0$, $\Omega(x) \cap S_0 \neq \emptyset$. $\quad\square$

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