Permanence for Replicator Equations

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1. Introduction

Many dynamical systems display strange attractors and hence orbits that are so sensitive to initial conditions as to make any long-term prediction (except on a statistical basis) a hopeless task. Such a lack of Ljapunov stability is not always crucial, however: Lagrange stability may be more relevant. Thus, for some models the precise asymptotic behavior – whether it settles down to an equilibrium or keeps oscillating in a regular or irregular fashion - is less important than the fact that all orbits wind up in some preassigned bounded set. The former problem can be impossibly hard to solve and the latter one easy to handle.

Permanence is a stability notion of Lagrangian type which (like the related ones of strong or weak persistence) applies especially well to population dynamical systems, where questions of survival and extinction occur.

The dynamics will be of the form

$$\dot{x}_i = x_i f_i(\mathbf{x}) \tag{1}$$

on $\mathbf{R}^n_+$, or

$$\dot{x}_i = x_i [f_i(\mathbf{x}) - \bar{f}] \tag{2}$$

on the simplex

$$S_n = \{ \mathbf{x} \in \mathbf{R}^n_+ : \sum x_i = 1 \}$$

where

$$\bar{f} = \sum x_i f_i(\mathbf{x}) \tag{3}$$

guarantees that the vector field is tangent to S_n. The variables x_i are

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densities or relative frequencies of replicating populations. Such equations describe the effect of selection in a wide variety of fields in theoretical biology, e.g., ecology, genetics, evolutionary game theory, or chemical kinetics (for a survey see Sigmund, 1985).

The boundary of the state space (where some x_i vanish) is invariant. So is the interior, where all types are present. If an orbit in the interior converges to the boundary, this spells extinction for one or several types. The system is called *permanent* if there exists a compact set K in the interior such that all orbits in the interior end up in K. This means that the boundary is a repellor (for $\mathbf{R}_+^n$, we consider the points at infinity as part of the boundary). Equivalently, permanence means that there exists a $k > 0$ such that

$$k < \liminf_{t \to +\infty} x_i(t) \tag{4}$$

for all i, whenever $x_i(0) > 0$ for all i [and for equation (1), in addition, that

$$\limsup_{t \to +\infty} x_i(t) < \frac{1}{k} \tag{5}$$

for all i].

Condition (5) means that orbits are uniformly bounded for $t \to +\infty$, a minimal concession to reality. Condition (4) means that if all types are initially present, selection will not lead to extinction. Even a series of small (but infrequent) perturbations will not be able to wipe out any type. Conversely, if some originally missing component is introduced through mutation, it will spread. The "threshold" k is a uniform one, independent of the initial condition. Thus, permanence is a more stringent property than strong persistence [which requires condition (4) with $k = 0$] and persistence [which requires

$$\limsup x_i(t) > 0$$

for all orbits in the interior of the state space]. Permanence was introduced in Schuster *et al.* (1979). For related stability concepts, we refer to Svirezev and Logofet (1983) and Butler *et al.* (1985).

There are basically only one necessary and one sufficient condition for permanence known so far: we describe them in Section 2. But for most examples, the terms f_i in equations (1) and (2) are linear (see Schuster and Sigmund, 1983, and Hofbauer and Sigmund, 1984). This yields

$$\dot{x}_i = x_i[r_i - (A\mathbf{x})_i] \tag{6}$$

resp.