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# PERSISTENCE IN FOOD WEBS

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1. Introduction. Of the stability concepts associated with population dynamics models, the notion of persistence seems to have emerged as most important to ecologists. (See, for example, Holling (1973), Botkin and Sobel (1974), Innis (1974), Maynard Smith (1974).) Persistence, generally, refers to that quality of such models whereby population density levels remain within certain acceptable bounds despite perturbations of model parameters or initial values. Various specific mathematical formulations of persistence have been given by Innis (1974), Botkin and Sobel (1974), Wu (1974), Freedman and Waltman (1977), McGehee and Armstrong (1977), and Harrison (1979a) for models taking the form of systems of ordinary differential equations. All of these definitions of persistence are closely related to the dynamical system concept of flow-invariance. Here this relationship will be discussed, and an extension to food webs of Freedman and Waltman's definition of food chain persistence will be exhibited for the Lotka-Volterra case. In particular, a sufficient condition for top predator persistence in terms of model parameters will be given. Although the discussion will be restricted to ordinary differential equation models, some brief remarks about persistence in dynamical models of other types are in order first.

For stochastic systems, in particular systems subject to random perturbations, Ludwig (1975) has suggested the exit time from a specified set as a measure of system persistence. The exit time is a random variable whose statistics can be estimated using perturbation techniques in this case. Tier and Hanson (1981) have carried out such a program, for example, for a single species population undergoing demographic as well as environmental random fluctuations. Allen (1981) has extended the Freedman-Waltman definition of persistence to systems incorporating spatial effects via different diffusion mechanisms. She has studied both discrete (patch type), and continuous (reaction-diffusion) models for prey-predator, competition, and mutualism systems. The importance of taking into account random fluctuations and spatial heterogeneity in ecosystem models, along with the development of mathematical tools for the analysis of stochastic and reaction-diffusion models, makes this a promising area for future research.

2. Persistence and flow-invariance. All of the persistence definitions cited above for models involving ordinary differential equations require or have as an immediate consequence the existence of a flow-invariant set in state space. To be precise, in this case the model takes the form

$$\frac{dx(t)}{dt} = f(x(t),a(t)) \tag{1}$$

where for each $t$,

$$x(t) = \{x_i(t)\} \in R^n_+ = \{x = \{x_i\} \in R^n \mid x_i \geq 0,\ 1 \leq i \leq n\} \quad ,$$

representing the population densities of $n$ species at time $t$, and $a$ belongs to some admissible class $\mathcal{A}$ so that $a(t) = \{a_j(t)\} \in R^m$ gives the state of the environment at time $t$; the function $f = \{f_i\}: R^n_+ \times R^m \to R^n$ denotes the species' net growth rates. Under mild assumptions on $f$ and $\mathcal{A}$, given an $a \in \mathcal{A}$ and $x_0 \in R^n_+$ there exists a unique solution $x(t)$ of (1) which satisfies $x(t_0) = x_0$ and represents the evolution of species' population densities on some time interval. A set $M \subseteq R_+^n$ is flow-invariant with respect to (1) if each solution $x(t)$ of (1) having initial value $x(0) \in M$ satisfies $x(t) \in M$ for all $t > 0$. Equilibrium points and periodic trajectories are examples of flow-invariant sets. Redheffer and Walter (1975), Seifert (1976), and Gard (1980) review the mathematical literature on flow-invariance. Most of the results give criteria for checking whether or not a given set is flow-invariant. Generally, determining flow-invariant sets for a particular model is a difficult task.

Harrison (1979a) defines a subset $M$ of

$$R_+^{n,o} = \{x = \{x_i\} | x_i > 0, 1 \leq i \leq n\} ,$$

(sometimes referred to as the feasible region), as persistent with respect to (1) and an admissible class $\mathcal{A}$ provided $M$ is flow-invariant with respect to (1) for each $a \in \mathcal{A}$; he also allows $M$ to vary with time (i.e., require $x(t) \in M(t)$, if $x(0) \in M(0)$) and points out that the persistence definitions given by Innis (1974), Botkin and Sobel (1974), and Wu (1974) are special cases of his definition. Furthermore Harrison (1979b) has shown how persistent sets can be determined from Lyapunov functions; the sets so obtained are Lyapunov-stable. It seems reasonable to require the asserted flow-invariant set to be stable for persistence; otherwise, for example, a system which preserves, under various environments, an equilibrium, even an unstable one, would be ruled persistent. The existence of a stable flow-invariant set in $R_+^{n,o}$ corresponds to the definition of persistence used by McGhee and Armstrong (1977) in their treatment of competition systems.

Freedman and Waltman (1977) take a different approach in their analysis of food chain models. Persistence here means that for each solution $x(t) = \{x_i(t)\}$ of (1) with initial value $x(0) \in R_+^{n,o}$, and maximal interval of existence $[0,T)$,

$$\limsup_{t \to \tau} x_i(t) > 0 \qquad (2)$$

for each $i$, $1 \leq i \leq n$, and each $\tau \in (0,T]$. That is, persistence means that no solution having all components positive initially experiences any component tending to zero in finite or infite time. This is a stronger requirement than the definition given previously; for autonomous systems having bounded trajectories in $R_+^{n,o}$, it implies the existence of a one or more stable flow-invariant sets in $R_+^{n,o}$, toward which all trajectories must move as $t \to \infty$. It is easy to see, for food chain models, that this definition of persistence is equivalent to persistence of the top predator; that is, if $x_n$ denotes the density of the top predator, (2) is equivalent to

$$\limsup_{t \to \tau} x_n(t) > 0 , \qquad (3)$$

for each $\tau \in (0,T]$, for each solution $x(t) = \{x_i(t)\}$ with initial value $x(0) \in R_+^{n,o}$ and maximum interval of existence $[0,T)$. For food web models, a natural extension of this persistence definition is, then, that given any population with all species initially present, at least some top predator survives indefinitely, which one survives being possibly dependent on the initial population configuration. This notion of persistence asserts the preservation of the web's trophic structure rather than all species in the web, which may be significant from the point of view of assessing ecological effects. (Paine (1966), in his studies of intertidal communities, has shown that removal of a top predator can drastically reduce community structure.) A disadvantage of this approach to persistence is that, although the existence of flow-invariant sets is asserted, the location of such sets in the feasible region is not addressed. Indeed, for food webs, these sets will not necessarily be situated in $R_+^{n,o}$ ; however, at least one species from each trophic level will be represented in each such set. The situation is somewhat mitigated by the improved mathematical tractability of the problem which is demonstrated in the next section where a criterion in terms of model parameters is deduced for Lotka-Volterra food webs. It is emphasized that these models are primarily of theoretical, as opposed to predictive, value at least at their current stage of development. Freedman (1980) has given a detailed mathematical treatment of the basic properties of Lotka-Volterra models.

3. Persistence in Lotka-Volterra food webs. In this section, the Lotka-Volterra food web, represented by the system of ordinary differential equations

$$\frac{dx_i}{dt} = x_i\left(a_i - \sum_{j=1}^{k} b_{ij}x_j - \sum_{j=1}^{m} c_{ij}y_j\right), \qquad 1 \le i \le k$$

$$\frac{dy_i}{dt} = y_i\left(-d_i + \sum_{j=1}^{k} e_{ij}x_j - \sum_{j=1}^{p} f_{ij}z_j\right), \qquad 1 \le i \le m \tag{4}$$

$$\frac{dz_i}{dt} = z_i\left(-g_i + \sum_{j=1}^{m} h_{ij}y_j\right), \qquad 1 \le i \le p$$

is considered. In this model $x_i(t)$, $y_i(t)$, and $z_i(t)$ denote the population densities at time $t$ of the $i$th prey, intermediate predator, and top predator respectively; the $a_i$, $b_{ij}$, $c_{ij}$, $d_i$, $e_{ij}$, $f_{ij}$, $g_i$, and $h_{ij}$ are positive constants representing the various intrinsic growth and interaction rates. Solutions of (4) with initial values in

$$R^n_+ = \{(x_1,\dots,x_k,y_1,\dots,y_m,z_1,\dots,z_p) \mid x_i \ge 0,\ y_i \ge 0\ z_i \ge 0,\ \text{each } i\},$$
$$n = k + m + p,$$

are unique, bounded, and remain in $R^n_+$ on their entire interval of existence. (These facts are easily deduced from the basic theory of ordinary differential equations.) Of primary interest here are solutions of (4) with initial values in

$$R^{n,o}_+ = \{(x_1,\dots,x_k,y_1,\dots,y_m,z_1,\dots,z_p \mid x_i > 0,\ y_i > 0,\ z_i > 0,\ \text{each } i\}$$

Top predator persistence means that for any solution

$$\varphi(t) = (x_1(t),\dots,x_k(t),y_1(t),\dots,y_m(t),z_1(t),\dots,z_p(t))$$

with initial value $\varphi(0) \in R^{n,o}_+$

$$\limsup_{t\to\tau} z_i(t) > 0 \tag{5}$$

for any $\tau \in (0,T]$, the maximal interval of existence of $\varphi(t)$, and some index $i$, $1 \le i \le p$, which may depend on choice of $\varphi(0)$. Similarly to the corresponding proof in Gard and Hallam (1979) for food chain models, it can be shown that any such solution $\varphi(t)$ is defined on the entire interval $[0,\infty)$ and remains in $R^{n,o}_+$ for all finite time. Thus top predator persistence (5) becomes, for some $i$,

$$\limsup_{t\to\infty} z_i(t) > 0 . \tag{6}$$

The basic problem addressed here is to obtain a criterion in terms of the model parameters which will guarantee (6).

A procedure for obtaining such a criterion involves the construction of a Lyapunov type function

$$\rho(x_1,\dots,x_k,y_1,\dots,y_m,z_1,\dots,z_p)$$

which is positive on $R^{n,o}_+$ and satisfies

$$\rho \to 0 \quad \text{if any} \quad z_i \to 0 \tag{7}$$

Assuming, by way of contradiction, that there is a solution $\varphi(t)$ of (4) with initial value $\varphi(0) \in R^{n,o}_+$ which exhibits $z_i(t) \to 0$, as $t \to \infty$, for all $i$, $1 \le i \le p$, one considers the function

$$\rho(\varphi(t)) = \rho(x_1(t),\dots,x_k(t),y_1(t),\dots,y_m(t),z_1(t),\dots,z_p(t)) .$$

If a differential inequality of the form

$$\dot{\rho} = \frac{d\rho(\varphi(t))}{dt} = \nabla\rho \cdot \left(\frac{dx_1}{dt},\dots,\frac{dx_k}{dt},\frac{dy_1}{dt},\dots,\frac{dy_m}{dt},\frac{dz_1}{dt},\dots,\frac{dz_p}{dt}\right) \ge \lambda\rho , \tag{8}$$

for some positive constant $\lambda$, can be established for sufficiently large $t$, then the required contradiction is obtained. Indeed, inequality (8) holding for sufficiently large $t$ implies $\rho(\varphi(t)) \not\to 0$ as $t \to \infty$ which itself contradicts that $z_i(t) \to 0$ as $t \to \infty$.

For the food web model (4) one chooses $\rho$ of the form

$$\rho = \prod_{i=1}^{k} x_i \prod_{i=1}^{m} y_i^{r_i} \prod_{i=1}^{p} z_i^{s_i}$$

where the constants $r_i$ and $s_i$ are to be determined. Then

$$\begin{aligned}\dot{\rho} = \rho\{ &\sum_{i=1}^{k} (a_i - \sum_{j=1}^{k} b_{ij}x_j - \sum_{j=1}^{m} c_{ij}y_j) \\ &+ \sum_{i=1}^{m} r_i(-d_i + \sum_{j=1}^{k} e_{ij}x_j - \sum_{j=1}^{p} f_{ij}z_j) \\ &+ \sum_{i=1}^{p} s_i(-g_i + \sum_{j=1}^{m} h_{ij}y_j)\}\end{aligned} \tag{9}$$

follows from (4). It is convenient to rewrite (9) as

$$\begin{aligned}\dot{\rho} = \rho\{ &\sum_{i=1}^{k} a_i - \sum_{i=1}^{m} d_i r_i - \sum_{i=1}^{p} g_i s_i \\ &+ \sum_{i=1}^{k} x_i(\sum_{j=1}^{m} e_{ji}r_j - \sum_{j=1}^{k} b_{ji}) \\ &+ \sum_{i=1}^{m} y_i(\sum_{j=1}^{p} h_{ji}s_j - \sum_{j=1}^{k} c_{ji}) \\ &- \sum_{i=1}^{p} z_i \sum_{j=1}^{m} f_{ji}r_j\}\end{aligned} \tag{10}$$

Now let the constants $r_i$ and $s_i$ be nonnegative numbers satisfying the inequalities

$$\sum_{j=1}^{m} e_{ji}r_j - \sum_{j=1}^{k} b_{ji} \geq 0 \,, \quad 1 \leq i \leq k \tag{11}$$

$$\sum_{j=1}^{p} h_{ji}s_j - \sum_{j=1}^{k} c_{ji} \geq 0 \,, \quad 1 \leq i \leq m \tag{12}$$

and let

$$\mu = \mu(\{r_i\},\{s_i\}) = \sum_{i=1}^{k} a_i - \sum_{i=1}^{m} d_i r_i - \sum_{i=1}^{p} g_i s_i \ .$$

Theorem. Top predator persistence holds in (4) if

$$\mu = \mu(\{r_i\},\{s_i\}) > 0 \tag{13}$$

Proof. Suppose $\varphi(t)$ is a solution of (4) with initial value $\varphi(0) \in R_+^{n,o}$ having $z_i$-component $z_i(t)$ tending to zero as $t \to \infty$, for all $i$. Taking $\rho$ defined as above with the $r_i$ and $s_i$ satisfying (11) and (12), it follows from (10) that

$$\frac{d\rho(\varphi(t))}{dt} = \dot{\rho}(\varphi(t)) \geq \rho(\varphi(t))\{\mu - \sum_{i=1}^{p} z_i(t) \sum_{j=1}^{m} f_{ji}r_j\} \tag{14}$$

The assumption that $z_i(t) \to 0$ as $t \to \infty$, for all $i$, $1 \leq i \leq p$ means that the second term in the bracket in (14) becomes arbitrarily small for sufficiently large $t$. Therefore if $\lambda$ is any positive constant less than $\mu$,

$$\dot{\rho}(\varphi(t)) \geq \lambda\rho(\varphi(t))$$

for sufficiently large $t$, and this completes the proof.

The biological interpretation of (13) is straightforward: if the combined intrinsic growth rate of the prey exceeds a linear combination of the intrinsic death rates of the predators where the coefficients of the linear combination are required to satisfy certain relations involving the interaction rates, then top predator persistence is assured. It is clear that the "best" such persistence criterion (13) is obtained by choosing coefficients $r_i$ and $s_i$ which solve the linear programming problem:

$$\text{minimize} \sum_{i=1}^{m} d_i r_i + \sum_{i=1}^{p} g_i s_i$$

subject to the constraints $r_i \geq 0$, $s_i \geq 0$, (11) and (12). The corresponding criterion is "best" in the sense that it places the weakest restriction on the prey growth rates possible. That the result is sharp is indicated by the fact that for $\mu$ obtained in the same way for food chains in Gard and Hallam (1979), it was shown that $\mu < 0$ implied top predator extinction.

The main result can be extended to food webs with more than three trophic levels, food webs exhibiting competition for space among predators, and food webs with arbitrary degrees of omnivory. It is not difficult to see the modifications of the persistence criterion and constraints required in each of these situations. In particular, that omnivory enhances top predator persistence can be readily observed from the form of the corresponding constraint relations.

Example. Consider the Lotka-Volterra model of the two intermediate predator food web given by

$$\begin{aligned} \frac{dx}{dt} &= x(a - b\,x - c_1y_1 - c_2y_2) \\ \frac{dy_i}{dt} &= y_i(-d_i + e_ix - f_iz) \ , \ i = 1,2 \qquad (15) \\ \frac{dz}{dt} &= z(-g + h_1y_1 + h_2y_2) \ . \end{aligned}$$

For $\rho = xy_1^{r_1}y_2^{r_2}z^s$, (10) has the form

$$\begin{aligned} \dot{\rho} = \{&a - d_1r_1 - d_2r_2 - gs \\ &+ x(e_1r_1 + e_2r_2 - b) \\ &+ y_1(h_1s - c_1) + y_2(h_2s - c_2) \\ &- z(f_1r_1 + f_2r_2)\} \end{aligned}$$

Then, from the theorem,

$$\mu = a - d_1r_1 - d_2r_2 - gs > 0 \qquad (16)$$

implies persistence if the nonnegative constants $r_1$, $r_2$, and $s$ are chosen so that

$$e_1r_1 + e_2r_2 \geq b \qquad (17)$$

and

$$h_is \geq c_i \ , \ i = 1,2 \ . \qquad (18)$$

The sharpest such criterion obtains from a solution of the problem

$$\begin{aligned} &\text{minimize} \ \ d_1r_1 + d_2r_2 + gs \\ &\text{subject to} \ \ r_1, r_2, \text{ and } \ s \geq 0, \ (17), \text{ and } (18). \end{aligned} \qquad (19)$$

The solution of (19) consists of taking

$$s = \max \{c_1/h_1, c_2/h_2\} \ ,$$

and $r_1 \geq 0$, $r_2 \geq 0$ minimizing $d_1r_1 + d_2r_2$ subject to (17), i.e., either

$r_1 = b/e_1$ and $r_2 = 0$ if $d_1e_2 < d_2e_1$ ,

$r_1 = 0$ and $r_2 = b/e_2$ if $d_1e_2 > d_2e_1$, or

$r_1$ and $r_2$ are the coordinates of any point on the line $e_1r_1 + e_2r_2 = b$ in the nonnegative quadrant if $d_1e_2 = d_2e_1$.

The corresponding persistence criterion then is

$$a - b \min \{d_1/e_1, d_2/e_2\} - g \max \{c_1/h_1, c_2/h_2\} > 0.$$

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