Journal of Mathematical Biology 3, 5—7 (1976)

On the Differential Equations of Species in Competition

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Received January 9, 1976

Summary

It is shown that the ordinary differential equation commonly used to describe competing species are compatible with any dynamical behavior provided the number of species in very large.

The goal is to show that the ordinary differential equations used in ecology to describe competing species do not say much in case the number of species is more than three or four. In fact these equations are compatiable with any dynamical behavior in a certain reasonable sense.

More precisely consider an ecological system of n competing species with state space

$$R^n_+ = \{x \in R^n \mid x = (x_1, \ldots, x_n),\ x_i \geq 0\}$$

where x_i represents the population of the i-th space.

We suppose the dynamics of population growth is given by the system of ordinary differential equations:

$$\frac{d x_i}{d t} = x_i M_i(x), \quad i = 1, \ldots, n$$

For background on these matters see references [1], [2], [3], [4], [5], [6].

We will impose the following conditions:

(1) $M_i : R^n_+ \to R$ are C^∞ (i.e., have continuous derivative to all orders).

(2) For all pairs i and j between 1 and n, if $x_i > 0$, $\dfrac{\partial M_i(x)}{\partial x_j} < 0$. This is a classic condition of competition which can be interpreted simply as "crowding inhibits growth".

(3) There is a constant $K > 0$ with the property: For each i, $M_i(x) < 0$ if $\| x \| > K$ (i.e., the planet is finite).

Example 1: Let $M_i(x)=1-\sum_{j=1}^{n} x_j$ for each $i=1,\dots,n$. This choice satisfies the conditions (1)—(3). In this case the boundary $\partial R_+^n=\{x\in R_+^n \mid \text{some } x_i=0\}$ is invariant under the flow generated by the differential equations and all other solutions tend as $t\to\infty$ to the invariant "attractor"

$$\Delta_1=\{x\in R_+^n \mid \Sigma x_i=1\}.$$

On Δ_1 the flow is stationary, a very degenerate situation which is remedied by the next example.

Example 2: Define $\Delta_0=\{x\in R^n \mid \Sigma x_i=0\}$, $1_0=(1,\dots,1)\in R_+^n$ and let $\beta: R\to R$ be a C^∞ function which is 1 in a neighborhood of 1 and $\beta(t)=0$ if $t\le\frac{1}{2}$ or if $t\ge 1-\frac{1}{2}$. Now define $h: R_+^n\to\Delta_0$ by

$$h(x)=\left(\frac{1}{n}\right)1_0-\frac{x}{\Sigma x_i}$$

and let $m_i: R_+^n\to\Delta_0\subset R^n$ be defined by

$$m_i(x)=\frac{1}{x_i}\beta(\Sigma x_i)\left(\prod_{j=1}^{n} x_j\right)h(x).$$

The equations of Example 2 are then $\frac{dx_i}{dt}=x_i(M_i+\eta m_i)=x_i N_i$, $\eta>0$, where the M_i are as in Example 1. Then clearly $N_i: R_+^n\to R$ is C^∞ and N_i satisfies Property (2) since for large $\|x\|$, $N_i=M_i$. Also if we choose η small enough, which we do, then (3) is also satisfied.

Let us check properties of solutions of $\frac{dx_i}{dt}=x_i N_i$. Any solution $t\to x(t)$ not lying on the boundary of R_+^n must satisfy $\Sigma x_i(t)\to 1$ as $t\to\infty$. This follows since $\Sigma m_i=0$, and from the form of the M_i. Thus Δ_1 is the attracting set. On Δ_1, the $M_i=0$, and the flow is determined by the $\eta x_i, m_i$, or up to a scalar factor, h restricted to Δ_1. On Δ_1, the differential equation $\frac{dx}{dt}=h(x)$ has $\frac{1}{n}1_0$ as a global linear sink. Thus in Example 2 every solution not on the boundary ∂R_+^n, tends to $\frac{1}{n}1_0\in R_+^n$ as $t\to\infty$.

Example 3: Let $h_0:\Delta_1\to\Delta_0$ be *any* C^∞ map and $h: R_+^n\to\Delta_0$ any C^∞ map which agrees with h_0 on Δ_1. Example 3 then is Example 2 where h is replaced by the above. As in Example 2 with η chosen small enough, conditions (1), (2), and (3) will be satisfied. Furthermore as in Example 2, Δ_1 will be the attractor for all non-boundary solutions, so that after a period of transitions, the dynamics of Example 3 will be the dynamics of $\frac{dx}{dt}=h_0(x)$ on Δ_1 (up to a scalar factor, which doesn't affect the qualitative behavior). But this was arbitrary. The system $\frac{dx}{dt}=h_0(x)$ could be any prescribed system!

We end with a sequence of remarks.

1. Let $n=2$. Then in Example 3, since Δ_1 is one-dimensional. solutions on Δ_1 tend to equilibria which will be stable in general. Thus the same will be true in general for solutions in Example 3. This is consistent with earlier results, see e.g., [5], [1].

2. If $n=3$, in Example 3 one can put on Δ_1 a system with a stable limit cycle γ; in fact we can suppose that every solution on Δ_1 will tend to γ and that perturbations of this system on Δ_1 will have the same properties. Thus every solution in the interior of R^n_+ will oscillate after a period of transition and this property will be true for perturbed systems. Compare this to the results of May and Leonard [4].

3. Suppose $n \geq 5$. Then since Δ_1 is at least 4-dimensional, one may impose on Δ_1 many of the complicated dynamical systems that have been found in recent years (see e.g., [7]). In particular the system of Example 3 may not be approximated by a structurally stable, dynamical system, or it may have strange attractors with an infinite number of periodic solutions, etc.

4. If the constant η as in Example 3 has been chosen small enough, then by the theory of invariant manifolds, after small perturbations of the system, there will remain an invariant manifold near Δ_1. Then in fact if the system on Δ_1 is structurally stable so will be the system on R^n_+.

References

[1] Hirsch, M., Smale, S.: Differential Equations, Dynamical Systems, and Linear Algebra. New York: Academic Press 1974.

[2] Kolomogorov, A. N.: Sulla Teoria di Volterra della Lotta per l'Esistenza, Giorn. Istituto Ital. Attuari *7*, 74—80 (1936).

[3] May, R.: Stability and Complexity in Model Ecosystems. Princeton, N. J.: Princeton University Press 1973.

[4] May, R., Leonard, W.: Nonlinear aspects of competition between three species. SIAM Jour. of Appl. Math. *29*, 243—252 (1975).

[5] Rescigno, A., Richardson, I.: The struggle for life: I, two species. Bull. Math. Biophys. *29*, 377—388 (1967).

[6] Rescigno, A.: The struggle for life: II, three competitors. Bull. Math. Biophys. *30*, 291—298 (1968).

[7] Smale, S.: Differential Dynamical Systems, Bull. Amer. Math. Soc. *73*, 747—817 (1967).

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