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Defining a stability boundary for three species competition models

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ABSTRACT

A periodic steady state is a familiar phenomenon in many areas of theoretical biology and provides a satisfying explanation for those animal communities in which populations are observed to oscillate in a reproducible periodic manner. In this paper we explore models of three competing species described by symmetric and asymmetric May–Leonard models, and specifically investigate criteria for the existence of periodic steady states for an adapted May–Leonard model:

$$\dot{x} = r(1 - x - \alpha y - \beta z)x$$
$$\dot{y} = (1 - \beta x - y - \alpha z)y$$
$$\dot{z} = (1 - \alpha x - \beta y - z)z.$$

Using the Routh–Hurwitz conditions, six inequalities that ensure the stability of the system are identified. These inequalities are solved simultaneously, using numerical methods in order to generate three-dimensional phase portraits to illustrate the steady states. Then the "stability boundary" is defined as the almost linear boundary between stability and instability. All the mathematics discussed is suitable for advanced undergraduate mathematics or applied mathematics students, offering them the opportunity to incorporate a computer algebra system such as Mathematica, DERIVE or Matlab in their investigations. The adapted May–Leonard model provides a practical application of steady states, stability and possible limit cycles of a nonlinear system.

1. Introduction

In the biological sciences, stable periodic states or stable limit cycles are constantly being sought, since they may provide a satisfying explanation for those animal communities in which populations are observed to oscillate in a periodic manner (May, 1972). Stability, in ecological terms, refers to an ability of a living system to persist in spite of perturbation. Obviously this is a highly desirable situation for any ecosystem where populations interact. If a valid and adequate mathematical model is built to represent the dynamics of a biological community, then the stability properties of the real system can be deduced by investigating the model's stability. It is therefore useful to define conditions that will ensure stability of the mathematical model, which will in turn indicate under which conditions the ecological system will prove to be stable over time.

The models developed can seldom be solved analytically; therefore these models should be studied numerically or using qualitative methods. Furthermore, Van der Vaart (1976) warns that although we have come a long way in developing mathematical models to describe ecosystems dynamics, these models are still deemed elementary, and should only be seen as an aid in decision making processes.

In this paper we examine a generalization of the classical three competing species model proposed by May and Leonard (1975) and investigate for which parameter values the new model will prove to have stable responses over time. We define the existence of a boundary between stability and instability as an almost linear curve, where for certain parameter values lying underneath the curve the system is stable, above the curve it is unstable and for values situated precisely on the curve a periodic steady state occurs. By stability we mean bounded periodic oscillatory response over time.

First a brief overview of the symmetric and asymmetric May–Leonard models, as applied to a system of three competing species, is given. A new adapted model of the classical May–Leonard type is then proposed, and using computer-generated data, a condition for the existence of families of periodic steady states are identified. Mathematica (Wolfram, 1996) is used to graphically demonstrate the periodic steady states found under these special conditions.

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2. The symmetric May–Leonard model

In order to provide the basic principles for this paper, consider the classic quadratic population model for three interacting species, namely

$$\begin{aligned}\dot{x} &= (a_0 + a_1 x + a_2 y + a_3 z)x\\ \dot{y} &= (b_0 + b_1 x + b_2 y + b_3 z)y\\ \dot{z} &= (c_0 + c_1 x + c_2 y + c_3 z)z.\end{aligned} \tag{1}$$

As usual, $\dot{x}$ denotes the rate of change of population x, and likewise for $\dot{y}$ and $\dot{z}$. Since this model has 12 parameters to deal with, May and Leonard (1975) made it more manageable by reducing the number of parameters in making the following assumptions:

(i) Let the population growth rates be $a_0 = b_0 = c_0 = r$.
(ii) By rescaling t, it can be assumed that $r = 1$.
(iii) With respect to inter-species competition, population y affects population x similarly as z affects y and as x affects z, so that $a_2 = b_3 = c_1 = \alpha$.
(iv) Similarly let $a_3 = b_1 = c_2 = \beta$.
(v) By rescaling the populations, it can be assumed with respect to intra-species competition, that $a_1 = b_2 = c_3 = 1$

Consequently the May–Leonard model describing a system for three competing species is given by:

$$\begin{aligned}\dot{x} &= (1 - x - \alpha y - \beta z)x\\ \dot{y} &= (1 - \beta x - y - \alpha z)y\\ \dot{z} &= (1 - \alpha x - \beta y - z)z.\end{aligned} \tag{2}$$

with α and β positive.

May and Leonard (1975) note that "the values of the competition coefficients α and β which lead to cycles, may be seen to correspond to the biological circumstance where in purely pair-wise competition population x beats y, y beats z and z beats x. Such circumstances are not plausible. It is this transitivity in the pair-wise competition which underlies the cyclic behaviour; the phenomenon clearly requires at least three competitors, which is why it cannot occur in models with two competitors."

With eigenvalue analysis it can be shown that the only equilibrium point of this system is located at $(1/(\beta+\alpha+1), (1/(\beta+\alpha+1), (1/(\beta+\alpha+1))$ Considering the variational matrix at this point, May and Leonard (1975) prove that a necessary and sufficient condition to ensure stability would be if $\alpha+\beta<2$, and that consequently, independent of initial conditions, a limit cycle will exist if $\alpha+\beta<2$. Using randomly chosen initial conditions and assuming values of $\alpha = 1.2$ and $\beta = 0.8$ so that $\alpha+\beta<2$ as an example, a number of stable limit cycles are observed in the phase plane of the May–Leonard model, as illustrated in Fig. 1.

It may be noted that, according to the mathematical definition of limit cycles, these are not truly limit cycles but rather periodic steady states (PSS), since trajectories resulting from nearby initial conditions do not spiral into the same periodic steady state, but appear to be forming their own unique steady states. However, stability of the mathematical system (and consequently of the ecological system represented by the model) is clearly indicated by the existence of the steady states.

3. The asymmetric May–Leonard model

In an interesting adaptation of the classical May–Leonard model, Chi et al. (1998) investigate the effect on stability when varying the inter-species competition parameters. They analyze the global asymptotic behaviour of what they call the asymmetric May–Leonard model. Their rescaled system models the competition between three species, with the same intrinsic growth rate and intra-species competition parameters but different inter-species competition coefficients. The asymmetric May–Leonard model under these circumstances is

$$\begin{aligned}\dot{x} &= (1 - x - \alpha_1 y - \beta_1 z)x\\ \dot{y} &= (1 - \beta_2 x - y - \alpha_2 z)y\\ \dot{z} &= (1 - \alpha_3 x - \beta_3 y - z)z\end{aligned} \tag{3}$$

Under the assumptions $A_i = 1 - \alpha$ and $B_i = \beta_i - 1$ for $i = 1, 2, 3$, Chi et al. (1998) prove the existence of neutrally stable periodic solutions if $B_1B_2B_3 = A_1A_2A_3$, as graphically illustrated in Fig. 2.

The question now arises: what would be the effect on stability when varying the growth and competition parameters of one of the three species? An example illustrating such a situation is given by Greeff and Fay (2008). They discuss a three species competition model for nyala, impala and duiker in the Ndumo Game Reserve, where the growth and inter- and intra-species competition parameters for nyala and impala are almost equal, but the parameter values for duiker is much lower. Under what conditions

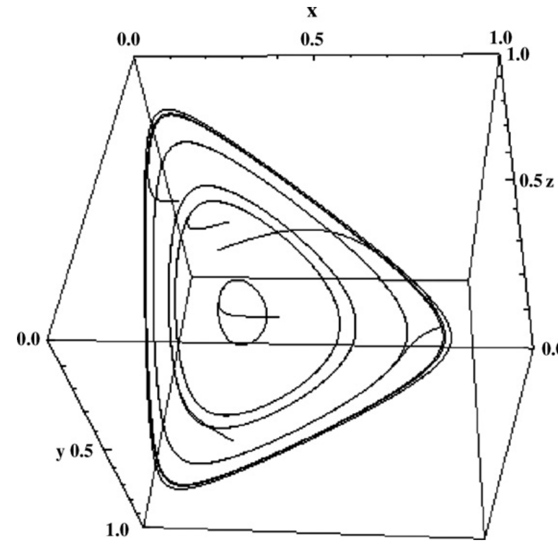

Fig. 1. For chosen values $\alpha = 1.2$ and $\beta = 0.8$ and randomly chosen initial conditions, limit cycles are graphically observed for the May–Leonard model for three competing species.

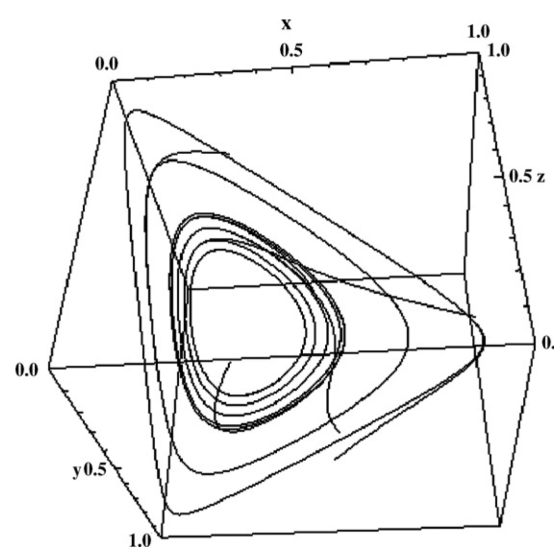

Fig. 2. As an example, stable periodic solutions for the *asymmetric* May–Leonard model are illustrated when choosing random values of $\alpha_1 = 0.2$, $\alpha_2 = 0.3$ and $\alpha_3 = 0.0857142$, and $\beta_1 = 1.7$, $\beta_2 = 1.5$ and $\beta_3 = 2.4628571$, so that $B_1B_2B_3 = A_1A_2A_3 = 0.512$.