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Quantitative analysis of competition models

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We study a 2-species Lotka–Volterra type differential system, modeling competition between two species and having a coexistence equilibrium in the first quadrant. In case that this equilibrium is of saddle type, its stable manifold divides the first quadrant into two zones. Then, depending on the zone where the initial condition lies, one of the species will extinct and the other will go to an equilibrium. Using this separatrix we introduce a measure to discern which species has more chance of surviving. This measure is given by a non-negative real number κ, that we will call *persistence ratio*, that only depends on the parameters of the system. In some cases, we can give simple explicit expressions for κ. When this is not possible, we use several dynamical tools to obtain effective approximations of it.

1. Introduction

In competition models two or more species struggle for a limited source, like food or territory. Following Murray [1, Sec. 3.5], in this work we consider a simple 2-species Lotka–Volterra competition model for which each species has logistic growth in absence of the other. More specifically, we consider the quadratic differential system

$$\begin{aligned} \dot{x} &= \frac{dx}{dt} = x(\lambda - \alpha_1 x - \alpha_2 y), \\ \dot{y} &= \frac{dy}{dt} = y(\mu - \beta_1 x - \beta_2 y), \end{aligned} \tag{1}$$

where $\alpha_1, \alpha_2, \beta_1, \beta_2, \lambda$ and μ are positive parameters and $t \in \mathbb{R}$ is the time. For short we name $\mathcal{X}$ and $\mathcal{Y}$ the species with respective populations x and y.

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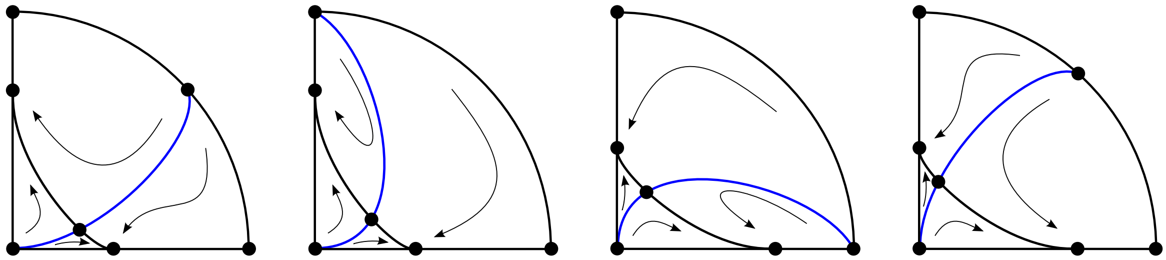

(a) $1 \leq \frac{\mu}{\lambda} < \min\{\frac{\alpha_2}{\beta_2}, \frac{\beta_1}{\alpha_1}\}$. (b) $\frac{\alpha_2}{\beta_2} \leq 1\frac{\mu}{\lambda} < \frac{\beta_1}{\alpha_1}$. (c) $\frac{\mu}{\lambda} < \frac{\beta_1}{\alpha_1} \leq 1 < \frac{\alpha_2}{\beta_2}$. (d) $\frac{\mu}{\lambda} < 1 < \min\{\frac{\alpha_2}{\beta_2}, \frac{\beta_1}{\alpha_1}\}$.

Fig. 1. Phase portraits in the first quadrant of the Poincaré sphere of system (1) having a saddle in the open first quadrant. The separatrix $\mathcal{S}$ of the saddle is presented in blue. Note that either (a) and (d), and (b) and (c), are equivalent after swapping variables. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We will study the case when the above system has an equilibrium $\mathbf{p}$ in the open first quadrant which is of saddle type. Recall that this situation allows to show for this 2-species model the so called *Principle of competitive exclusion:* when two species compete for the same limited resources, one of them usually becomes extinct. System (1) is known to be a good model for several kinds of species in competition, as shown in the classical works of Gause and Leslie, see [2,3].

To the best of our knowledge, there is not a quantitative version of this principle. The aim of this paper is to fill this gap. We will introduce a non-negative real (even infinity) number κ, that we will call *persistence ratio*, that will measure which of both species has more chance of surviving and that depends only on the parameters of the model. As we will see, the computation of this number relays on the knowledge of the expression of the stable manifold of $\mathbf{p}$, $\mathcal{S} = \mathcal{W}^s(\mathbf{p})$, where $\mathbf{p}$ is a hyperbolic saddle in the open first quadrant. Since for the most of the cases this manifold is not algebraic, this computation is not easy. In this work we will approach κ by looking for algebraic approximations of $\mathcal{S}$. These approximations will be obtained following similar tools to the ones developed in [4–6]. For fixed values of the parameters of the model, an alternative approach for obtaining κ would be to apply numerical methods to compute $\mathcal{S}$. However, in this work, we center our efforts in obtaining analytic results.

Next we introduce κ for system (1), in the case that it has a saddle point in the first open quadrant. In fact, in this situation it can be seen that the system has two more equilibria on the positive axes $(0, \mu/\beta_2)$ and $(\lambda/\alpha_1, 0)$ that correspond to extinction of the first or the second species, respectively. The different phase portraits of system (1) having a saddle in the first quadrant of the Poincaré disk are given in Fig. 1, where the arc of circle corresponds to the points at infinity. See [7–9] for more information about the Poincaré compactification. In fact, phase portraits and integrability of general quadratic Lotka–Volterra systems have been studied in many works, see for instance [10–12] and the references therein.

Given any positive real number $R > 0$, consider the two areas

$$\begin{aligned} A^+(R) &= \mu_{\mathcal{L}}\big(\{z_0 \in [0,R]^2 \,:\, \omega(\gamma_{z_0}) = (0, \mu/\beta_2)\}\big), \\ A^-(R) &= \mu_{\mathcal{L}}\big(\{z_0 \in [0,R]^2 \,:\, \omega(\gamma_{z_0}) = (\lambda/\alpha_1, 0)\}\big), \end{aligned}$$

where $\mu_{\mathcal{L}}$ is the Lebesgue measure, γ_{z_0} is the orbit with initial condition $z_0 = (x_0, y_0)$ and $\omega(\gamma_{z_0})$ is its ω-limit set. The *persistence ratio of $\mathcal{Y}$ with respect to $\mathcal{X}$* is

$$\kappa_{[\mathcal{Y}\,:\,\mathcal{X}]} = \lim_{R\to\infty} \kappa_{[\mathcal{Y}\,:\,\mathcal{X}]}(R), \quad \text{where } \kappa_{[\mathcal{Y}\,:\,\mathcal{X}]}(R) = \frac{A^+(R)}{A^-(R)}.$$

Note that we can also define $\kappa_{[\mathcal{X}\,:\,\mathcal{Y}]} = 1/\kappa_{[\mathcal{Y}\,:\,\mathcal{X}]}$. We will see that the above limit always exists, including infinity. Indeed when it is infinity it means that $\kappa_{[\mathcal{X}\,:\,\mathcal{Y}]} = 0$. Note that it is non-negative because it comes from a quotient of areas. When there is no confusion we will simply write $\kappa = \kappa_{[\mathcal{Y}\,:\,\mathcal{X}]}$ or $\kappa(R) = \kappa_{[\mathcal{Y}\,:\,\mathcal{X}]}(R)$.