Original Research Article

Basins of attraction of the classic model of competition between two populations

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ABSTRACT

In this paper we revisit the classic Lotka–Volterra model of competition between two populations and present some new results on the regime of bistability presented by this model. Initially, we review the results on the global stability analysis of the system and present a new global energy function. Then, we extend the model analysis in the case of strong competition, when the system has two asymptotically stable equilibria. The influence of parameters on the size and shape of the basins of attraction of these equilibria was characterized. The results show that the higher the rate of interspecific competition of a population, the greater the basin of attraction of the stable equilibrium that corresponds to the predominance of the same. In addition, the relative birth rate of population influences the curvature of the boundary between the basins of attraction which is the stable manifold of a saddle point. The influence analysis of this parameter reveals an interesting relation. Which population has more chances to survive depends on the context in which the initial conditions take place. In the case where populations begin with a large number of individuals, the one with a smaller birth rate will survive; in the case where populations begin with few individuals, the one with a greater birth rate will survive. We showed this result analytically by using the Picard method to approximate invariant manifolds and to obtain the expression for the curvature of the stability boundary. Finally, the analysis of the joint influence of competition and reproduction on the thresholds for initial conditions was made and the biological implications were discussed. We conclude that in terms of strategy for survival of a population, it is more efficient to adjust its reproductive rate than to improve its ability to withdraw resources from the environment.

1. Introduction

The task of estimating basins of attraction is common and important in the analysis of dynamic systems that describe electric power systems, and many tools have been developed for this purpose (Alberto, 2006; Chiang et al., 1988; Genesio et al., 1985). In mathematical biology, the determination of the basin of attraction of a locally asymptotically stable (LAS) equilibrium point is also an important problem (Gatto and Rinaldi, 1977). In 1973, in his seminal paper about resilience (Holling, 1973), Holling raised the issue of studying in more detail, from the resilience point of view, biological systems presenting multistability. While the stability view emphasizes the equilibrium, the maintenance of a predictable world, and the harvesting of nature's excess production with as little fluctuation as possible, the resilience view emphasizes basins of attraction and the need for persistence,

where extinction results from the interaction of random events with those deterministic forces that define the shape, size, and characteristics of the basin of attraction.

Global results on bistability are important because of the biological meaning of equilibrium points. If, an equilibrium point represents the extinction of a population that should be preserved, it is thus desirable that the initial conditions are not in its basin of attraction. One can study control strategies on system parameters so that this basin of attraction decreases, therefore increasing the chances that an initial condition does not lead to extinction of the population.

Several works have dealt with this issue from a biological standpoint (Holling, 1973; May, 1977; Scheffer et al., 2001; Walker et al., 2004; Folke et al., 2004), but as far as we know, there has been no global analysis and comprehensive description of the bistability regime and the influence of parameters on size and shape of the basins of attraction in population dynamics models. From the mathematical point of view, the most common approach has been through the construction of Lyapunov functions that in general are difficult to devise and do not provide the estimation of

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the entire basin of attraction (Gatto and Rinaldi, 1977; Genesio et al., 1985; Goh, 1978).

In this work we perform a comprehensive description of the regime of bistability presented by the classical model of competition between two populations (Murray, 2000), which is a modification of the well-known Lotka–Volterra predator–prey model:

$$\begin{cases} \dfrac{dN}{dt} = r_N N\left(1 - \dfrac{N}{K_N} - a_{21}\dfrac{I}{K_N}\right) \\ \dfrac{dI}{dt} = r_I I\left(1 - \dfrac{I}{K_I} - a_{12}\dfrac{N}{K_I}\right). \end{cases} \tag{1}$$

This is a classical model, frequently presented in the beginning of the study of population dynamics, and has been a basis model for various other more complex phenomena of biological invasions (Fassoni and Martins, 2014). In the strong interspecific competition regime, this system presents the interesting dynamic phenomenon of bistability. The two equilibrium points corresponding to the survival of only one of the populations are LAS, and the phase space is divided into two basins of attraction. However, this phenomenon of bistability is treated only in a general way, and it is said only that the trajectories beginning above the separatrix between the basins of attraction lead to the extinction of the first population, and that the trajectories beginning below the separatrix lead to extinction of the other population (Murray, 2000).

The main objective of this work is to answer the question of what the biological implication of the different configurations of size and shape of the basins of attraction is, and to study how these properties are governed by parameters. It is expected that, for example, the greater the competitiveness of a population, the greater the basin of attraction of the point corresponding to its survival and the extinction of the other is. On the other hand, what is expected with respect to the reproduction rate of each population? Does a population that reproduces faster have more chances of survival? Together with numerical and analytical results and the combination of tools of differential geometry with qualitative theory of differential equations, we answer this question and extend the global analysis of this classic model. We showed that the rates of reproduction of the species, despite their not having any influence on the linear stability of equilibria, do have an influence on the curvature of the entire separatrix between the basins of attraction. Therefore, these rates play a crucial role in the shape of the basins. This role translates into an interesting biological mechanism that reveals the chance of survival of a population is not always increasing with the rate of reproduction of the population. The results show that this relation depends heavily on the context from which the initial conditions are taken.

The paper is organized as follows. In Section 2, we revisit the model, describing the linear stability analysis of equilibrium points; also, we discuss some general results on invariant manifolds and basins of attraction of LAS equilibrium points that allow us to characterize each basin of attraction. In Section 3, results on the influence of parameters on basins are presented and biological implications of the results are discussed. By using the Picard method to approximate invariant manifolds, a relation between the rates of reproduction of the populations and the curvature of stability boundary is found. The proofs of analytical results of Section 3 are in Appendix A. Finally, in Section 4 some conclusions are drawn.

2. Revisiting the model – local and global stability analysis

Along this paper, we call N the native population and I the invader population. System (1) assumes that each population presents a Verhulst growth and that populations compete for limited resources available in the environment. All parameters are positive; r_N and r_I represent the birth rate of the native and invader populations, respectively; K_N and K_I represent the carrying capacity of these populations; a_{21} represents the competitive pressure made by the invader population on the native population, and a_{12} is analogous. System (1) can be reduced to a dimensionless form by considering $\overline{N} = N/K_N$, $\overline{I} = I/K_I$ and $\overline{t} = r_N t$. Omitting the bars, the dimensionless form of (1) is

$$\begin{cases} \dfrac{dN}{dt} = N(1 - N - \alpha I) \\ \dfrac{dI}{dt} = \delta I(1 - I - \beta N), \end{cases} \tag{2}$$

where N and I now represent the density of the populations with respect to their carrying capacity. The dimensionless parameters are $\alpha = a_{21}(K_I/K_N)$, $\beta = a_{12}(K_N/K_I)$ and $\delta = (r_I/r_N)$. α and β represent the competitive pressures made by each population and $\delta = (r_I/r_N)$ is the ratio between the reproduction rates of I and N; note that $\delta > 1$ implies that I reproduces faster than N, and $\delta < 1$ implies that N reproduces faster.

System (2) has the trivial equilibrium point $P_0 = (0, 0)$, which is a source, since its eigenvalues are 1 and δ. In consequence, both populations will never be led to extinction simultaneously. Further, system (2) also has the equilibrium points

$$P_1 = (1, 0) \text{ and } P_2 = (0, 1),$$

which represent the extinction of the invader population and the extinction of the native population, respectively. The eigenvalues of the Jacobian matrix in P_1 are -1 and $\delta(1 - \beta)$, while the eigenvalues of the Jacobian matrix in P_2 are $-\delta$ and $1 - \alpha$. Therefore, we conclude that if a population competes strongly, it can eliminate the other population. Since in this work we are interested in analyzing only the hyperbolic equilibrium points, from now on we consider $\alpha \neq 1$ and $\beta \neq 1$.

If $\alpha, \beta < 1$ or $\alpha, \beta > 1$, there is another equilibrium point,

$$P_3 = \left(\frac{\alpha - 1}{\alpha\beta - 1}, \frac{\beta - 1}{\alpha\beta - 1}\right),$$

which represents the coexistence of both populations. As to the eigenvalues of $J(P_3)$, it is possible to show (see Murray, 2000) that they have a real negative part if $\alpha < 1$ and $\beta < 1$, and that they are real and have opposite signs if $\alpha > 1$ and $\beta > 1$. Thus, if both populations compete weakly, coexistence may occur. If both compete strongly, coexistence is not possible. And if one of them competes strongly and the other is a weak competitor, the strong one eventually will eliminate the weak.

These results lead to the well known *principle of competitive exclusion*, a fairly general principle which is observed to hold true in nature. Note that the parameter δ plays no role in the stability analysis.

If $\alpha > 1$ and $\beta > 1$, system (2) has two LAS equilibrium points, $P_1 = (1, 0)$ and $P_2 = (0, 1)$. The outcomes will depend on the initial conditions: there are some that lead to P_1 and others that lead to P_2. Results above are only local and reveal nothing about this global behavior of the system, i.e., the division of the phase space in two regions with different asymptotic behavior of the solutions. Thus, a global study in this respect is necessary. For this purpose, we discuss some general results on invariant manifolds and basins of attraction of LAS points. For more information see Alberto (2006) and Chiang et al. (1988).

Let $\mathbf{f} : \Omega \to \mathbb{R}^n$ be a C^1 vector field, where $\Omega \subset \mathbb{R}^n$ is an open subset, and consider the nonlinear system $\mathbf{x}' = \mathbf{f}(\mathbf{x})$. We say that a hyperbolic equilibrium point $\mathbf{x}^*$ of $\mathbf{f}$ is a type k equilibrium point if the matrix $J(\mathbf{x}^*) = D\mathbf{f}(\mathbf{x}^*)$ has exactly k eigenvalues with positive real parts. The Stable Manifold Theorem (Coddington and Levinson, 1972; Perko, 2001) ensures that in a neighborhood of a type k equilibrium point $\mathbf{x}^*$, there is a stable manifold $S \subset \Omega$ of dimension