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Rethinking the logistic approach for population dynamics of mutualistic interactions

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HIGHLIGHTS

- We introduce a new population dynamics model for mutualistic communities.
- The new model preserves the original logistic formulation.
- We perform an analytical stability analysis to study the model behavior.
- We perform numerical simulations to test the model behavior.
- The model shows as much richness or even more than other mutualistic models.

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ABSTRACT

Mutualistic communities have an internal structure that makes them resilient to external perturbations. Late research has focused on their stability and the topology of the relations between the different organisms to explain the reasons of the system robustness. Much less attention has been invested in analyzing the systems dynamics. The main population models in use are modifications of the $r-K$ formulation of logistic equation with additional terms to account for the benefits produced by the interspecific interactions. These models have shortcomings as the so-called $r-K$ formulation diverges under some conditions. In this work, we introduce a model for population dynamics under mutualism that preserves the original logistic formulation. It is mathematically simpler than the widely used type II models, although it shows similar complexity in terms of fixed points and stability of the dynamics. We perform an analytical stability analysis and numerical simulations to study the model behavior in general interaction scenarios including tests of the resilience of its dynamics under external perturbations. Despite its simplicity, our results indicate that the model dynamics shows an important richness that can be used to gain further insights in the dynamics of mutualistic communities.

1. Introduction

Despite its long history, there are still several open issues in the research of ecological population dynamics. Some of these questions were highlighted in the 125th anniversary issue of the journal *Science* (Kennedy and Norman, 2005; Pennisi, 2005; Stokstad, 2005). For example, aspects such as the mechanisms determining species diversity in an ecosystem are under a very active scrutiny by an interdisciplinary scientific community (Williams and Martínez, 2000; Dunne et al., 2002; Olesen et al., 2007; Allesina et al., 2008; Bascompte, 2009; Saavedra et al., 2009; Bastolla et al., 2009; Fortuna et al., 2010; Encinas-Viso et al., 2012). Quantitative population dynamics goes back to 1202 when Leonardo Fibonacci, in his *Liber Abaci*, described the famous series that follows the growth of rabbit population (Sigler, 2002). Classical population theory began, however, in 1798 with Robert Malthus' *An Essay on the Principle of Population* (Malthus, 1798). Malthus argued that population growth is the result of the difference between births and deaths, and that these magnitudes

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are proportional to the current population. Mathematically, this translates into the differential equation:

$$\frac{dN}{dt}=r_0N, \tag{1}$$

where N is the population size, r_0 is the *intrinsic rate* of growth of the population and equals the difference between the rates of birth and death (assuming no migrations).

The Malthusian model predicts an exponential variation of the population, which if $r_0>0$ translates into an unbounded growth. In this model, r_0 remains constant along the process ignoring thus limiting factors on the population such as the lack of nutrients or space. In 1838 Verhulst introduced an additional term, proposing the so-called *logistic* equation (see Verhulst, 1845). The growth rate must decrease as N increases to limit population growth and the simplest way to achieve this is by making r_0 a linear function of N: $r_0=r-\alpha N$, where r is the intrinsic growth rate and α a positive (friction) coefficient that is interpreted as the intraspecific competition. This approach leads to the $r-\alpha$ model:

$$\frac{dN}{dt}=rN-\alpha N^2. \tag{2}$$

The term with α acts as a biological *brake* leading the system to a point of equilibrium for the dynamics with a population value approaching $K=r/\alpha$, usually called the *carrying capacity* of the system.

The logistic equation is best known in the form that Raymond Pearl introduced in 1930 (see Mallet, 2012 for an excellent historical review). In this formulation, the carrying capacity appears explicitly, and so it is known as $r-K$:

$$\frac{dN}{dt}=rN\left(1-\frac{N}{K}\right). \tag{3}$$

The solution of this equation is a sigmoid curve that asymptotically tends to K. This formulation has some major mathematical drawbacks (Kuno, 1991; Gabriel et al., 2005). The most important is that it is not valid when the initial population is higher than the carrying capacity and r is negative. Under those conditions, it predicts an unbounded population growth. This issue was noted by Richard Levins, and consequently is called Levins' paradox (Gabriel et al., 2005). It is important to stress that all mutualistic models derived from Pearl's formula inherit its limitations in this sense.

These seminal models of population dynamics did not take into account interactions between species. When several species co-occur in an community there can be a rich set of relationships among them that can be represented as a complex interaction network. In 1926, Vito Volterra proposed a two-species model to explain the behavior of some fisheries in the Adriatic sea (Volterra, 1926). Volterra's equations describe prey $N(t)$ and predator populations $P(t)$ in the following way:

$$\frac{dN}{dt}=N(a-bP),$$
$$\frac{dP}{dt}=P(cN-d), \tag{4}$$

where a, b, c, and d are positive constants. In the Lotka–Volterra model, as it is known today, the prey population growth is limited by the predator population, while the latter benefits from the prey and is bounded by its own growth. This pair of equations has an oscillatory solution that in the presence of further species can even become chaotic.

While prey–predator and competition interactions have been extensively studied, mutualistic interactions, which are beneficial for all the species involved, have received a lower level of attention. Interestingly, back in the XIX century, Charles Darwin had already noticed the importance of a mutualistic interaction between orchids and their pollinators (Darwin, 1862). Actually, the relations between plants and their pollinators and seed dispersers are the paradigmatic examples of mutualism. In this context, Ehrlich and Raven (1964) alluded to the importance of plant–animal interactions in the generation of Earth's biodiversity. The simplest mutualistic model without '*an orgy of mutual benefaction*' was proposed by May (1981). Each of May's equations for two species is a logistic model with an extra term accounting for the mutualistic benefit. It is the same idea as in the Lotka–Volterra model but interactions between species always add to the resulting population. May's equations for two species can be written as

$$\frac{dN_1}{dt}=r_1N_1\left(1-\frac{N_1}{K_1}\right)+r_1N_1\beta_{12}\frac{N_2}{K_1},$$
$$\frac{dN_2}{dt}=r_2N_2\left(1-\frac{N_2}{K_2}\right)+r_2N_2\beta_{21}\frac{N_1}{K_2}, \tag{5}$$

where N_1 (N_2) is the population of the species 1 (2); $r_{1,2}$ is the intrinsic growth rate of population 1 (2) and K_1 (K_2) the carrying capacity. This is the maximum population that the environment can sustain indefinitely, given food, habitat, water and other supplies available in the environment. Finally, β_{12} (β_{21}) is the coefficient that embodies the benefit for population 1 (2) of each interaction with population 2 (1). May model's major drawback is that it also leads to unbounded growth. This model has been, anyhow, an inspiration for subsequent mutualist models that incorporate terms to solve this problem.

Different strategies to avoid the unlimited growth have been adopted. Wright (1989) proposed a two-species model with saturation as a result of restrictions on handling time, T_H, which corresponds to the time needed to process resources (food) produced by the mutualistic interaction. The mutualistic term can be included as a type II functional response

$$\frac{dN_1}{dt}=r_1N_1-\alpha_1N_1^2+\frac{abN_1N_2}{1+aN_2T_H},$$
$$\frac{dN_2}{dt}=r_2N_2-\alpha_2N_2^2+\frac{abN_1N_2}{1+aN_1T_H}, \tag{6}$$

where a is the effective search rate and b is a coefficient that accounts for the rate of encounters between individuals of species 1 and 2. Wright analyzes two possible behaviors of mutualism: *facultative* and *obligatory*. In the facultative case, $r_{1,2}$ are positive, *i.e.*, mutualism increases the population but it is not indispensable to species subsistence. If $r_{1,2}$ are negative mutualism is obligatory to the species survival. This model has different dynamics depending on the parameter values, but for a very limited region of parameters shows three fixed points. One stable at both species extinction, another also stable at large population values and a saddle point separating both basins of attractions. Using a mutualistic model with a type II functional, Bastolla et al. (2005, 2009) show the importance of the structure of the interaction network to minimize competition between species and to increase biodiversity. The type II models are, however, hard to treat analytically due to the fractional nature of the mutualistic term. Other recent alternatives have been proposed as, for instance, that of Johnson and Amarasekare (2013). Still, these works go in the direction of adding extra features to the type II functional rendering more difficult an eventual analytical treatment.

Recently, the research in this area has focused on system stability, looking for an explanation of the resilience of these communities in the interaction networks (Saavedra et al., 2009; Bastolla et al., 2009; Thébault and Fontaine, 2010; Fortuna et al., 2010; Staniczenko et al., 2013). The dynamics is, however, as important since changes in the parameters that govern the equations induced by external factors can lead the systems to behave differently and to modify their resilience to perturbations in the population levels. Here, we revisit the basic model