Generic model of population dynamics

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Population dynamics has been modelled using differential equations since Malthus, more than two centuries ago. At this moment, there is no unified or general model that encapsulates all biotic interactions, given that the most used models, denominated as Holling's types I, II and III functionals, involves too many variations and ad hoc premises. Here we discuss a different approach in order to model ecological equations, based on the logistic-mutualistic model of García-Algarra *et al.* [1]. We propose that Holling's types functionals reflect only a self-saturation limit and that García-Algarra's model, once generalised, reflects both inter and intraspecific saturation limits. *Any ecological model can be formulated by specific growth rate terms plus the competition terms that limits the population growth.* Even when a complete ecological model surely must involve both limits, population dynamics tend to stay within only one of the regimes.

In this general model one can include in the equation of species i any species interacting with it, even itself. The interaction between individuals of the same species can be beneficial, namely, *cooperation*, or detrimental, as can be *cannibalism* or violent competition. In any case, it is possible to include the effect of the own species in its growth rate, so the general ecological interaction model can be written as

$$\dot{X}_i = X_i \left[\left(r_i + \sum_{j=1}^n b_{ij} X_j \right) (1 - \epsilon_i X_i) \right], \quad (1)$$

where the subscript i runs from 1 to n. Note that the effective growth rate term includes the interaction between individuals of the same species in the summand $j = i$, where the coefficient b_{ii} is positive if it represents *cooperation* or negative if it represents violent competition.

One can go one step further if one considers the intrinsic growth rate r_i as an *interaction* with the environment, in such a way that the parameter r_i can be written as

$$r_i = b_{i0} X_0, \quad (2)$$

where X_0 can be considered constant. The identification of the intrinsic growth rate r_i as another interaction term allows us to reformulate Eq. (1) as a Verhulst equation with a growth rate given by the addition/subtraction of all the beneficial/detrimental interactions terms, including the environment and the own species. Now in Eq. (1) the sum can be extended from $j = 0$ to $j = n$ and a generic ecological
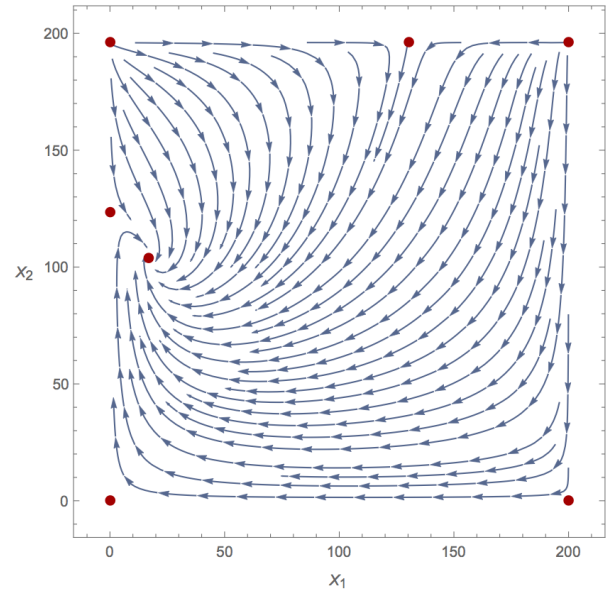

Fig. 1. Space phase with different fixed points in red.

interaction model can be expressed as

$$\dot{X}_i = \sum_{j=0}^n b_{ij} X_j (1 - \epsilon_i X_i) X_i, \quad (3)$$

where i runs from $i = 1$ to $i = n$ (as long as X_0 is considered constant), and the term $b_{i0} X_0$ represents the intrinsic growth rate r_i. Note that there are n equations for n interacting species, and the coefficients b_{ij} can be positive, negative or null, for a beneficial, detrimental or negligible interaction, respectively. Now Eq. (3) consists of three independent factors, namely, the Malthusian factor X_i, the effective growth rate $\sum_j b_{ij} X_j$, and the Verhulst or intraspecific-interaction factor $1 - \epsilon_i X_i$. The Verhulst term allows for a particular carrying capacity for each species given by $K_i = 1/\epsilon_i$.

We show a rich dynamical behaviour in our unified model using the lineal stability analysis.

[1] J. García-Algarra, J. Galeano, J. M. Pastor, J. M. Iriondo, and J. J. Ramasco, Rethinking the logistic approach for population dynamics of mutualistic interactions, J. Theor. Biol. **363**, 332-343 (2014).