

Richards-like two species population dynamics model

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Abstract The two-species population dynamics model is the simplest paradigm of inter- and intra-species interaction. Here, we present a generalized Lotka–Volterra model with intraspecific competition, which retrieves as particular cases, some well-known models. The generalization parameter is related to the species habitat dimensionality and their interaction range. Contrary to standard models, the species coupling parameters are general, not restricted to non-negative values. Therefore, they may represent different ecological regimes, which are derived from the asymptotic solution stability analysis and are represented in a phase diagram. In this diagram, we have identified a forbidden region in the mutualism regime, and a survival/extinction transition with dependence on initial conditions for the competition regime. Also, we shed light on two types of predation and competition: weak, if there are species coexistence, or strong, if at least one species is extinguished.

Keywords Complex systems · Population dynamics (ecology) · Pattern formation ecological

Introduction

Population growth models are important for understanding and predicting the time dependent behavior in several disciplines. As instances of such systems, one has: oscillatory behavior in a chemical concentration (Motoike and Adamatzky 2005); immune system cells growth dynamics and the viral load (Nowak et al. 1991); tumor cells growth (Araujo and McElwain 2004); human population growth (Bettencourt et al. 2007; Strzalka 2009); defectors and cooperators dynamics in game theory (Pereira et al. 2008; Pereira and Martinez 2010); etc. However, most of the growth models proposed deal with a specific situation, or a specific system. For example, the Verhulst model (Murray 2002) is used to describe a system which presents a logistic growth curve; the Gompertz model (Gompertz 1825) is used to describe the human life span (among others applications); and the Richards' model (Richards 1959), which unifies the previous models, was initially introduced to describe plant growth dynamics. Researchers try to find generalized models to retrieve each of these specific models as particular cases (Barberis et al. 2011; Cabella et al. 2011; dOnofrio 2009; Mombach et al. 2002a, b; Strzalka and Grabowski 2008). A more general model could be useful not only to describe a vast spectrum of systems, but also to help find universal growth laws (Guiot et al. 2003; West et al. 2001).

Interactions between species are generally formalized with the Lotka–Volterra equations (Murray 2002), which explain prey–predator behavior in its original formulation, but present stability problems. A more realistic approach is

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to consider that species grow in limited environments. Besides the predatory interaction, there are many other different kinds of interaction taking place between two species. If species disfavor each other, when their niches overlap, there is competition. If species favor each other, as in pollination/seed dispersion by insects, there is *mutualism* or *symbiosis*. If only one of these species affect the fitness of the other, there are two possibilities: *amensalism*, if one of them has a negative effect on the other; and *commensalism*, otherwise. Finally, when species do not interact at all there is the so-called *neutralism*. Part of this ecological richness is present in the Verhulst–Lotka–Volterra model, which naturally unveils other ecological regimes and does not have the stability problem of the standard Lotka–Volterra model.

The aim of this work is to present a generalization of the Verhulst–Lotka–Volterra model. We present the asymptotic solution stability analysis in a non-trivial phase diagram. We show that the generalization parameter is related to the fractal dimension of species habitat and also to the range of interactions between con-specifics. This relation enables us to demonstrate the emergence of population growth (macroscopic behavior) from the microscopic behavior, given by the interaction range and dimensionality of underlying topological structure.

Our presentation is structured as follows. In Sect. 2, we present a generalized two-species model. This model describes species interaction by a Richards-like term and retrieves the Verhulst–Lotka–Volterra equations as a particular case. The model steady state solutions are obtained and extinction and coexistence phases are discussed. In Sect. 3, we describe the ecological regimes that emerge from the model, that is: amensalism, commensalism, neutralism, mutualism, competition and predation. Finally, we draw our conclusions in Sect. 4

Generalized two-species model

Before introducing the two-species generalized model, let us present an one-parameter generalization of the logarithmic and exponential functions and some of their properties. These functions (Arruda et al. 2008; Martinez et al. 2008, 2009; Tsallis 1988, 1994) allow us to easily formulate and write the solutions of the models we present. The \tilde{q} -logarithm function is:

$$\ln_{\tilde{q}}(x) = \lim_{\tilde{q}' \rightarrow \tilde{q}} \frac{x^{\tilde{q}'} - 1}{\tilde{q}'} = \int_1^x \frac{dt}{t^{1-\tilde{q}}}, \tag{1}$$

which is the area under the hyperbola, controlled by \tilde{q} . This is a generalization of the natural logarithm function, which is retrieved for $\tilde{q} = 0$. For $\tilde{q} < 0$, $\ln_{\tilde{q}}(\infty) = -1/\tilde{q}$; for

$\tilde{q} > 0$, $\ln_{\tilde{q}}(0) = -1/\tilde{q}$; for all \tilde{q} , $\ln_{\tilde{q}}(1) = 0$; $\ln_{\tilde{q}}(x^{-1}) = -\ln_{-\tilde{q}}(x)$; $d \ln_{\tilde{q}}(x)/dx = x^{\tilde{q}-1}$. The inverse of the \tilde{q} -logarithm function is the \tilde{q} -exponential function:

$$e_{\tilde{q}}(x) = \begin{cases} \lim_{\tilde{q}' \rightarrow \tilde{q}} (1 + \tilde{q}'x)^{\frac{1}{\tilde{q}'}} & \text{if } \tilde{q}x > -1 \\ 0 & \text{otherwise} \end{cases}, \tag{2}$$

with $e_{\tilde{q}}(0) = 1$, for all \tilde{q} and $[e_{\tilde{q}}(x)]^a = e_{\tilde{q}/a}(ax)$, where a is a constant. For $a = -1$, one has: $1/e_{\tilde{q}}(x) = e_{-\tilde{q}}(-x)$.

The interaction among species is fundamentally addressed in the M. A. Savageau seminal paper (Savageau 1979). In general lines, the scope of the mass-action law for k species is enlarged by means of the product of the species-density $X_i \geq 0$ raised to the powers $g_{i,j}$ and $h_{i,j}$, as expressed in its Eq. 13; (Savageau 1979). In this equation, the variation of X_i , with respect to time t , depends on non-negative factors α_i and β_i , which takes into account the growth and shrinkage of species i , respectively:

$$\frac{dX_i}{dt} = \alpha_i \prod_{j=1}^k X_j^{g_{i,j}} - \beta_i \prod_{j=1}^k X_j^{h_{i,j}}, \tag{3}$$

with $i = 1, 2, \dots, k$. To compare models addressed by the Savageau's equations (S-system), we consider one- and two-species models in terms of the generalized logarithm function.

Calling the variable $p = (\alpha_1/\beta_1)^{1/\tilde{q}} X_1$ and the parameters: $\tilde{q} = g_{1,1} - h_{1,1}$ and $\kappa = -\beta_1(\alpha_1/\beta_1)^{\tilde{q}} \tilde{q}$, the one species model ($k = 1$) $dX_1/dt = \alpha_1 X_1^{g_{1,1}} - \beta_1 X_1^{h_{1,1}}$ can be written as:

$$\frac{d \ln(p)}{d(\kappa t)} = -p^{h_{1,1}-1} \ln_{\tilde{q}}(p), \tag{4}$$

which is a particular instance of the Tsoularis-Wallace model (Tsoularis and Wallace 2002): $d \ln(p)/d(\kappa t) = p^{h_{1,1}-1} [-\ln_{\tilde{q}}(p)]^\gamma$, with $\gamma = 1$ (Cabella et al. 2011). In particular, if $h_{1,1} = 1$, one retrieves the Richards' model (Richards 1959). Notice that with this mapping between notations, one is able to give an empirical interpretation to \tilde{q} -logarithm parameter in terms of the species-density powers.

Calling $p_i = (\alpha_i/\beta_i)^{1/\tilde{q}_i} X_i$, $\tilde{q}_i = g_{i,i} - h_{i,i}$ and $\kappa_i = -\beta_i \tilde{q}_i (\alpha_i/\beta_i)^{\tilde{q}_i - i/(h_{i,i}) - 1}$, the Savageau two-species model ($k = 2$) is written as:

$$d \ln(p_1)/dt = -\kappa_1 p_1^{h_{1,1}-1} X_2^{g_{1,2}} \ln_{\tilde{q}_1}(p_1) \tag{5}$$

$$d \ln(p_2)/dt = -\kappa_2 p_2^{h_{2,2}-1} X_1^{g_{2,1}} \ln_{\tilde{q}_2}(p_2) \tag{6}$$

These equations have the the Lotka–Volterra model (among others) as a particular limit. Although the Savageau's model is very general, it does not retrieve the stable version of the Lotka–Volterra model, i.e. the Verhulst-like.

Here, we are also concerned with a formalism which includes the stable version of Lotka–Volterra model as a particular case. Consider now a Richards-like two-species population dynamic model, which describes species growing in a limited environment:

$$\frac{dN_1}{dt} = -\kappa_1 N_1 \left[\ln_{\tilde{q}_1} \left(\frac{N_1}{K_1} \right) - \epsilon_1 \frac{N_2}{K_2} \right] \tag{7}$$

$$\frac{dN_2}{dt} = -\kappa_2 N_2 \left[\ln_{\tilde{q}_2} \left(\frac{N_2}{K_2} \right) - \epsilon_2 \frac{N_1}{K_1} \right], \tag{8}$$

where $N_i \geq 0$, κ_i and $K_i > 0$ are the number of individuals (population size), net reproductive rate, and the carrying capacity of species i ($= 1, 2$), respectively. In fact, K_1 represents the resources restriction considering any kind of external factors, except the ones relative to species 2, similarly for K_2 . The non-dimensional population interaction parameters ϵ_1 and ϵ_2 can assume positive or negative values and represent the different ecological interactions. To compare the species abundance with its own carry capacity, call $p_i = N_i/K_i \geq 0$, for $i = 1, 2$, with $N_i \geq 0$. To use an non-dimensional time measure, for instance, relative to species 1 net reproductive rate, consider $\tau \equiv \kappa_1 t \geq 0$. The two net reproductive rates produce a single parameter $\rho = \kappa_2/\kappa_1 > 0$, fixing a second time scale to the system: $\tau' \equiv \rho \tau = \kappa_2 t$. With these new quantities Eqs. 7 and 8 can be rewritten as:

$$\frac{dp_1}{d\tau} = p_1 [-\ln_{\tilde{q}_1}(p_1) + \epsilon_1 p_2] = f(p_1, p_2) \tag{9}$$

$$\frac{dp_2}{d\tau} = \rho p_2 [-\ln_{\tilde{q}_2}(p_2) + \epsilon_2 p_1] = g(p_1, p_2), \tag{10}$$

The term $p_1 \ln_{\tilde{q}_1}(p_1)$ in Eq. 9 represents the competition between individuals of the same species (intraspecific competition), and $\epsilon_1 p_1 p_2$ represents the interaction between individuals of different species (interspecific interaction) (Edelstein-Keshet 2005; Murray 2002). Similar analysis applies to Eq. 10. Contrary to ρ , which has no major relevance to this model, the product $\epsilon_1 \epsilon_2$ plays an important role, so that: $\epsilon_1 \epsilon_2 < 0$ means predation; $\epsilon_1 \epsilon_2 = 0$ means commensalism, amensalism or neutralism and $\epsilon_1 \epsilon_2 > 0$ means either mutualism or competition (see diagram of the Fig. 1).

The dynamic of the model is quite similar to the so-called theta-logistic model (Sibly 2005), which is a generalization of the Verhulst model. However, the Richards' model has as particular cases not only the Verhulst model but also the Gompertz one. Moreover, the population dynamics are governed by a Richards' term, instead of the Malthus one in the standard Lotka–Volterra equations. When these interactions are given by the Verhulst equation ($\tilde{q}_1 = \tilde{q}_2 = 1$), one retrieves the Verhulst–Lotka–Volterra model, which does not belong to the Savageau modeling

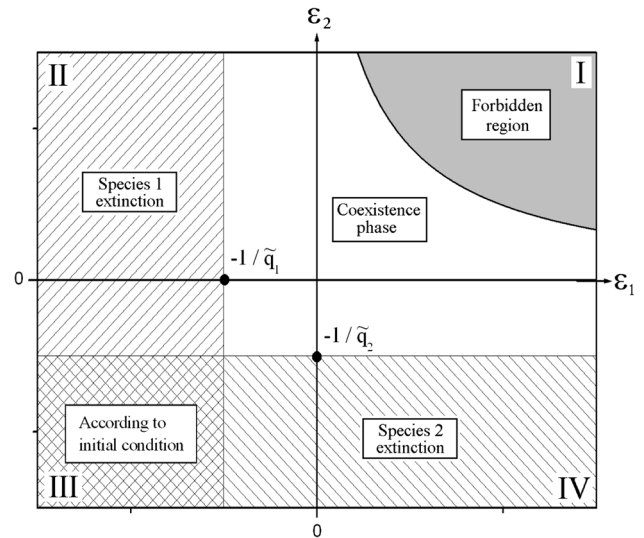


Fig. 1 Diagram of ecological regimes according to the interaction parameters pair (ϵ_1, ϵ_2) . The origin $(\epsilon_1, \epsilon_2) = (0, 0)$ represents neutralism; the axis, amensalism and commensalism and the quadrants **I** mutualism; **II** and **IV** predation; **III** competition. Extinction occurs for $\epsilon_i < -1/\tilde{q}_i$. If $\epsilon_1 < -1/\tilde{q}_1$ and $\epsilon_2 < -1/\tilde{q}_2$, contrary to complementary case, extinction depends on the initial conditions. In the mutualism regime, a forbidden region emerges where the two populations grow infinitely at the region border

category. Here, we analyze the two-specie dynamical system obtained through Eqs. 9 and 10, enhancing the scope of single species growth models (Cabella et al. 2011, 2012).

Generalization parameter interpretation

The generalization parameter \tilde{q} links the microscopic with the macroscopic behavior of population growth. From the microscopic perspective, it addresses the interaction range among individuals in fractal media. The macroscopic consequences of these interactions are sigmoid growth curves, such as the ones of Gompertz or Verhulst model.

A microscopic model to describe cell proliferation in D -dimensional medium, which supports a population with fractal structure dimension D_f was first proposed by Mombach et al. (2002a). This fractal dimensional hypothesis is consistent with experimental data (Cross 1997; Guiot et al. 2003; Kozusko et al. 2007). The cell replication rate is considered to be a balance between its intrinsic properties of self-replication and the inhibitory factor from the presence of neighboring cells. This inhibitory factor $I(r)$ depends only on the distance r between two cells, in the form $I(r) = 1/|r|^\gamma$. The analytical solution for this equation leads to the Richards' model at the macroscopic level, which can be rewritten in terms of Eq. 1, with $\tilde{q} = 1 - \gamma/D_f$ (Cabella et al. 2011).

In population dynamics, the intraspecific per capita growth rate $G_{\text{intra}}(p_i) = -\kappa_i \ln_{\tilde{q}}(p_i)$, with $i = 1, 2$ is the average number of individuals that each individual generates at time t . The inhibitory factor is the intraspecific competition according to Eqs. 9 and 10. Considering a population in a spatial structure of dimension D_f , $I(r)$ can be rewritten in terms of the \tilde{q} parameter: $I(r) = |r|^{D_f(\tilde{q}-1)}$. The fractal dimension of habitats may reflect its quality (Imre 2004) and biodiversity level (Tokeshi 2012). For $\tilde{q} < 1$, $G_{\text{intra}}(p_i)$ is a concave function of p_i ($d^2G_{\text{intra}}/dp_i^2 > 0$). In this case, G_{intra} is strongly affected by the increase of population size, even for low population densities. Insects and some fishes belong to this case (Saether 2002; Sibly and Hone 2002), where species have a high intrinsic growth rate (Sibly 2005). For $\tilde{q} = 1$, the interaction strength does not depend on distance among individuals, i.e. the mean field case. Finally, for $\tilde{q} > 1$, $G_{\text{intra}}(p_i)$ is a convex function of p_i ($d^2G_{\text{intra}}/dp_i^2 < 0$) and species are particularly unaffected by the increase of p_i until the population size is near the carrying capacity, where G_{intra} rapidly decreases. Examples of this case are species living in a wide plain (Fowler 1981; Sibly 2005). Using $d^2N/dt^2 = 0$, one can show that maximum population growth rate is $N_t = K/(1 + \tilde{q})^{1/\tilde{q}}$, where K is the carrying capacity.

Steady state solutions

In Eqs. 9 and 10, the nullclines are denoted by nullA $f(p_1, p_2) = 0$ and by nullB, for $g(p_1, p_2) = 0$. There are trivial nullclines $p_1 = 0$ (nullA0) or $p_2 = 0$ (nullB0) and nontrivial ones:

$$p_2 = \frac{1}{\epsilon_1} \ln_{\tilde{q}_1}(p_1) \quad (\text{nullA1}) \tag{11}$$

$$p_2 = e_{\tilde{q}_2}[\epsilon_2 p_1] \quad (\text{nullB1}) \tag{12}$$

The crossing of nullA and nullB in the plane $p_2 \times p_1$ generates a steady state solution. The trivial solution ($p_{1,t}^* = 0$ and $p_{2,t}^* = 0$) is the crossing of nullA0 with nullB0 and is restricted to the case $\tilde{q}_1 > 0$ and $\tilde{q}_2 > 0$, to avoid a division by zero in Eqs. 9 and 10 via definition (1). Semi-trivial solutions ($p_{1,\text{st}}^* = 0$ and $p_{2,\text{st}}^* = 1$, restricted to $\tilde{q}_1 > 0$; or $p_{1,\text{st}}^* = 1$ and $p_{2,\text{st}}^* = 0$, restricted to $\tilde{q}_2 > 0$) are the crossing of nullA1 with nullB0 or nullA0 with nullB1. The crossing of nullA1 with nullB1 produces the nontrivial solutions:

$$p_{1,\text{nt}}^* = e_{\tilde{q}_1}[\epsilon_1 e_{\tilde{q}_2}(\epsilon_2 p_{1,\text{nt}}^*)] \tag{13}$$

$$p_{2,\text{nt}}^* = e_{\tilde{q}_2}[\epsilon_2 e_{\tilde{q}_1}(\epsilon_1 p_{2,\text{nt}}^*)], \tag{14}$$

in which the analytical solution cannot be obtained, since they are transcendental equations.

For the particular case $\tilde{q}_1 = \tilde{q}_2 = 1$ (Verhulst-like) with competition interaction (i.e. $\epsilon_1 < 0$ and $\epsilon_2 < 0$), the solutions are: $p_1^* = 0$ and $p_2^* = 0$ (trivial solution and not stable); $(p_1^*, p_2^*) = (1, 0)$ or $(p_1^*, p_2^*) = (0, 1)$ (semi-trivial solutions); $p_1^* = (1 + \epsilon_1)/(1 - \epsilon_1\epsilon_2)$ and $p_2^* = (1 + \epsilon_2)/(1 - \epsilon_1\epsilon_2)$ (non-trivial solution).

These steady state solutions (p_1^*, p_2^*) are stable if $-\text{Tr}[A(p_1^*, p_2^*)] > 0$ and $\text{Det}[A(p_1^*, p_2^*)]/\rho > 0$, where $A(p_1^*, p_2^*) = \begin{pmatrix} \partial_{p_1} f & \partial_{p_2} f \\ \partial_{p_1} g & \partial_{p_2} g \end{pmatrix}_{p_1^*, p_2^*}$ is the stability matrix (community matrix).

Equations 13 and 14 are real-valued functions if: $\tilde{q}_1 \epsilon_1 e_{\tilde{q}_2}(\epsilon_2 p_{1,\text{nt}}^*) > -1$ and $\tilde{q}_2 \epsilon_2 e_{\tilde{q}_1}(\epsilon_1 p_{2,\text{nt}}^*) > -1$ (according to Eq. 2), leading to:

$$\epsilon_1 > \frac{-1}{\tilde{q}_1 e_{\tilde{q}_2}(\epsilon_2 p_{1,\text{nt}}^*)} \quad \text{and} \quad \epsilon_2 > \frac{-1}{\tilde{q}_2 e_{\tilde{q}_1}(\epsilon_1 p_{2,\text{nt}}^*)}. \tag{15}$$

The phase plane $\epsilon_2 \times \epsilon_1$ of Fig. 1 presents the diagram of the ecological regimes accessible to the system according to the pair (ϵ_1, ϵ_2) , given by the numerical solution of Eqs. 13 and 14. The forbidden region in this phase diagram (see Fig. 1), the population sizes has not well defined due to the second condition in Eq. 2). In fact, the two populations grow infinitely at the forbidden region border. For $\tilde{q}_1 = \tilde{q}_2 = 1$, this border is simply $\epsilon_2 = 1/\epsilon_1$.

In particular, if $\tilde{q}_i = 1$ the nullcline nullA1 and nullB1 are linear functions. We stress that in general, they are either convex, if $\epsilon_i(\tilde{q}_i - 1) > 0$ or concave, if $\epsilon_i(\tilde{q}_i - 1) < 0$. The nullclines convexity is analyzed in the following.

The trivial steady states $p_{1,t}^* = 0$ and $p_{2,t}^* = 0$ mean extinction of both species (synnecrosis), therefore $-\text{Tr}[A(0, 0)] = -1/\tilde{q}_1 - \rho/\tilde{q}_2$ and $\text{Det}[A(0, 0)] = \rho/(\tilde{q}_1\tilde{q}_2)$. Since $\rho > 0$, $\text{Det}[A(0, 0)] > 0$ if, and only if, $\tilde{q}_1\tilde{q}_2 > 0$, i.e., \tilde{q}_1 and \tilde{q}_2 must have the same signal, either positive or negative. Since $-\text{Tr}[A(0, 0)] > 0$, \tilde{q}_1 and \tilde{q}_2 must be negative. However, when both \tilde{q}_1 and \tilde{q}_2 are negative the trivial solution is undetermined, as discussed in the beginning of this subsection. When \tilde{q}_1 and \tilde{q}_2 are positive, the synnecrosis is a unstable fixed point, as in the case for Verhulst–Lotka–Volterra model ($\tilde{q}_1 = \tilde{q}_2 = 1$). Thus, synnecrosis is not an accessible ecological regime.

The semi-trivial solutions are either: $(p_{1,\text{st}}^*, p_{2,\text{st}}^*) = (0, 1)$ or $(p_{1,\text{st}}^*, p_{2,\text{st}}^*) = (1, 0)$, where one species extinguishes and the other survives. For instance, considering species 1 extinction, one has: $-\text{Tr}[A(0, 1)] = -\epsilon_1 - 1/\tilde{q}_1 + \rho$ and $\text{Det}[A(0, 1)] = -\rho(\epsilon_1 + 1/\tilde{q}_1)$. The stability condition $-\text{Tr}[A(0, 1)] > 0$, implies $\epsilon_1 < \rho - 1/\tilde{q}_1$ and $\text{Det}[A(0, 1)] > 0$ implies $\epsilon_1 < -1/\tilde{q}_1$, since $\rho > 0$. Thus, species 1 extinguishes for $\epsilon_1 < \epsilon_1^{(c)}$. Similarly, species 2 extinction is stable only for $\epsilon_2 < \epsilon_2^{(c)}$, where $\epsilon_i^{(c)} = -1/\tilde{q}_i$

($i = 1, 2$) is the transition critical value. It is interesting to point out that the Gompertz-like two-species model ($\tilde{q}_1 = \tilde{q}_2 = 0$) does not present the survival/extinction transition, since $\epsilon_i^{(c)} \rightarrow -\infty$. For the particular case ($\tilde{q}_1 = \tilde{q}_2 = 1$) this transition occurs at $\epsilon_1 = \epsilon_1^c = -1$. A Taylor expansion of the non-trivial solution allows us to write $p_{1,nt}^* = (\epsilon_1 - \epsilon_1^c)/(1 + \epsilon_2) + \mathcal{O}((\epsilon_1 - \epsilon_1^c)^2)$. Therefore, near the critical point ϵ_1^c (t), species 1 linearly goes extinct, i.e. $p_{1,nt}^* \sim (\epsilon_1 - \epsilon_1^c)$, where the critical exponent related to the order parameter is $\beta = 1$. Analogous for species 2.

The hatched diagram region of Fig. 1 characterizes the extinction of one species. The doubly hatched region ($\epsilon_1 < -1/\tilde{q}_1$ and $\epsilon_2 < -1/\tilde{q}_2$) the steady state solutions depend on initial conditions.

The non-trivial solutions, Eqs. 13 and 14, correspond to the coexistence phase and it is represented by the white region of the diagram ($\epsilon_1 > -1/\tilde{q}_1$, and $\epsilon_2 > -1/\tilde{q}_2$). The coexistence phase can occur in the mutualism, commensalism, amensalism, predation and competition regimes.

Transient dynamics is an important aspect of the predators and preys coexistence and also of competitors (Hastings 2004). Studies of outbreaks (insects or diseases) focus greatly on the transient dynamics (Cavaliere and Kocak 1995; Gavrillets and Hastings 1995; Harrison 2001; Kaitala 1999; Lai and Winslow 1995; Lai 1995a, b). In tuberculosis treatment for example, it can reveal important aspects beyond asymptotic states such as how

drug resistance emerges (Espíndola et al. 2011, 2012, 2014). The full solutions of Eqs. 9 and 10 must be dealt numerically. Differently from the Lotka–Volterra model, the oscillatory behavior around fixed points (limit cycle) is not observed in the proposed model. The solutions always converge to the fixed points. However, in the predation regime, our model depicts an interesting feature. It may happen that the species 1 population (prey) is greater than species 2 (predator) in the beginning of the dynamics, but the steady state solution is just the opposite, i.e. predator population is greater than the prey one. The long-term (steady state) analysis may not provide enough information about species abundance in the short-term dynamics i.e. before reaching equilibrium (Hastings 2004), as depicted in Fig. 2.

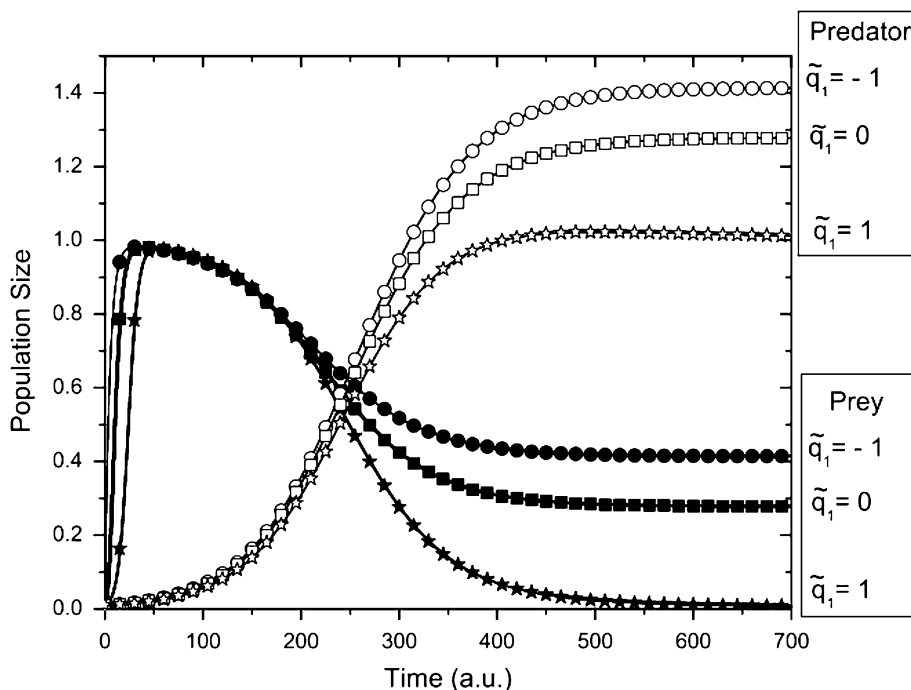
Ecological regimes

Now, we address the ecological regimes that emerge from the proposed model. These regimes are: amensalism, commensalism, neutralism, mutualism, competition and predation.

Neutralism, amensalism and commensalism

The situation $\epsilon_1 \epsilon_2 = 0$ in Eqs. 9 and 10 leads to an independent growth of at least one species. For instance, when both interaction parameters vanish, the two species evolve independently. That is the neutralism, so the steady state

Fig. 2 Prey and predator regime for $\tilde{q} = -1; 0$ and 1 . Although the initial conditions are the same, $p_1(0) = p_2(0) = 0.01$, in the beginning of the dynamics the prey population is greater than the predator one. However the steady state solution is just the opposite, i.e. more predators than preys



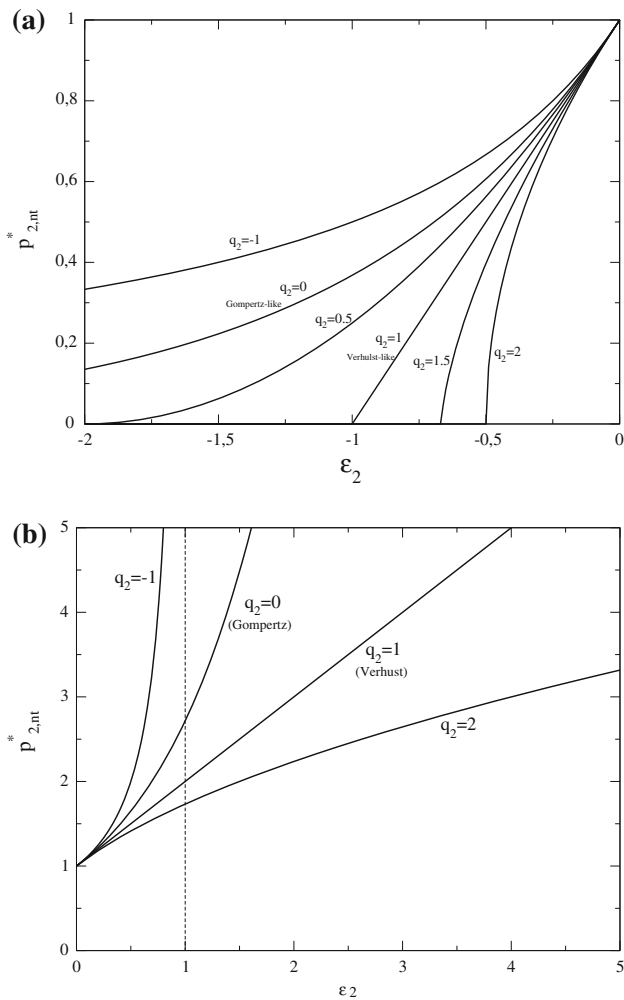


Fig. 3 Plots of $p_{2,nt}^* = e^{\tilde{q}_2 \epsilon_2}$. For amensalism (a) species 1 growth is independent of species 2 ($\epsilon_1 = 0$ and $\epsilon_2 < 0$). When $\tilde{q}_2 \epsilon_2 < -1$, then $p_{2,nt}^* = 0$, meaning extinction of species 2. For $\tilde{q}_2 \leq 0$ the one species extinction phase is suppressed and the coexistence phase becomes stable. For commensalism (b) species 1 grows independently of species 2 ($\epsilon_1 = 0$ and $\epsilon_2 > 0$). For $\tilde{q}_2 \geq 0$, the steady state diverges only at $\epsilon_2 \rightarrow \infty$. However, for $\tilde{q}_2 < 0$ (see the case $\tilde{q}_2 = -1$), the steady state diverges at $\epsilon_2 = -1/\tilde{q}_2$ (vertical dashed line)

solutions of both species become unity, that is $(p_1^*, p_2^*) = (1, 1)$. Another case is to consider that only one species is unaffected by the other. For instance, considering $\epsilon_1 = 0$ and $\epsilon_2 \neq 0$ in Eqs. 9 and 10, the non-trivial steady state solutions Eqs. 13 and 14 become: $p_{1,nt}^* = 1$ and $p_{2,nt}^* = e^{\tilde{q}_2 \epsilon_2}$, which are plotted for $\epsilon_2 < 0$ (amensalism) in Figs. 3a and for $\epsilon_2 > 0$ (commensalism) in Figs. 3b. In this case, species 1 optimally uses the environment resources while species 2 may either coexist with species 1, for $\tilde{q}_2 \epsilon_2 > -1$; be extinguished or reach the forbidden region. In brief, the steady state $p_{2,nt}^*$ grows (as a function of ϵ_2): logarithmically, for $\tilde{q}_2 > 1$; linearly, for $\tilde{q}_2 = 1$ (Verhulst model); exponentially, for $0 \leq \tilde{q}_2 < 1$ and hyper-exponentially, for $\tilde{q}_2 < 0$. Following von Foerster et al. (1960)

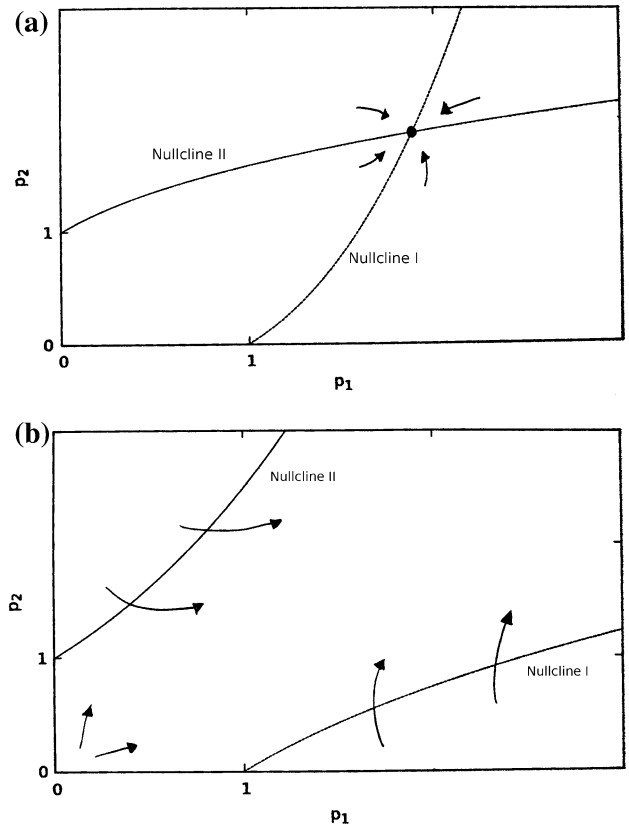


Fig. 4 Plot of the nullclines for mutualism between species ($\epsilon_1 > 0$ and $\epsilon_2 > 0$). a For $\tilde{q}_1 > 1$ and $\tilde{q}_2 > 1$, the crossing of the two nullclines produces a stable solution. b For $\tilde{q}_1 < 1$ and $\tilde{q}_2 < 1$, the two nullclines never intercept, so that populations grow indefinitely, which is not a stable ecological regime (forbidden region)

and Strzalka (2009) studies, in hyper-exponential growth the population diverges at a finite value of ϵ_2 , while in exponential growth the population diverges only when $\epsilon_2 \rightarrow \infty$.

Using the context of statistical physics (Yeomans 1992), one can interpret $p_{2,nt}^*$ as an order parameter of a second order survival/extinction transition, which occurs at $\epsilon_2^{(c)} = -1/\tilde{q}_2$. This transition is suppressed for $\tilde{q}_2 \rightarrow 0^+$, since $\epsilon_2^{(c)} \rightarrow -\infty$. When $\epsilon_2 \approx 0^-$, $p_{2,nt}^*$ is close to unity, regardless the value of \tilde{q}_2 . In the commensalism regime, the population may grow indefinitely for $\epsilon_2 \tilde{q}_2 \rightarrow -1^+$, i.e. $p_2^* \rightarrow \infty$. The steady state of the species 2 is undefined in the region $\epsilon_2 \tilde{q}_2 \leq -1$: that is the forbidden region. Analogous results are obtained when species 2 is independent of species 1, and species 1 is positively affected by species 2.

Mutualism, competition and predation

Now, consider $\epsilon_1 \epsilon_2 \neq 0$, which represents three kinds of species interaction: mutualism, competition and predation.

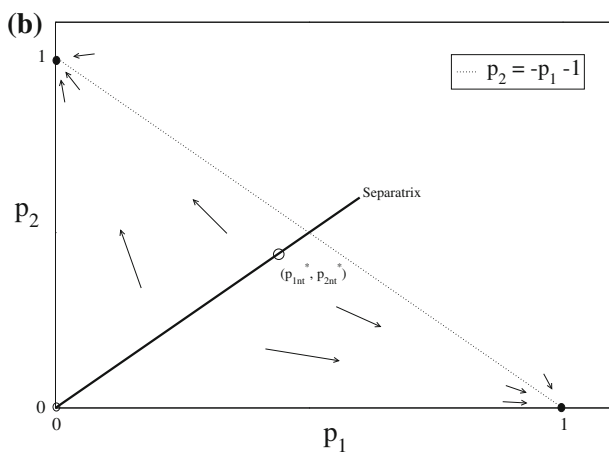
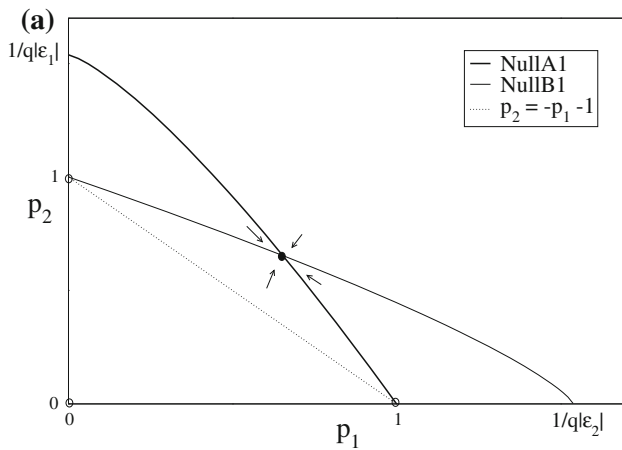


Fig. 5 Plot of the nullclines for the competition regime ($\epsilon_1 < 0$ and $\epsilon_2 < 0$). The plots depict the particular situation when \tilde{q}_1 and \tilde{q}_2 are positive. **a** If the two nullclines intercept (the non-trivial steady state) above the straight line $p_2 = -p_1 - 1$, the steady state solution is stable and represents weak competition. **b** If the non trivial steady state is below the dotted line, then it is *unstable* and the semi-trivial steady state becomes stable, giving rise to the strong competition. The separatrix divide the two regions of convergence according to the initial conditions

The case $\epsilon_1 \epsilon_2 > 0$ means that both species have the same kind of influence on each other. For instance, both species benefit each other ($\epsilon_1 > 0$ and $\epsilon_2 > 0$): mutualism; or both species impair each other ($\epsilon_1 < 0$ and $\epsilon_2 < 0$): competition. The case $\epsilon_1 \epsilon_2 < 0$ means that one species is the predator and the other is the prey.

In this context, the stable solutions for Eqs. 9) and 10 are $p_1^* = e_{\tilde{q}_1}(\epsilon_1 p_2^*)$ and $p_2^* = e_{\tilde{q}_2}(\epsilon_2 p_1^*)$, with the following transcendental equations as solutions:

$$\ln_{\tilde{q}_1} p_1^* = \epsilon_1 e_{\tilde{q}_2}(\epsilon_2 p_1^*) \quad \text{and} \quad \ln_{\tilde{q}_2} p_2^* = \epsilon_2 e_{\tilde{q}_1}(\epsilon_1 p_2^*). \quad (16)$$

For mutualism ($\epsilon_1 > 0$ and $\epsilon_2 > 0$), the steady state solutions are obtained through the crossing of the nullclines: Eqs. 11 and 12. On one-hand, when $\tilde{q}_1 > 1$ and $\tilde{q}_2 > 1$ the nullA1 is a convex function, while the nullB1 is concave.

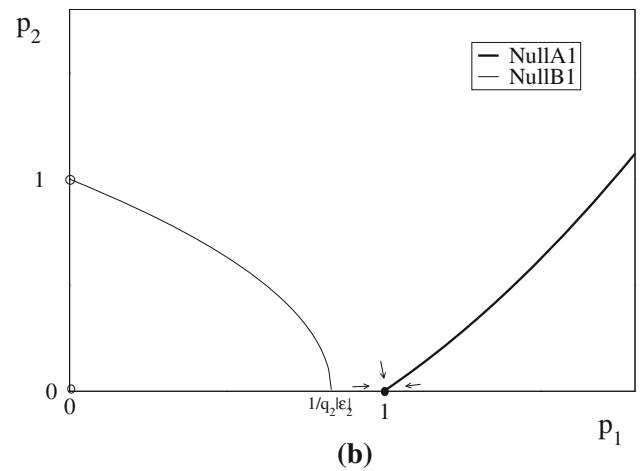
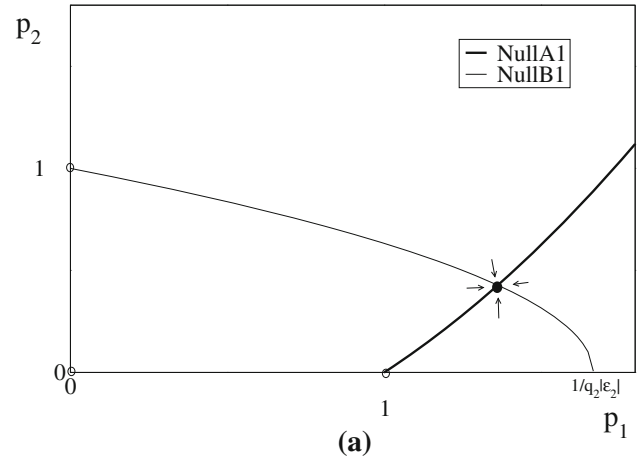


Fig. 6 Prey (species 2)/predator (species 1) regime ($\epsilon_1 > 0$ and $\epsilon_2 < 0$). **a** The plot depicts the case that $\tilde{q}_2 |\epsilon_2| < 1$, which implies that the non-trivial steady state solution (crossing of the nullclines) is stable. One has coexistence of the two species: weak predation. **b** When $1/(\tilde{q}_e |\epsilon_e|) < 1$, the steady state solution is the semi-trivial one: $(p_{1,st}^*, p_{2,st}^*) = (1, 0)$, i.e. strong predation

Thus, as presented in Fig. 4a, the two nullclines cross at the point in which simultaneously satisfy Eqs. 11 and 12: $\ln_{\tilde{q}_1}(p_{1,nt}^*) = \epsilon_1 e_{\tilde{q}_2}(\epsilon_2 p_{1,nt}^*)$ and $p_{2,nt}^* = \ln_{\tilde{q}_1}(p_{1,nt}^*)/\epsilon_1$. On the other hand, when $\tilde{q}_1 < 1$ and $\tilde{q}_2 < 1$, nullA1 is convex and greater than the concave nullB1, therefore they never cross each other, giving rise to the forbidden region.

When the nullclines intercept, one can find the steady state solution through the transcendental equation $p_{1,nt}^* = \ln_{\tilde{q}_2}[\ln_{\tilde{q}_1}(p_{1,nt}^*)/\epsilon_1]\epsilon_2$. Consequently $p_{2,nt}^*$ is calculated inserting $p_{1,nt}^*$ in the Eq. 11 or 12.

In the competition case ($\epsilon_1 < 0$ and $\epsilon_2 < 0$), the dynamics of the system presents two regimes. In the first, the two species coexist, that is weak competition. In the second, there is extinction of one species, that is strong competition. As in the mutualism case, the non-trivial steady state is given by the crossing of nullA1 and nullB1 (Eq. 16), which can be unstable in some cases. If the crossing point

is above the straight line $p_2 = -p_1 - 1$, then the non-trivial steady state is stable, see Fig. 5a. The equation $p_2 = -p_1 - 1$ leads us to the conclusion that if $p_{1,nt}^* + p_{2,nt}^* < 1$, then there is strong competition (extinction of one species); and when $p_{1,nt}^* + p_{2,nt}^* > 1$, then there is weak competition (coexistence of both species).

When $p_{1,nt}^* + p_{2,nt}^* < 1$, there is a line which passes through the origin and the non trivial steady state (an unstable point in this case). This line, the separatrix, divides the two regions of convergence according to the initial conditions (see Fig. 5b). In this case, one species is extinguished (strong competition).

Consider now that the species 1 is the predator and species 2 is the prey, thus $\epsilon_1 > 0$ and $\epsilon_2 < 0$. The interception of the two nullclines describes a stable non-trivial steady state, representing coexistence of both species: weak predation, see Fig. 6a. As expected, species 1 takes advantage from species 2 therefore $p_{1,nt}^* > 1$ and $p_{2,nt}^* < 1$. For $\tilde{q}_2|\epsilon_2| > 1$, the stable steady state is the semi-trivial solution $p_{1,st}^*, p_{2,st}^* = (1, 0)$. It can happen when: (1) the two nullclines intercept, see Fig. 6b; or (2) the intercept point coincides with the semi-trivial solution. In this case, species 2 is extinguished: strong predation. Analogous results occurs for species 2 as the predator.

Conclusion

We have generalized the Verhulst–Lotka–Volterra model to take into account several ecological regimes in a simple unified formulation. Based on Martínez et al. (2008), we showed that our model generalization parameter is related to the range of interaction between individuals and the fractal dimension of growth media. The interaction range parameter generates different concavities in the per capita growth rate curves. The richness of the proposed model can be explored through the steady state solutions stability analysis. We have identified several ecological phases according to species coexistence and extinction. In the competition regime, two distinct cases emerge: the weak competition when both species survive and strong competition when one is extinguished. The latter reveals a non-trivial survival/extinction transition, where the system is strongly dependent on the initial conditions when $\epsilon_1 < -1/\tilde{q}_1$ and $\epsilon_2 < -1/\tilde{q}_2$. Similarly, the weak/strong interaction also occurs in the predation regime. However, in this case, the survival/extinction transition does not depend on the initial conditions. In the mutualism regime, there is a forbidden region in the parameter space. Because its simplicity compared to the model of Wodarz and Komarova (2005), and since we have a microscopic basis for our generalization, we propose to study it as a paradigm for

tumor-selective replicating viruses in cancer therapy. Further, the presented model can be easily formulated to address an arbitrary number of interacting species, producing a more realistic ecological system with multiple trophic interactions.

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