A Verhulst-Like Two-Species Population Dynamics Model

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Abstract

The study of a two-species dynamics population model, which includes intraspecific competition to the Lotka-Volterra equation, is presented. Despite being simple, this model presents a very rich behavior, spanning on several ecological regimes. The ecological regimes are assigned according to the interaction parameter values (ϵ_1, ϵ_2) and they are neutralism, amensalism, comensalism, mutualism, predation, and competition. From the stability of the steady state solutions, two phases are obtained,namely extinction of one species or their coexistence. On one hand, extinction of one species occurs for $\epsilon_1 < -1$ and/or $\epsilon_2 < -1$; i. e., in predation, amensalism, or competition regimes. If $\epsilon_1 < 0$ and $\epsilon_2 < 0$ so that $\epsilon_1\epsilon_2 > 1$, one has an extinction phase where the solutions depend on the initial conditions. On the other hand, coexistence may occur for all the considered regimes as far as $\epsilon_1\epsilon_2 < -1$. If $\epsilon_1 > 0$ and $\epsilon_2 > 0$ so that $\epsilon_1\epsilon_2 > 1$, one has a forbidden regime with no biological reality. Full analytical solutions have been obtained for all ecological the regimes mentioned above.

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1. Introduction

The ecosystem is composed by a complex interaction network from which the removal of a single species may cause dramatic changes throughout the system. The interactions between species only became better known in population dynamics in the 1920s, with the Lotka-Volterra equation [1]. This is a simple mathematical model that explains the oscillatory behavior in a chemical concentration (Lotka) and in fish catches (Volterra), which observed in such systems has been interpreted as a consequence of predation. The introduction of Lotka-Volterra-like models for the cells of the immune system and the viral load (in immunology) may be considered one of the main contributions of population dynamics in the twentieth century [3].

Besides the Lotka-Volterra interaction, there are many other different kinds of interaction taking place between biological species. For instance, if only one of these species is independent of the other, one has two possible situations: *amensalism*, if the considered species has a *negative* effect on the other; and *commensalism*, if such effect is positive. As an example of amensalism consider that, in order to survive, an organism exudes a chemical compound as part of its normal metabolism, but this compound is detrimental to the other organism. An example of commensalism is the remoras that eat leftover food from the shark. If species favor each other, one has *mutualism* or *symbiosis*, which is the case of clear fish As example clear fish and pollination / seed dispersion by insects. If species unfavor each other, there is *competition*. This happens, for instance, when two species occupy the same ecological niche and use the same resources. If one species is benefited from the interaction while the other is in harm, one has *predation* which is a biological system where one species captures the biomass from the other. A typical example of predation is the hare-lynx interaction, which can be described by a Lotka-Volterra system. The interaction between parasite and the host, also called *parasitism*, also belongs to this class, although it is not exactly "predation" in the strict sense. Finally, when species do not interact at all there is the so-called *neutralism*. In fact, "true" neutralism is very rare or even nonexistent in the real world.

Here an analytical solution to a simple model for the description of the full dynamics of two interacting populations occupying limited environmental resources is presented. The solution exhibits all the abovementioned two-species interactions in the

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parameter space diagram. Although the particular situations of the considered model have been addressed in basic dynamics population textbooks, we show here that this model presents aspects that have not yet been sufficiently explored.

The text is organized as follows. In Sec. 2, interspecific competition to the Lotka-Volterra equations is presented, the domain of the interaction parameter between two species is extended, and analytical solutions are obtained. The steady state solutions of the model are also achieved analytically. These solutions correspond to the stable ecological regimes in the parameter space diagram. In Sec. 3, the full analytical solutions for the trivial case neutralism and the non-trivial ones amensalism and comensalism are depicted. In Sec. 4, the results for mutualism, predation, and competition are presented. Our conclusions are described in Sec. 5.

2. A Simple Two-Species Population Dynamics Model

A reasonable simple two-species population model, inspired in textbooks models [1, 2], is

$$\frac{dN_1}{dt} = \kappa_1 N_1\left(1 - \frac{N_1}{K_1} + \alpha_1\frac{N_2}{K_1}\right) \quad (1)$$

$$\frac{dN_2}{dt} = \kappa_2 N_2\left(1 - \frac{N_2}{K_2} + \alpha_2\frac{N_1}{K_2}\right) . \quad (2)$$

This model incorporates limit environmental resources, logistic growth of one species in the absence of the other, and interspecific interaction. In Eqs. (1) and (2), $N_i \geq 0$, κ_i and $K_i > 0$ are the number of individuals (size), natality rate, and the carrying capacity of species i $(= 1, 2)$, respectively. In Eq. (1), $-\kappa_1 N_1^2/K_1$ can be understood as a competition between individuals of the same species (intraspecific competition), and $-\kappa_1 N_1 N_2/K_1$ represents the interaction between individuals of different species(interspecific interaction). The same is valid for Eq. (2). The carrying capacity represents the fact that the two species are not isolated from the rest of the world. In fact, K_1 represents the feeding resource that comes from any kind of external factors, but that does not have to do with species 2. The same is valid for K_2.

For $\alpha_1 < 0$ and $\alpha_2 > 0$ (or vice-versa), Eqs. (1) and (2) lead to a class of models called *competitive Lotka-Volterra models*. In this case, species 2 (predator) acts negatively on species 1 and species 1 (prey) acts positively on species 2. In a more specific case, when the prey (N_1) grows exponentially in the absence of the predator (N_2); i.e., $K_1 \to \infty$; and the predator dies in the absence of the prey, giving $N_2 \gg K_2$, one retrieves the *simple Lotka-Volterra model*. The *simple Lotka-Volterra model* presents two steady-state solutions, namely $(N_1^*, N_2^*) = (0, 0)$ and $(N_1^*, N_2^*) = (\kappa_2/\alpha_2, \kappa_1/\alpha_1)$. The stability analysis shows that the trivial solution $(0, 0)$ is unstable (saddle point); i.e., if the prey population is slightly greater than zero and the predator population vanishes, the prey population diverges. However, if the predator population is slightly greater than zero and there is no prey, predators become extinct. The non-trivial solution $(\kappa_2/\alpha_2, \kappa_1/\alpha_1))$ leads to a limit cycle; i.e., both populations oscillate with a fixed amplitude. For the competitive Lotka-Volterra model, the non-trivial solution is still unstable; however, it is not a saddle point. For the non-trivial solution, one has a damped oscillation for the transient cycle while limit cycle vanishes, giving rise to non-periodic stable solutions.

The novelty of the present work is a new interpretation of Eqs. (1) and (2), since we consider that the interaction parameter α_i, is not restricted, as is usually done in other studies. In fact, this absence of restriction to the interaction parameters allows retrieval of many different ecological regimes, like competition, predation, and mutualism; by the same unified mathematical approach. Note that, for instance, if $\alpha_1 < 0$, species 2 is unfavourable to species 1; if $\alpha_1 = 0$, it is indifferent; and if $\alpha_1 > 0$, it is favourable. The parameter α_2 behaves similarly. The model is fully analytically soluble.

To use non-dimensional quantities, we write $p_i = N_i/K_i \geq 0$, for $i = 1, 2$. Time is measured with respect to the natality rate of species 1, $\tau = \kappa_1 t \geq 0$. Here, we restrict ourselves to the case $\kappa_i > 0$. The scaled time is positive since we take the initial condition as $t_0 = 0$. Moreover, the two natality rates form a single parameter $\rho = \kappa_2/\kappa_1 > 0$, because we shall deal with positive natality rates. The non-dimensional population interaction parameters are given by $\epsilon_1 = \alpha_1 K_2/K_1$ and $\epsilon_2 = \alpha_2 K_1/K_2$, which are not restricted and represent the different ecological interactions. With these quantities, Eqs. (1) and (2) become:

$$\frac{dp_1}{d\tau} = p_1[1 - p_1 + \epsilon_1 p_2] = f(p_1, p_2) \quad (3)$$

$$\frac{dp_2}{d\tau} = \rho p_2[1 - p_2 + \epsilon_2 p_1] = g(p_1, p_2) . \quad (4)$$

Observe that ρ fixes a second time scale to the system: $\tau' \equiv \rho\tau = \kappa_2 t$. Therefore, the interaction between two species is represented by the pair of parameters (ϵ_1, ϵ_2). The diagram of Figure (1) depicts the several ecological interactions according to (ϵ_1, ϵ_2) values. Contrary to ρ, which has no major relevance to this model (since we consider only $\rho > 0$), 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.

2.1. Stability of Steady State Solutions

To obtain the steady state solution $p_1^* = p_1(\tau \to \infty)$ and $p_2^* = p_2(\tau \to \infty)$ of Eqs. (3) and (4), we have to impose $dp_1/d\tau = dp_2/d\tau = 0$, which implies $f(p_1^*, p_2^*) = g(p_1^*, p_2^*) = 0$ and leads to

$$p_1^*(1 - p_1^* + \epsilon_1 p_2^*) = 0 \quad (5)$$

and

$$p_2^*(1 - p_2^* + \epsilon_2 p_1^*) = 0. \quad (6)$$

One has the following trivial ("t"), semi-trivial ("st"), and non-trivial ("nt") solutions:

$$p_{1,t}^* = 0 \quad \text{and} \quad p_{2,t}^* = 0; \quad (7)$$

$$p_{1,st}^* = 1 \quad \text{and} \quad p_{2,st}^* = 0; \quad (8)$$

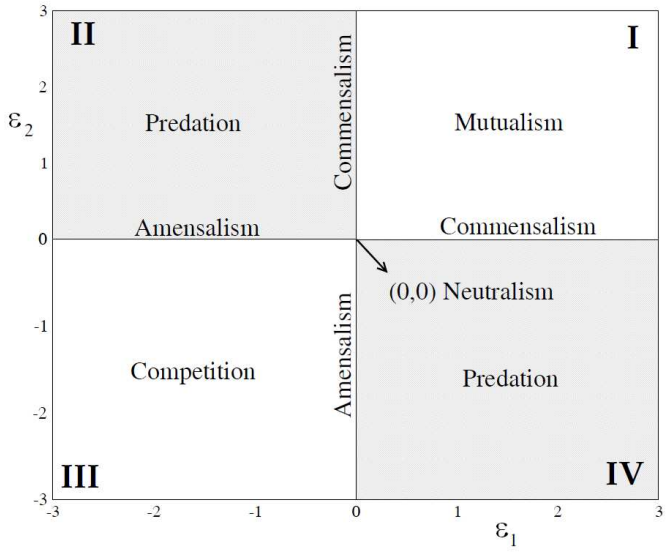

Figure 1: Diagram of ecological interaction between two species according to the interaction parameters (ϵ_1, ϵ_2). In this diagram, each quadrant represents one kind of interaction: I:mutualism; II and IV: predation ; III: competition. The abscissa and ordinate represent either amensalism or commensalism. The origin represents neutralism.

$$p^*_{1,st} = 0 \qquad \text{and} \qquad p^*_{2,st} = 1; \tag{9}$$

$$p^*_{1,nt} = \frac{1+\epsilon_1}{1-\epsilon_1\epsilon_2} \qquad \text{and} \qquad p^*_{2,nt} = \frac{1+\epsilon_2}{1-\epsilon_1\epsilon_2}. \tag{10}$$

These asymptotic solutions characterize the system according to their stability. The stability matrix, also called *community matrix*, is:

$$\begin{aligned} A(p^*_1, p^*_2) &= \left(\begin{array}{cc} \partial_{p_1} f & \partial_{p_2} f \\ \partial_{p_1} g & \partial_{p_2} g \end{array} \right)_{p^*_1, p^*_2} \\ &= \left(\begin{array}{cc} 1 - 2p^*_1 + \epsilon_1 p^*_2 & \epsilon_1 p^*_1 \\ \rho\epsilon_2 p^*_2 & \rho(1 - 2p^*_2 + \epsilon_2 p^*_1) \end{array} \right). \end{aligned} \tag{11}$$

The steady state solutions p^*_1 and p^*_2 are stable if the trace and the determinant of the community matrix are negative and positive, respectively. Considering Eq. (11), one has:

$$\text{Tr}[A(p^*_1, p^*_2)] = 1 + \rho + (\rho\epsilon_2 - 2)p^*_1 + (\epsilon_1 - 2\rho)p^*_2 \tag{12}$$

$$\begin{aligned} \text{Det}[A(p^*_1, p^*_2)] &= \rho\{1 + p^*_1[\epsilon_2 - 2(1 + \epsilon_2 p^*_1)] + \\ &\quad p^*_2[\epsilon_1 - 2(1 + \epsilon_1 p^*_2)] + 4p^*_1 p^*_2\} \end{aligned} \tag{13}$$

One must analyze the possible four instances (7-10).

2.2. Trivial Solutions

Let us start with the stability analysis of the trivial solutions of Eqs. (7), which means extinction of both species (synnecrosis). One has:

$$\text{Tr}[A(0,0)] = 1 + \rho \tag{14}$$

$$\text{Det}[A(0,0)] = \rho\,. \tag{15}$$

Since $\rho > 0$, $\text{Det}[A(0,0)] > 0$ but $\text{Tr}[A(0,0)] > 1$. The pair of trivial solution is not stable anywhere in the parameter space, so synnecrosis never occurs in our model.

2.3. Semi-Trivial Solutions

The semi-trivial solutions are given by Eqs. (8) or (9) and they mean that one of the species is extinguished. Considering the steady state solution Eq. (8) (species 1 extinction), one has:

$$\text{Tr}[A(0,1)] = 1 + \epsilon_1 - \rho \tag{16}$$

$$\text{Det}[A(0,1)] = -\rho(1 + \epsilon_1)\,. \tag{17}$$

For these solutions to be stable, it is necessary that $\epsilon_1 < -1$, regardless of the ρ value. A similar analysis leads us to conclude that the steady state Eq. (9) (species 2 extinction) is stable only for $\epsilon_2 < -1$.

2.4. Non-Trivial Solutions

The non-trivial solution Eq. (10) lead to:

$$\text{Tr}[A(p^*_{1,nt}, p^*_{2,nt})] = \frac{1 + \epsilon_1 + \rho(1+\epsilon_2)}{\epsilon_1\epsilon_2 - 1} \tag{18}$$

$$\text{Det}[A(p^*_{1,nt}, p^*_{2,nt})] = -\frac{(1+\epsilon_1)(1+\epsilon_2)\rho}{\epsilon_1\epsilon_2 - 1}\,. \tag{19}$$

On one hand, if $\epsilon_1\epsilon_2 < 1$, the denominator is positive and the numerator of $p_{1,nt}$ and $p_{2,nt}$ must vanish or be positive. From the condition $p^*_{1,nt} \geq 0$, this solution is only stable if $\epsilon_1 \geq \epsilon_c^{(1)} = -1$; otherwise, $p^*_{1,t} = 0$ is the stable solution. This produces a transition from the regime where species 1 coexists with species 2 to the regime where species 1 is extinguished. The same transition occurs for the parameter ϵ_2. On the other hand, if $\epsilon_1\epsilon_2 > 1$, the denominator is positive and the numerator of $p_{1,nt}$ and $p_{2,nt}$ must vanish or be positive. From the condition, $p^*_{1,nt} \geq 0$, this solution is only stable if $\epsilon_1 < \epsilon_c^{(1)} = -1$; otherwise, $p^*_{1,t} = 0$ is the stable solution. This produces a transition from the regime where species 1 coexists with species 2 to the regime where species 1 is extinguished. The same transition occurs for ϵ_2.

From the stability criteria, we conclude that species can coexist only if $\epsilon_1 > -1$ and $\epsilon_2 > -1$. According to the values of ϵ_1 and ϵ_2, the various ecological regimes may present a stable non-trivial solution, as shown below.

2.5. Stable Steady State Solutions in the Parameter Space: Phase Diagram

In Fig. 2, the stable steady state solutions Eqs. (8), (9), and (10) of Eqs. (3) and (4) are represented. It is a more detailed figure than the one shown in of Fig. 1, which only accounts for ecological regimes. The diagram summarizes our findings: the coexistence phase and one species extinction phase can be seen. These phases span on different ecological regimes, which means that different ecological interactions may lead to the same phase.

It is important to stress that the non-trivial solutions [Eqs. (10)] are stable in all quadrants, where $\epsilon_1 > -1$, $\epsilon_2 > -1$ and $\epsilon_1\epsilon_2 < 1$. In this region, the populations coexist, regardless of the kind of ecological interaction. Modifying the values of the pair (ϵ_1, ϵ_2), but restricting ourselves to this region ($\epsilon_1 > -1$, $\epsilon_2 > -1$, and $\epsilon_1\epsilon_2 < 1$), one can change the regime of interaction (for instance, from competition to mutualism), but one can say that the system continues in the same phase. It is in

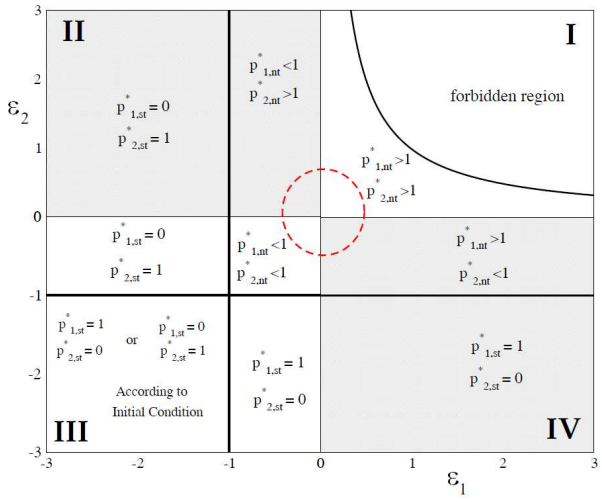

Figure 2: Diagram of ecological interaction between two species according to the pair (ϵ_1, ϵ_2). In this diagram, each quadrant represents one kind of interaction: I:mutualism; II and IV: predation ; III: competition. The abscissa and ordinate represent either ammensalism or commensalism. The origin represents neutralism. The non-trivial solutions ($\epsilon_1 > -1$, $\epsilon_2 > -1$, and $\epsilon_1\epsilon_2 < 1$) correspond to the coexistence phase. In this phase mutalism, comensalism, amensalism, predation, competition, and neutralism can occur, for instance, around and inside the dashed circe. The complementary region is characterized by an extinction phase and a forbidden region. The extinction phase ($\epsilon_1 < -1$ and/or $\epsilon_2 < -1$) reveals a region for $\epsilon_1 < 0$ and $\epsilon_2 < 0$ where, contrary to the other cases, the steady state solutions depend on the initial condition. For $\epsilon_1 > 1$ and $\epsilon_2 > 0$ and $\epsilon_2 > 1/\epsilon_1$, there exists a forbidden region with non biological reality (negative number of individuals).

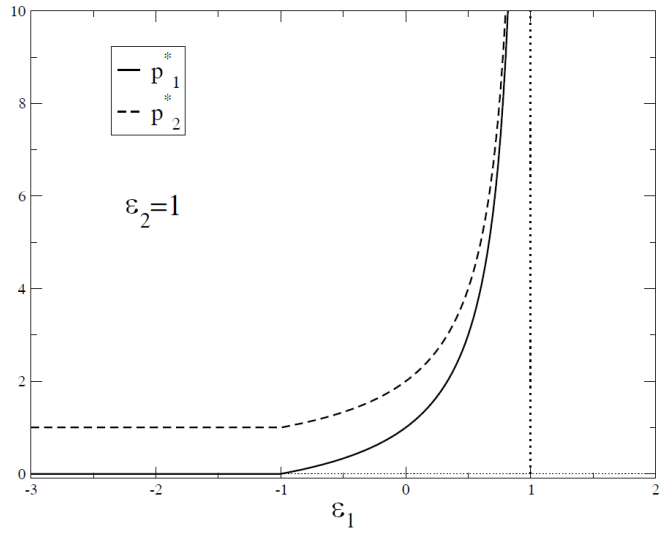

Figure 3: Plot of steady steady solutions [Eqs. (9) and (10)] of the model [Eqs. (3) and (4)] as a function of ϵ_1, keeping $\epsilon_2 = 1$ fixed. In this plot one sees two phase transitions. The first is the extinction-coexistence (predation) transition which occurs at $\epsilon_1 = -1$. The second is the transition from coexistence (mutualism) to a forbidden region (with no ecological reality).

the same phase because the population size, regardless of the change in regime, continues being governed by the same steady state solution (10). To exemplify this situation, consider that we change the values of the pair (ϵ_1, ϵ_2) of the system describing a path around the origin of the parameter space $\epsilon_1 \times \epsilon_2$, as represented in Fig. 2 by the dashed line. One sees that, in this path, the system passes throught all possible regimes; nevertheless, it remains in the same phase; In other words, the population size remains governed by the nontrivial solution Eq. (10).

In the first quadrant of the diagram of Fig. 2, as $\epsilon_1\epsilon_2 \to 1^-$, $p_{i,nt} \sim (1 - \epsilon_1\epsilon 2)^{-\beta}$ diverges with the exponent $\beta = 1$ (see Fig. 3). In this case, the mutual cooperation conducts to unbounded growth of both populations. The region $\epsilon_2 > 1/\epsilon_1$ is forbidden; since $p^*_{i,nt} < 0$, it does not have ecological reality.

The plot of Fig. (3) shows the stable steady solutions for both populations as a function of ϵ_1, for a fixed value of ϵ_2. One sees that both solutions diverge as $\epsilon_1 \to 1/\epsilon_2$; in the second quandrant (predation), species 1 is extinguished for $\epsilon_1 < -1$.

The other regions of this diagram are characterized by the semi-trivial solutions [Eqs. (8) and (9)]. Differently from all the other regions in the phase diagram, in the case of the specific region in the third quadrant, with $\epsilon_1 < -1$ and $\epsilon_2 < -1$, the steady state solutions depend on the initial condition. In this region, there is a separatrix for the initial conditions [1]. Another interesting characteristic of this phase diagram is the reflexion symmetry about $\epsilon_2 = \epsilon_1$.

3. $\epsilon_1\epsilon_2 = 0$

This section is restricted to the particular case $\epsilon_1\epsilon_2 = 0$, where only one or both parameters vanish. This corresponds to parameter space axis $\epsilon_2 \times \epsilon_1$ [see Fig. 2]. Thus, three ecological regimes are allowed in this specific situation:

- amensalism: $\epsilon_1 = 0$ and $\epsilon_2 < 0$ (species 2 extinction, if $\epsilon_2 \leq -1$ and species coexistence otherwise) or $\epsilon_2 = 0$ and $\epsilon_1 < 0$ (species 1 extinction, if $\epsilon_1 \leq -1$ and species coexistence otherwise);
- neutralism: $\epsilon_1 = \epsilon_2 = 0$; and
- comensalism: $\epsilon_1 > 0$ and $\epsilon_2 = 0$ or $\epsilon_1 = 0$ and $\epsilon_2 > 0$.

In these cases, one can obtain full analytical solutions of Eqs. (3) and (4). Below we address each case in more detail.

3.1. Neutralism

Neutralism is a special case where each population grows independent of the other (no interaction between the species), so the species coexist. This ecological regime is represented by Eqs. (3) and (4), with $\epsilon_1 = \epsilon_2 = 0$, leading to independent equations:

$$\frac{dp_1}{d\tau} = p_1[1 - p_1] \tag{20}$$

$$\frac{dp_2}{\rho d\tau} = p_2[1 - p_2]\,, \tag{21}$$

which are the Verhulst equations for isolated species. The solutions, with different time scales and parameters, for each species are:

$$p_1(\tau) = \frac{1}{1 + (p_{1,0}^{-1} - 1)e^{-\tau}} \tag{22}$$

$$p_2(\tau) = \frac{1}{1 + (p_{2,0}^{-1} - 1)e^{-\rho\tau}} \,, \tag{23}$$

where $p_{i,0} = p_i(0)$ is the initial condition for species $i = 1, 2$.

Eqs. (22) and (23) are driven by different characteristic times $\tau = \kappa_1 t$ and $\tau' = \rho\tau = \kappa_2 t$, respectively. For $\tau \gg 1$, so that $\rho\tau \gg 1$, the asymptotic behaviors $p_1^* = p_1(\infty) = 1$ and $p_2^* = p_2(\infty) = 1$ are obtained, so that species end exploring all the available environmental resources. Fig. 4 shows the dynamics of the population given by Eqs. (22) and (23). In this figure the effect of the parameter ρ on the system is also compared. For the same initial conditions, there are no differences between species evolution for $\rho = 1$. For $\kappa_2 > \kappa_1$; i.e., $\rho > 1$, species 2 grows more rapidly than species 1, given the same initial condition. For $\kappa_2 < \kappa_1$; i.e., $\rho < 1$, the inverse occurs.

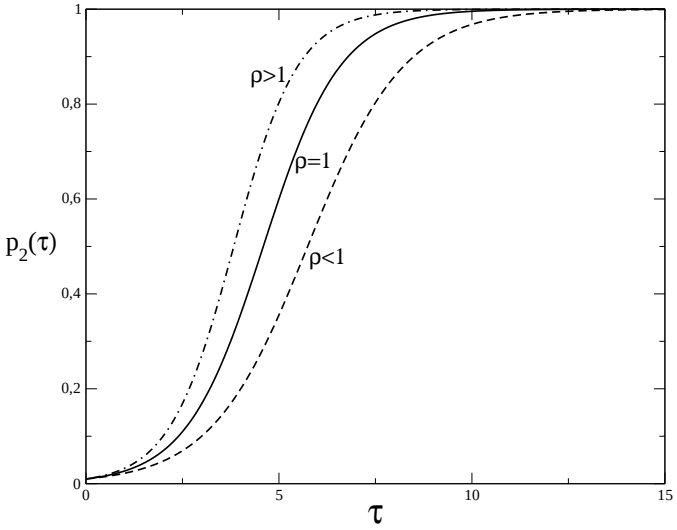

Figure 4: Plots of the evolution of $p_2(\tau)$ by Eq. (23) for different ρ values. When $\rho = 1$, the evolution of both populations ($p_1(\tau)$ and $p_2(\tau)$) is the same. The plots have qualitatively the same shape, and the effect of ρ is to retard or advance one solution with respect to the other. The asymptotic values are the unit. The initial conditions was $p_1(0) = 1/100$.

3.2. Comensalism and Amensalism

Consider that two species interact asymmetrically. For instance, consider that individuals of species 1 are unaffected by species 2, although, individuals of species 2 are adversely affected by species 1. This is the amensalism regime. The commensalism regime has the same structure as amensalism, except that one species is favorably affected by the other. These interactions can be mathematically represented by Eqs. (3) and (4):

$$\frac{dp_1}{d\tau} = p_1(\tau)\left[1 - p_1(\tau)\right] \tag{24}$$

$$\frac{dp_2}{\rho d\tau} = p_2(\tau)\left[1 - p_2(\tau) + \epsilon_2 p_1(\tau)\right] \,, \tag{25}$$

where ϵ_2 is negative for amensalism and positive for commensalism.

In this kind of interaction, species 1, described by Eq. (24), follows the Verhulst model, whose solution is given by Eq. (22). The dynamics of species 2 follows the time-dependent Verhulst-Schaefer model [9, 10, 11] [Eq. (25)], whose solution is:

$$p_2(\tau) = \left\{ \frac{1}{1 + \epsilon_2 p_1(\tau)} + \frac{e^{-\rho\tau\left[1+\epsilon_2 \overline{p}_1(\tau)\right]}\left(1 - p_{2,0} + \epsilon_2 p_{1,0}\right)}{p_{2,0} + \epsilon_2 p_{1,0} p_{2,0}} \right\}^{-1} \tag{26}$$

where the mean relative size of species 1 up to τ is:

$$\begin{aligned} \overline{p}_1(\tau) &= \frac{1}{\tau}\int_0^\tau d\tau' p_1(\tau') = \int_0^\tau \frac{d\tau'}{1 + (p_{1,0}^{-1} - 1)e^{-\tau'}} \\ &= \ln[1 + p_{1,0}(e^\tau - 1)] \,, \end{aligned} \tag{27}$$

with $p_1(\tau)$ given by Eq. (22).

Using Eqs. (22) and (27) in Eq. (26), one obtains:

$$p_2(\tau) = \left\{ \frac{e^{-\tau}\left[1 + (-1 + e^\tau)\, p_{1,0}\right]^2}{p_{1,0}\left\{1 + \left[-1 + e^\tau\left(1 + \epsilon_2\right)\right] p_{1,0}\right\}} + \right. \tag{28}$$

$$\left. \frac{e^{-\rho\tau}\left[1 + (-1 + e^\tau)\, p_{1,0}\right]^{-\epsilon_2\rho\tau}\left(1 + \epsilon_2 p_{1,0} - p_{2,0}\right)}{p_{2,0} + \epsilon_2 p_{1,0} p_{2,0}} \right\}^{-1} \tag{29}$$

The plots of $p_2(\tau)$ for several ϵ_2 values are depicted in Fig. 5.

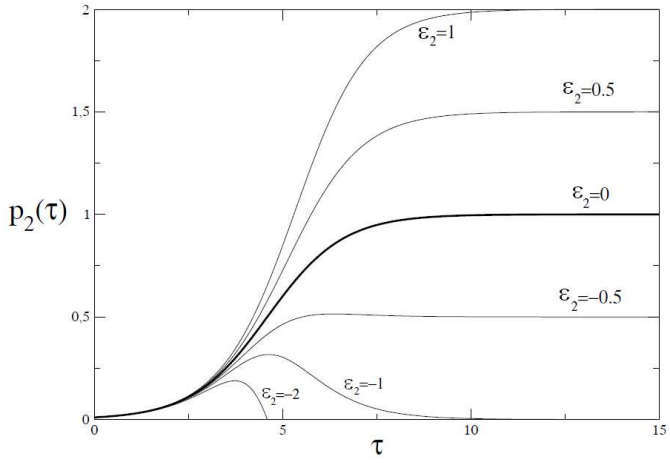

Figure 5: Plots of the solution of Eq. (25), given by Eq. (29), for different values of interaction parameter ϵ_2 and $\rho = 1$. The comensalism regime is obtained for $\epsilon_2 > 0$, where the asymptotic value, due to the other species, is greater than unity. The neutralism regime is retrived for $\epsilon_2 = 0$ (see Fig. 4). The amensalism regime is obtained for $\epsilon_2 < 0$, where the asymptotic value does not vanish (meaning species coexistence) for $\epsilon_2 > -1$ and vanishes (meaning species extinction) for $\epsilon_2 \leq -1$.

The steady state solutions of Eqs. (24) and (25) are, respectively

$$p_1^* = p_1(\infty) = 1 \tag{30}$$

$$p_2^* = p_2(\infty) = \begin{cases} 1 + \epsilon_2 & \text{if } \epsilon_2 > -1 \\ 0 & \text{otherwise} \,. \end{cases} \tag{31}$$

One sees that $\epsilon_2^{(c)} = -1$ is a critical value that separates two distinct phases: $\epsilon_2 \leq -1$, where species 2 is extinguished; and $\epsilon_2 > -1$, where species 2 coexists with species 1. The former case occurs in the amensalism regime, while in the latter one it may occur in the amensalism ($\epsilon_2 < 0$), neutralism ($\epsilon_2 = 0$), or

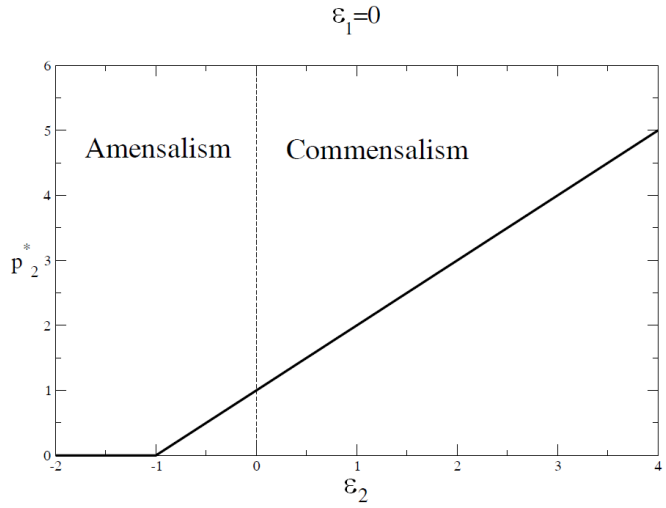

Figure 6: The plot of the steady state solution of Eq. (25), given by Eq. (31), as a function of the interaction parameter ϵ_2. For $\epsilon_2 \leq -1$, species 2 is extinguished, while for $\epsilon_2 > -1$ it coexists with species 1. This coexistence can occur in an amensalism regime, if $\epsilon_2 < 0$, or comensalism, if $\epsilon_2 > 1$. Since $\epsilon_1 = 0$, there is no forbidden region. The nontrivial solution grows linearly as a function of ϵ_2.

in the comensalism ($\epsilon_2 > 0$) regimes. The plot $p_2^*(\epsilon_2)$ is shown in Fig. 6.

The same conclusions are valid for $\epsilon_2 = 0$ and $\epsilon_1 \neq 0$. One finds the same behaviors and a critical point $\epsilon_1^{(c)} = -1$, so that similarly for $\epsilon_1 < \epsilon_1^c$ species 1 is extinguished.

4. $\epsilon_1\epsilon_2 \neq 0$

In the following, we deal with the case $\epsilon_1\epsilon_2 \neq 0$, which addresses mutualism, competition, and predation. If $\epsilon_1\epsilon_2 > 0$, each species has the same kind of influence on the other. This corresponds to either the competition or the mutualism regime. The following regimes occur:

- $\epsilon_1 > 0$ and $\epsilon_2 > 0$, mutualism, which corresponds to the first quadrant of the space parameter phase space, restrict to the region $\epsilon_2 < 1/\epsilon_1$;
- $\epsilon_1 < 0$ and $\epsilon_2 < 0$, competition, which corresponds to the third quadrant of the space parameter phase space.

If $\epsilon_1\epsilon_2 < 0$, the predation regime occurs, which belongs to the second and fourth quadrants of the parameter space (see Fig. 2). For $\epsilon_2 > 0$ and $\epsilon_1 < 0$, there is species coexistence for $\epsilon_1 > \epsilon_1^{(c)} = -1$ and species 1 extinction for $\epsilon_1 \leq -1$.

These ecological regimes are special cases of Eqs. (3) and (4), whose solutions can be worked out to have the form:

$$p_1(\tau) = \left\{ \frac{1}{1+\epsilon_1 p_2(\tau)} + \frac{e^{-\tau\left[1+\epsilon_1 \overline{p}_2(\tau)\right]}\left(1 - p_{1,0} + \epsilon_1 p_{2,0}\right)}{p_{1,0} + \epsilon_1 p_{1,0} p_{2,0}} \right\}^{-1} \quad (32)$$

where $p_2(\tau)$ is given by Eq. 26, and the relative populations sizes mean values up to instant τ are

$$\overline{p}_1(\tau) = \frac{1}{\tau}\int_0^\tau d\tau' p_1(\tau') \quad (33)$$

$$\overline{p}_2(\tau) = \frac{1}{\tau}\int_0^\tau d\tau' p_2(\tau') \, . \quad (34)$$

Using Eq. (26) in (32), we obtain a quadratic equation for $p_1(\tau)$, eliminating its dependence on $p_2(\tau)$. In fact, we can write $p_1(\tau)$ as dependent only on the initial condition and $\overline{p}_2(\tau)$. The population size $p_2(\tau)$ behaves analogously. Thus, the coupling between the two population sizes is given only by the mean values (33) and (34). The solutions Eqs. 32 and (26) are presented in Fig. (7) for the three regimes where $\epsilon_1\epsilon_2 \neq 0$. As $\tau \to \infty$, the steady state solutions of Eqs. (10) are reached.

Notice that considering $\epsilon_1 = 0$ in Eqs. (32) and (26), one retrieves Eqs. (22), (26), and (27), which correspond to the amensalism, neutralism, and comensalism regimes. In this way, these evolution equations can be seen as a general solution that is valid for all kinds of interaction regime.

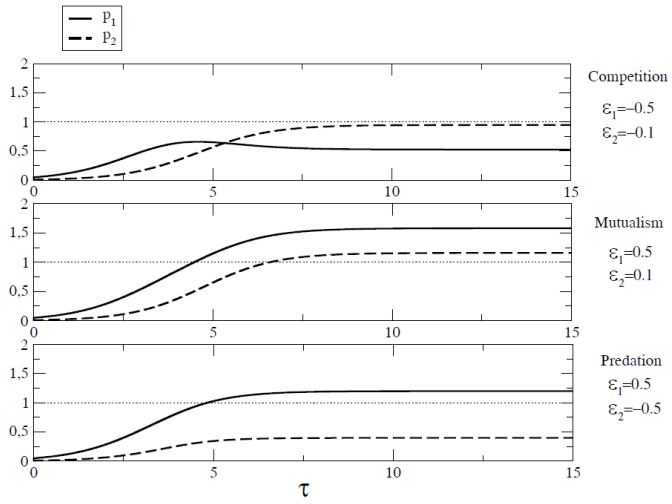

Figure 7: Plots of the evolution equations Eqs. (32) and (26), which are solutions of Eqs. (3) and (4). The initial condition is $p_{1,0} = p_{2,0} = 1/100$ and $\rho = 1$. The species interaction parameters $\epsilon_1\epsilon_2 \neq 0$ so that for competition: $\epsilon_1 = -1/2$ and $\epsilon_2 = -1/10$; mutualism: $\epsilon_1 = -1/2$ and $\epsilon_2 = -1/10$; and predation: $\epsilon_1 = 1/2$ and $\epsilon_2 = -1/2$.

5. Conclusion

The simple model we addressed here illustrates that one can interpret the interaction of two species at several levels. From the interaction parameters ϵ_1 and ϵ_2, which act at the individual level of species, one is able to tell about the different ecological regimes, classified in a higher level according to the product of the interaction parameter $\epsilon_1\epsilon_2$. If it vanishes, one or two species are independent from each other. If $\epsilon_1\epsilon_2 > 0$, one has either mutualism (both positive) or competition (both negative). For $\epsilon_1\epsilon_2 < 0$, one has predation. A collective level is obtained from the stability of the steady state solution, from where one obtains three phases: extinction of one species ($\epsilon_i < -1$) (synnecrosis

is not a stable phase in our model), species coexistence, and a forbidden phase ($\epsilon_2 > 1/\epsilon_1$). Although the studied model has been considered in several isolated instances, our study reveals the very general aspect of a simple mathematical set of equations, which represents very rich ecological scenarios that can be described analytically.

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