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Mutualism as a stabilizing effect on the population densities of two interacting species
Mutualismo como un efecto estabilizador de las densidades poblacionales de dos especies interactuando

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Abstract

Mathematical models are a very useful tool to understand, describe or predict the population dynamics of species interacting. Ecologists and mathematicians have extensively studied the predator-prey, victim-exploiter, competition and mutualistic relationships. However, mutualism between species has not received the same attention as the other ecological interactions. In this work, we exclude periodic solutions of three types of systems by the construction of Dulac functions. These systems can be used to describe the population dynamics of mutualistic species. The system type I includes a wide variety of mutualistic models in which both the intrinsic rate of increase and the carrying capacity of each species increase by the interaction between species. In particular, the system type I can be applied to exclude periodic solutions of models with conditioned interactions such that mutualism occurs at low population densities and competition occurs at high population densities. The system type II includes mutualistic models that describe a consumer-resources interaction. In these models, it is assumed that the net change of benefits-costs due to the interaction depends on the densities of the recipient species and the partner one. The system type III describes mutualistic models in which the per capita growth rate of each species is affected by a weak Allee effect. We also apply the results of this work to models mentioned in a historical list of mutualistic models provided in [1]. From the results obtained, we conclude that mutualism leads to the exclusion of periodic behaviors in the population dynamics of interacting species. Therefore, the population densities of the mutualistic species converge to an equilibrium point. Then, when the population densities oscillate, the oscillatory behaviors are transient. These results are relevant since the dynamics of mutualistic species has not been deeply characterized and the discussion about the existence of sustained oscillatory behavior in mutualistic species is relevant from an ecological perspective.

Keywords . Mutualism, conditioned interaction, consumer-resources model, Allee effect, Dulac function, periodic solution.

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Resumen

Los modelos matemáticos son una herramienta muy útil para comprender, describir o predecir la dinámica poblacional de especies que interactúan. Ecólogos y matemáticos han estudiado ampliamente las relaciones depredador-presa, víctima-explotador, competencia y mutualismo. Sin embargo, el mutualismo entre especies no ha recibido la misma atención que las otras interacciones ecológicas. En este trabajo, excluimos soluciones periódicas de tres tipos de sistemas mediante la construcción de funciones de Dulac. Estos sistemas pueden utilizarse para describir la dinámica poblacional de especies mutualistas. El sistema tipo I incluye una amplia variedad de modelos mutualistas en los que tanto la tasa de aumento intrínseca como la capacidad de carga de cada especie se incrementa por la interacción entre especies. En particular, el sistema tipo I puede aplicarse para excluir soluciones periódicas de modelos con interacciones condicionadas, de manera que el mutualismo ocurre a bajas densidades poblacionales y la competencia a altas densidades poblacionales. El sistema tipo II incluye modelos mutualistas que describen una interacción consumidor-recursos. En estos modelos, se supone que el cambio neto de beneficios-costos debido a la interacción dependen de las densidades de la especie receptora y de la especie socia. El sistema tipo III describe modelos mutualistas en los que las tasas de crecimiento per cápita de cada especie se ve afectado por un efecto Allee débil. También aplicamos los resultados de este trabajo a los modelos mencionados en una lista histórica de modelos mutualistas proporcionados en [1]. A partir de los resultados obtenidos, concluimos que el mutualismo conduce a la exclusión de comportamientos periódicos en la dinámica poblacional de especies que interactúan. Por lo tanto, las densidades poblacionales de especies mutualistas convergen a un punto de equilibrio. En consecuencia, cuando las densidades poblacionales oscilan, los comportamientos oscilatorios son transitorios. Estos resultados son relevantes ya que la dinámica de las especies mutualistas no ha sido caracterizada profundamente y la discusión sobre la existencia de un comportamiento oscilatorio sostenido en especies mutualistas es relevante desde una perspectiva ecológica.

Palabras clave. Mutualismo, interación condicionada, modelo consumidor-recursos, efecto Allee, función de Dulac, solución periódica.

1. Introduction. In nature, species interact in three fundamental ecological relationships: predation-prey, competition and mutualism. Among these relationships, mutualism has gotten short attentiveness even though mutualistic species play a major role in biodiversity and ecosystem function. In the ecological literature, it is very common to find other words that might be used as synonyms of mutualism, which are cooperation, protocooperation, mutual aid, entraide, facilitation, reciprocal altruism and symbiosis [2]. Mutualism can be classified into four categories: pollination, protection, seed dispersal and resource exchange.

In this work, we say that two species are in a mutualistic relationship when individuals of the recipient species receive benefits from the interaction with individuals of the partner species. Mutualism is divided into direct mutualism and indirect mutualism since mutualistic species increase directly or indirectly their fitness through the interaction between their individuals. In general, species in a direct mutualism interact physically. That is, there is a direct contact among individuals of different species. In contrast, species in an indirect mutualism are benefited from the other's presence, but there is not a direct contact among their individuals. By mutualism, species can increase either its per capita growth rate or its carrying capacity or both [3].

Direct mutualism can be divided into symbiotic and nonsymbiotic mutualism. Generally, symbiotic species exchange nutritional benefits or supply energy (resource exchange) while nonsymbiotic species exchange services such as transport (pollination and dispersal) and protection. Commonly, species in a symbiotic relation are in an obligate mutualism while species in a nonsymbiotic relation are in a facultative mutualism. In this cases, the modifiers (obligate or facultative) are used to specify dependence on the interaction. On the other hand, indirect mutualism might occur among competing species. For example, if the species u competes with the species v and v competes with w, the net interaction between u and w might be mutualistic. An opposite scenario occurs if the species u and v are in a mutualistic relationship with the species w, u and w can benefit each other indirectly. Other indirect mutualism occurs if the presence of the species u and v reduce predation on each other [2].

Hale and Valdovinos in [1] present an exhaustive historical review of mathematical models that describe pairwise mutualisms. Most of these models are given by differential equations. In some of these models, mutualism is modeled as a static interaction. In these cases, the parameters associated to the interaction are constant. In other models, it is assumed that mutualism can change to other ecological relationship as a function of the population densities. When this is the case, models with conditioned interaction rates are used [3, 4, 5, 6, 7]. Other mathematical tools have also been used in modeling mutualism. For example, integrodifferential equations [8], delay differential equations [9, 10, 11], and discrete equations [12, 13, 14].

Mutualistic models are known to show scenarios of exclusion or coexistence of species. However, scenarios of coexistence of species can be associated with different qualitative behaviors of the population densities. For example, in a first case, solutions of the models tend to a stable equilibrium. When this is the case, the solutions have a damped oscillatory behavior or a monotone one [1, 15, 7, 16, 17, 8, 9, 10, 11, 12, 13, 14]. In a second case, mutualistic models show coexistence scenarios through a limit cycle. In this case, the solutions show sustained oscillations [7, 18, 19, 20, 21, 22]. Limit cycles in a mutualism system were recorded in laboratory conditions [22].

From an ecological perspective, scenarios in which the population densities of both species converge to equilibrium points are more wished that scenarios in which both populations densities show sustained oscillations. This is true since populations are more resilient to perturbations if they are converging towards an equilibrium. In contrast, periodic or oscillatory behaviors have important conservation implications since periods of low population density can make species more vulnerable to extinction. Therefore, from a perspective of sustainability of species, it is of paramount importance to understand what type of ecological or demographic mechanisms discard the existence of periodic population densities.

Excluding the existence of periodic solutions in planar systems of differential equations is hard work. However, periodic solutions of planar systems can be excluded if these systems admit a Dulac function. In [23, 24, 25, 26, 27, 28], the authors propose a method to constructing Dulac functions for diverse planar systems. In particular, Dulac functions for ecological and epidemiological models can be constructed [29, 30, 26, 31]. Other important result related to the existence of a Dulac function is mentioned as follows. If a planar system admits a Dulac function, then the global stability of an equilibrium point can be proved when some conditions over the model are satisfied [32].

In this work, we propose three general systems for which periodic solutions are excluded. Each of these systems can be used to describe the dynamics of mutualistic species. This result is relevant since oscillations resulting from mutualism has been sometimes discussed in literature for each model analyzed but not in a general way. To do this, in Section 2, mathematical results to exclude periodic solutions of planar systems are mentioned. In section 3, we prove that each general system proposed admits a Dulac function. In Section 4, to exemplify, we propose six mutualistic models in which periodic solutions are excluded by using the results in this work. We also apply our results to the historical list of models given in [1]. Finally, in Section 5, we discuss the results of this work.

2. Criteria for the exclusion of periodic orbits of planar systems.

We mention three theorems used in this work.

Theorem 2.1 (Bendixon-Dulac criterion). *Let $\Omega \subset \mathbb{R}^2$ a simply connected subset and $f_1(x,y), f_2(x,y)$ and $h(x,y) \in C^1_\Omega$. If $\frac{\partial(h(x,y)f_1(x,y))}{\partial x} + \frac{\partial(h(x,y)f_2(x,y))}{\partial y}$ does not change of sign and it is not identically zero in Ω, then the system*

$$\begin{aligned} \tfrac{dx}{dt} &= f_1(x,y), \\ \tfrac{dy}{dt} &= f_2(x,y) \qquad (x,y) \in \Omega, \end{aligned} \tag{2.1}$$

does not admit periodic orbits in Ω. The function $h(x,y)$ is called a Dulac function.

Theorem 2.2. *If there exists $C(x,y) := \Omega \to \mathbb{R}$ and $h(x,y)$ is a solution of the system*

$$f_1(x,y)\frac{\partial h(x,y)}{\partial x} + f_2(x,y)\frac{\partial h(x,y)}{\partial y} = h(x,y)\left[C(x,y) - \nabla \cdot (f_1(x,y), f_2(x,y))\right], \tag{2.2}$$

where $h(x,y)C(x,y)$ is continuous, with constant sign and not identically zero in any subregion of Ω, then $h(x,y)$ is a Dulac function for (2.1) on Ω.

Notice that, the challenge now, it is to find a function $C(x,y)$ and a solution, $h(x,y)$, of the partial differential equation (2.2), such that $C(x,y)h(x,y)$ is a continuous function not identically zero with constant sign. For more details about the method see [29, 30].

3. Dulac functions for three types of mutualistic models.

In this section, we propose three general systems for which periodic solutions are excluded. To do this, for each system, we construct an auxiliary function $C(x,y)$ to solve the partial differential equation given by (2.2) whose solution is a Dulac function for the system.

3.1. System Type I.

Theorem 3.1. *[System Type I]. Let $r_1, r_2 \in \mathbb{R}^+$, $s_1, s_2 \in \mathbb{R}$, $g_1(y), g_2(x) : \mathbb{R}^+ \to \mathbb{R}$, $h_1(y), h_2(x) : \mathbb{R}^+ \cup \{0\} \to \mathbb{R}^+ \cup \{0\}$ and $m_1(x), m_2(y) \in C^1$ such that $\frac{dm_1(x)}{dx} > 0$, $\frac{dm_2(y)}{dy} > 0$.*

The system

$$\begin{aligned} \tfrac{dx}{dt} &= x\left(r_1 + h_1(y)\right)\left(s_1 + g_1(y) - m_1(x)\right), \\ \tfrac{dy}{dt} &= y\left(r_2 + h_2(x)\right)\left(s_2 + g_2(x) - m_2(y)\right), \end{aligned} \tag{3.1}$$

admits the Dulac function $h(x,y)=\frac{1}{xy}$ *on* $\mathbb{R}^2_+ := \{(x,y)\in\mathbb{R} : x>0, y>0\}$.

Therefore, there are no periodic solutions of system (3.1) *on* $\mathbb{R}^2_+ := \{(x,y)\in\mathbb{R} : x>0, y>0\}$.

Proof: To prove the result, we use theorem 2.2. First, observe that the divergence of model (3.1) is given by

$$-\nabla\cdot(f_1,f_2) = -\left(\frac{f_1}{x}+\frac{f_2}{y}\right) + x(r_1+h_1(y))\frac{dm_1(x)}{dx} + y(r_2+h_2(x))\frac{dm_2(y)}{dy}. \tag{3.2}$$

Notice that, equation (2.2) becomes

$$\left[f_1(x,y)\frac{\partial z(x,y)}{\partial x} + f_2(x,y)\frac{\partial z(x,y)}{\partial y}\right]\frac{dh(x,y)}{dz(x,y)} = h(x,y)\left[C(x,y)-\nabla\cdot(f_1(x,y),f_2(x,y))\right], \tag{3.3}$$

if $h=h(z)$ with $z(x,y)$.

To simplify equation (3.3), we propose the function

$$C(x,y) = -\left(x(r_1+h_1(y))\frac{dm_1(x)}{dx} + y(r_2+h_2(x))\frac{dm_2(y)}{dy}\right), \tag{3.4}$$

which is negative in $\mathbb{R}^2_+$.

With $C(x,y)$ given in (3.4), equation (3.3) is reduced to

$$\frac{\frac{\partial h}{\partial z}}{h} = \frac{-\left(\frac{f_1}{x}+\frac{f_2}{y}\right)}{f_1\frac{\partial z}{\partial x}+f_2\frac{\partial z}{\partial y}}. \tag{3.5}$$

Taking $z(x,y)=xy$, equation (3.5) is simplified to

$$\frac{\frac{dh}{dz}}{h} \equiv \frac{\partial \log h}{\partial z} = -\frac{1}{z}. \tag{3.6}$$

Solving the differential equation (3.6), we obtain the solution $h(x,y)=\frac{1}{xy}$ which is positive in $\mathbb{R}^2_+$.

Since $C(x,y)h(x,y)$ has fixed sign in $\mathbb{R}^2_+$, it is continuous and not identically zero, by theorem 2.2, system (3.1) admits the Dulac function $h(x,y)=\frac{1}{xy}$ on $\mathbb{R}^2_+$. Therefore, there are no periodic solutions of system (3.1) in the positive quadrant.

Remarks: Regardless of the geometric characteristics of the functions $g_1(y)$ and $g_2(x)$ and the values of the parameters s_1 and s_2, in system (3.1), periodic solutions are excluded. This occurs because these functions and the parameters do not appear in the function $C(x,y)$ proposed.

3.2. System Type II. Theorem 3.2. *[System Type II]. Let* $r_1,r_2\in\mathbb{R}$, $d_1,d_2\in\mathbb{R}^+\cup\{0\}$ *and* $f_1(x,y)$, $f_2(x,y)$, $g_1(x,y)$, $g_2(x,y)\in C^1$. *If* $\left(\frac{\partial f_1}{\partial x}+\frac{\partial f_2}{\partial y}-\left(\frac{\partial g_1}{\partial x}+\frac{\partial g_2}{\partial y}\right)\right)<0$ *on* $\mathbb{R}^2_+ := \{(x,y)\in\mathbb{R} : x>0, y>0\}$, *then the system*

$$\begin{aligned}\frac{dx}{dt} &= r_1x-d_1x^2+(f_1(x,y)-g_1(x,y))\,xy,\\ \frac{dy}{dt} &= r_2y-d_2y^2+(f_2(x,y)-g_2(x,y))\,xy,\end{aligned} \tag{3.7}$$

admits the Dulac function $h(x,y)=\frac{1}{xy}$ *on* $\mathbb{R}^2_+ := \{(x,y)\in\mathbb{R} : x>0, y>0\}$.

Therefore, system (3.7) *does not admit periodic solutions on* $\mathbb{R}^2_+$.

Proof: The line of thought followed to prove this result is analogous to that used in the proof of the previous theorem. Calculating $-\nabla\cdot(f_1,f_2)$ and after factoring this expression, we obtain

$$\begin{aligned}-\nabla\cdot(f_1,f_2) &= -\left(\frac{f_1}{x}+\frac{f_2}{y}\right)+d_1x+d_2y+\\ &\quad -xy\left(\frac{\partial}{\partial x}f_1(x,y)-\frac{\partial}{\partial x}g_1(x,y)+\frac{\partial}{\partial y}f_2(x,y)-\frac{\partial}{\partial y}g_2(x,y)\right).\end{aligned} \tag{3.8}$$

We propose the expression

$$C(x,y) = xy\left(\frac{\partial f_1}{\partial x}+\frac{\partial f_2}{\partial y}-\left(\frac{\partial g_1}{\partial x}+\frac{\partial g_2}{\partial y}\right)\right)-d_1x-d_2y. \tag{3.9}$$

Since d_1 and d_2 are positive, the function $C(x,y)$ does not change of sign when $\left(\frac{\partial f_1}{\partial x}+\frac{\partial f_2}{\partial y}-\left(\frac{\partial g_1}{\partial x}+\frac{\partial g_2}{\partial y}\right)\right)<0$.

Assuming that $h(z)$ depends on $z(x,y)$ and applying the chain rule, equation (2.2) associated with this case becomes

$$\frac{\frac{\partial h}{\partial z}}{h}=\frac{-\left(\frac{f_1}{x}+\frac{f_2}{y}\right)}{f_1\frac{\partial z}{\partial x}+f_2\frac{\partial z}{\partial y}}. \tag{3.10}$$

Taking $z(x,y)=xy$, equation (3.10) is given by

$$\frac{\frac{dh}{dz}}{h}\equiv\frac{\partial\log h}{\partial z}=-\frac{1}{z}. \tag{3.11}$$

Solving the differential equation (3.11), we obtain the solution $h(x,y)=\frac{1}{xy}$, which is positive in $\mathbb{R}^2_+$. Since $C(x,y)h(x,y)$ is continuous, it is not identically zero and it has constant sign, by theorem 2.2, $h(x,y)=\frac{1}{xy}$ is a Dulac function of system (3.7). Therefore, the system does not present periodic solutions on $\mathbb{R}^2_+$.

3.3. System Type III.

Theorem 3.3. *[System Type III]. Let* $a_1,a_2\in\mathbb{R}^+\cup\{0\}$, $b_1,b_2\in\mathbb{R}^+$, $g_1(x)$, $g_2(y)$, $m_1(y)$, $m_2(x)$, $h_1(x)$, $h_2(y)$ $:\mathbb{R}^+\to\mathbb{R}^+$ *be. If* $\frac{d}{dx}g_1(x)>0$, $\frac{d}{dy}g_2(y)>0$, $g_1(x)\le x$, $g_2(y)\le y$, $h_1(x)\le x$ *and* $h_2(y)\le y$, *then the system*

$$\begin{array}{rcl}\frac{dx}{dt}&=&x(a_1-b_1x)g_1(x)+m_1(y)h_1(x),\\ \frac{dy}{dt}&=&y(a_2-b_2y)g_2(y)+m_2(x)h_2(y),\end{array} \tag{3.12}$$

admits the Dulac function $h(x,y)=\frac{1}{x^2y^2}$ *on* $\mathbb{R}^2_+:=\{(x,y)\in\mathbb{R}:x>0,y>0\}$.

Therefore, the system does not admit periodic orbits on $\mathbb{R}^2_+$.

Proof: We need to solve the partial differential equation given by (2.2) associated with system (3.12). To do this, we calculate the divergence of the model which is

$$\begin{array}{rcl}-\nabla\cdot(f_1,f_2)&=&-\left(a_1-b_1x\right)g_1\left(x\right)+xb_1g_1\left(x\right)-x\left(a_1-b_1x\right)\frac{d}{dx}g_1\left(x\right)-m_1\left(y\right)\frac{d}{dx}h_1\left(x\right)\\ &&-\left(a_2-b_2y\right)g_2\left(y\right)+yb_2g_2\left(y\right)-y\left(a_2-b_2y\right)\frac{d}{dy}g_2\left(y\right)-m_2\left(x\right)\frac{d}{dy}h_2\left(y\right).\end{array} \tag{3.13}$$

By factoring expression (3.13), it is obtained the following.

$$\begin{array}{rcl}-\nabla\cdot(f_1,f_2)&=&-2\left(\frac{f_1}{x}+\frac{f_2}{x}\right)+\left(g_1(x)-x\left(\frac{d}{dx}g_1(x)\right)\right)a_1+\left(g_2(y)-y\left(\frac{d}{dy}g_2(y)\right)\right)a_2+\\ &&+\frac{m_1(y)}{x}\left(h_1(x)-x\left(\frac{d}{dx}h_1(x)\right)\right)+\frac{m_2(x)}{y}\left(h_2(y)-y\left(\frac{d}{dy}h_2(y)\right)\right)+\\ &&+x^2\left(\frac{d}{dx}g_1(x)\right)b_1+y^2\left(\frac{d}{dy}g_2(y)\right)b_2+\frac{m_1(y)h_1(x)}{x}+\frac{m_2(x)h_2(y)}{y}.\end{array} \tag{3.14}$$

We propose the following function $C(x,y)$ to apply theorem 2.2.

$$\begin{array}{rcl}C(x,y)&=&-\left(g_1(x)-x\left(\frac{d}{dx}g_1(x)\right)\right)a_1-\left(g_2(y)-y\left(\frac{d}{dy}g_2(y)\right)\right)a_2+\\ &&-\frac{m_1(y)}{x}\left(h_1(x)-x\left(\frac{d}{dx}h_1(x)\right)\right)-\frac{m_2(x)}{y}\left(h_2(y)-y\left(\frac{d}{dy}h_2(x)\right)\right)+\\ &&-x^2\left(\frac{d}{dx}g_1(x)\right)b_1-y^2\left(\frac{d}{dy}g_2(y)\right)b_2-\frac{m_1(y)h_1(x)}{x}-\frac{m_2(x)h_2(y)}{y}.\end{array} \tag{3.15}$$

The function $C(x,y)$ is always negative in $\mathbb{R}^2_+$ since, by hypothesis, $g_1(x)$, $g_2(y)$, $h_1(x)$ and $h_2(y)$ satisfies the following Gronwall's differential inequalities.

$$\begin{array}{ll}\frac{d}{dx}g_1(x)\le\frac{g_1(x)}{x}, & \frac{d}{dy}g_2(y)\le\frac{g_2(y)}{y},\\ \frac{d}{dx}h_1(x)\le\frac{h_1(x)}{x} & \frac{d}{dy}h_2(y)\le\frac{h_2(y)}{y}.\end{array} \tag{3.16}$$

Assuming that $h(z)$ depends on $z(x,y)$ and applying the chain rule, equation (2.2) becomes

$$\frac{\frac{\partial h}{\partial z}}{h} = \frac{-2\left(\frac{f_1}{x}+\frac{f_2}{y}\right)}{f_1\frac{\partial z}{\partial x}+f_2\frac{\partial z}{\partial y}}. \tag{3.17}$$

Taking $z(x,y)=xy$, equation (3.17) is reduced to

$$\frac{\frac{dh}{dz}}{h} \equiv \frac{\partial \log h}{\partial z} = -\frac{2}{z}. \tag{3.18}$$

Solving equation (3.18), we obtain the solution $h(x,y) = \frac{1}{x^2y^2}$ which is positive in $\mathbb{R}^2_+$. Notice that, $C(x,y)h(x,y)$ is a continuous not identically zero function and it has constant sign. Then, by theorem 2.2, system (3.7) admits the Dulac function $h(x,y) = \frac{1}{x^2y^2}$ on $\mathbb{R}^2_+$. Therefore, the system does not admit periodic solutions in $\mathbb{R}^2_+$.

4. Examples. In this section, we propose six novel models which describe the dynamics of two mutualistic species. These models are particular cases of the systems analyzed in Section 3. Therefore, according to the results obtained, the population dynamics of these mutualistic species does not present periodic behaviors. By numerical simulations, we show the behavior of the solutions of the models for some values of the parameters. We also apply Theorems 3.1-3.3 to mutualistic models that were collected by Hale and Valdovinos in [1] to show what models do not present periodic solutions; see Appendix A.

4.1. Mutualistic models associated to the System Type I. In the two cases shown in the following, we assume that each species increases its carrying capacity by mutualism.

Example a. The population dynamics of each species, if the partner species is absent, is described by a θ-logistic model. When this is the case, the carrying capacity and the intrinsic growth rate for the species x (y) are given by $\sqrt[\theta_1]{K_1}$ ($\sqrt[\theta_2]{K_2}$) and r_1 (r_2), respectively. It is known that, if $0<\theta<1$, θ-logistic models are used to model population growth of species with an r survival strategy. In contrast, if $\theta>1$, θ-logistic models are used to model population growth of species with a K survival strategy. In the construction of the two models proposed, it is assumed that mutualism does not increase the intrinsic growth rate, then $h_1(y)$ and $h_2(x)$ are the function zero. In contrast, it is assumed that mutualism increases the carrying capacity of each species. To model these increments, we use the functions $g_1(y) = \gamma_1\frac{\alpha_1 y}{1+\alpha_1\beta_1 y}$ and $g_2(x) = \gamma_2\frac{\alpha_2 x}{1+\alpha_2\beta_2 x}$, which were used in [33]. The model proposed is given by

$$\begin{aligned} \dot{x} &= r_1 x\left[K_1 + \gamma_1\tfrac{\alpha_1 y}{1+\alpha_1\beta_1 y} - x^{\theta_1}\right], \\ \dot{y} &= r_2 y\left[K_2 + \gamma_2\tfrac{\alpha_2 x}{1+\alpha_2\beta_2 x} - y^{\theta_2}\right]. \end{aligned} \tag{4.1}$$

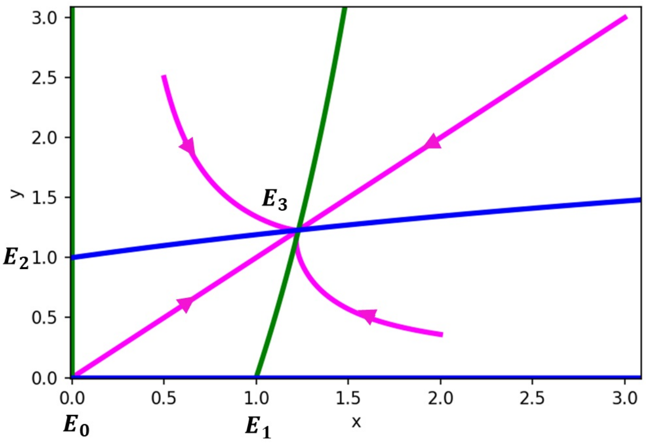

Figure 4.1: Model (4.1) has a global attractor. Therefore, for all initial condition, the solutions of the model converge to E_3.

System (4.1) satisfies the conditions in theorem 3.1. Then, we can conclude that $h(x,y) = \frac{1}{xy}$ is a Dulac function. Therefore, the model does not admit periodic solutions. So, the mutualistic species do not present sustained oscillations in their population densities.

In this case, the auxiliary function used to solve (2.2) is

$$C(x,y)=-\left(r_1\theta_1 x^{\theta_1}+r_2\theta_2 x^{\theta_2}\right). \tag{4.2}$$

In the following, we prove the global stability of the unique nontrivial equilibrium of the model that describes a scenario of coexistence of both species.

The nonzero nullclines, for model (4.1), are given by $\phi_1(y)=\left(K_1+\frac{g_1\alpha_1 y}{1+\alpha_1\beta_1 y}\right)^{\frac{1}{\theta_1}}$ and $\phi_2(x)=\left(K_2+\frac{g_2\alpha_2 y}{1+\alpha_2\beta_2 y}\right)^{\frac{1}{\theta_2}}$, respectively. By evaluating the nullclines at the origen, we obtain $\phi_1(0)=\sqrt[\theta_1]{K_1}$ and $\phi_2(0)=\sqrt[\theta_2]{K_2}$. The derivative of the nullclines are

$$\begin{aligned}
\frac{\phi_1(y)}{dy} &= \frac{\alpha_1\gamma_1\left(\frac{K_1+K_1\alpha_1\beta_1 y+\gamma_1\alpha_1 y}{1+\alpha_1\beta_1 y}\right)^{\frac{1}{\theta_1}}}{\theta_1\left(K_1+\frac{\alpha_1\gamma_1 y}{1+\alpha_1\beta_1}\right)}>0\\
\frac{\phi_2(x)}{dx} &= \frac{\alpha_1\gamma_2\left(\frac{K_2+K_2\alpha_2\beta_2 x+\gamma_2\alpha_2 x}{2+\alpha_2\beta_2 x}\right)^{\frac{1}{\theta_2}}}{\theta_2\left(K_2+\frac{\alpha_2\gamma_2 x}{2+\alpha_2\beta_2}\right)}>0.
\end{aligned} \tag{4.3}$$

Thus, both nullclines are increasing functions for all values of the parameters. Also, $\lim\limits_{y\to\infty}\phi_1(y)=\left(\frac{K_1\beta_1+\gamma_1}{\beta_1}\right)^{\frac{1}{\theta_1}}$ and $\lim\limits_{y\to\infty}\phi_2(x)=\left(\frac{K_2\beta_2+\gamma_2}{\beta_2}\right)^{\frac{1}{\theta_2}}$. Therefore, the nullclines are concave increasing functions. By the continuity of the nullclines, model (4.1) has a unique equilibrium point in $\mathbb{R}^+_2$, which is denoted by E^*. Therefore, by Poincare-Bendixson theory, all solutions in the positive quadrant approach E^* as $t\to\infty$. Thus, the equilibrium is globally asymptotically stable [32].

Figure 4.1 shows numerical solutions of the model for the values of the parameters $r_1=0.5, r_2=0.5, K_1=1, K_2=1, \gamma_1=0.5, \gamma_2=0.5, \alpha_1=0.3, \alpha_2=0.3, \beta_1=0.5, \beta_2=0.5, \theta_1=0.7, \theta_2=0.7$ and the initial conditions $(0.001, 0.001)$, $(2, 0.36)$, $(0.5, 2.5)$ and $(3, 3)$. Observe that, all solutions converge to the equilibrium E_3.

Example b. In this case, we model a scenario in which the species x and y are in a conditioned interaction. To do this, we assume that both species are in a mutualistic relationship in low population densities but they are in a competition relationship in higher population densities. To model this mechanism, we use the following functions: $g_1(y)=\left(\frac{b_1 y-y^2}{1+c_1 y^2}\right)y$ and $g_2(x)=\left(\frac{b_2 x-x^2}{1+c_2 x^2}\right)x$, which were used in [5]. All other parameters and functions used in the modelling process are the same as used in the example a. Thus, when there is no interaction between the species, the population dynamics is given by a θ-logistic model. The proposed model is

$$\begin{aligned}
\dot{x} &= r_1 x\left[K_1+\left(\frac{b_1 y-y^2}{1+c_1 y^2}\right)y-x^{\theta_1}\right],\\
\dot{y} &= r_2 y\left[K_2+\left(\frac{b_2 x-x^2}{1+c_2 x^2}\right)x-y^{\theta_2}\right].
\end{aligned} \tag{4.4}$$

Model (4.4) satisfies the conditions of theorem 3.1. Therefore, there are no periodic solutions of the model since the system given in (4.4) admits a Dulac function which is given by $h(x,y)=\frac{1}{xy}$. Then, both populations tend to a population equilibrium.

Models with conditioned interactions can show complex dynamics for different values of the parameters of the model [5]. Model (4.4) shows three border equilibrium points for all values of the parameters. Depending on the values of the parameters, the model can present from zero to five interior equilibrium points, which describe scenarios of coexistence. Depending the values of the parameters, these coexistence scenarios describe different ecological relationships such as mutualism, competition or a victim-exploiter relationship. Figure 4.2 shows the case in which there exists five interior equilibrium but only three equilibrium points are locally asymptotically stable. The stable equilibrium points describe a mutualism between the species. Depending on the initial conditions, solutions converge to different equilibrium points. For the numerical simulations, the values of the parameters are $\theta_1=0.7$, $\theta_2=0.7$, $r_1=1, K_1=0.1, b_1=3, c_1=0.1, r_2=1, K_2=0.1, b_2=3, c_2=0.1$. In Figure 4.2 (a), the initial conditions $(2, 0.5), (0.5, 2)$ were used. For Figure 4.2 (b) the initial conditions are $(0.5, 0.188), (0.001, 0.001), (0.1, 0.006), (0.03, 0.08), (0.01, 0.02)$ and $(0.02, 0.01)$. Notice that, according to Figure 4.2 (a), solutions can show an oscillatory behavior; however, sustained oscillations are discarded.

4.2. Mutualistic models associated to the System Type II. In the models proposed here, we describe a mutualistic relationship between the species x and y as a consumer-resource interaction.

Example c. In model (4.5), the parameter r_1 (r_2) denotes the growth rate for the species x (y) while the parameter d_1 (d_2) denotes the intraspecific competition rate for the species x (y).

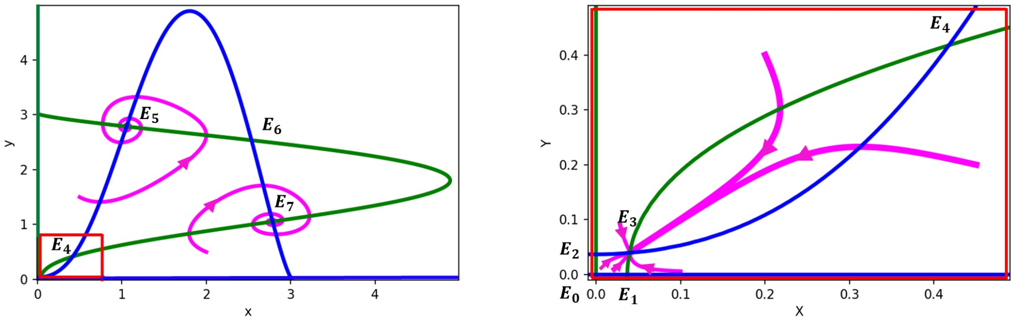

Figure 4.2: Model (4.4) presents three stable equilibrium points (E_3, E_5 and E_7) which describe coexistence scenarios. Very low values of K_1 and K_2 were used to describe a scenario in which both populations are in extreme adverse conditions when the partner species is absent. Numerical simulations show that changes in biotic or abiotic factors (for example, changes in the initial conditions) can lead to stable equilibrium points with a higher population densities, E_5 or E_7, or population densities close to the carrying capacities of each species when the partner species is absent E_3.

The functions $f_1(x,y) = \frac{1}{\alpha_1+\beta_1 x+\gamma_1 y}$ and $f_2(x,y) = \frac{1}{\alpha_2+\beta_2 x+\gamma_2 y}$ model the benefits related to the interaction. They describe how the services and resources acquired by x and y vary with the population densities of both species. The functional responses $g_1(x,y) = \frac{\delta_1 y}{\eta_1+\theta_1 y}$ and $g_2(x,y) = \frac{\delta_2 x^2}{\eta_2+\theta_2 x^2}$ model negative effects on population change of species x and y, respectively, due to supplying resources o services to the partner species. We model the net balance of benefits and cost receives for species x (y) from the interaction with species y (x) by $f_1(x,y) - g_1(x,y)$ ($f_2(x,y) - g_2(x,y)$). Notice that, the net balance $f_i(x,y) - g_i(x,y)$ can be positive or negative, for $i = 1, 2$. Therefore, depending on the population densities of the species x and y, when the net balance is positive, the interaction is beneficial while when it is negative, the interaction is detrimental. Model (4.5) generalizes a model proposed in [7].

$$\begin{aligned} \dot{x} &= x(r_1 - d_1 x) + \left[\frac{1}{\alpha_1+\beta_1 x+\gamma_1 y} - \frac{\delta_1 y}{\eta_1+\theta_1 y}\right] xy, \\ \dot{y} &= y(r_2 - d_2 y) + \left[\frac{1}{\alpha_2+\beta_2 x+\gamma_2 y} - \frac{\delta_2 x^2}{\eta_2+\theta_2 x^2}\right] xy. \end{aligned} \tag{4.5}$$

Model (4.5) satisfies the conditions in theorem 3.2. So, we can conclude that the model does not present periodic solutions since it admits a Dulac function, which is given by $h(x,y) = \frac{1}{xy}$.

In this case to simplify equation (3.3), we used

$$C(x,y) = -xy\left(\frac{\beta_1}{(\alpha_1+\beta_1 x+\gamma_1 y)^2} + \frac{\gamma_2}{(\alpha_2+\beta_2 x+\gamma_2 y)^2}\right) - d_1 x - d_2 y. \tag{4.6}$$

By an analysis of the nonzero nullclines of model (4.5), it can be proved that the model has a unique nontrivial equilibrium point in $\mathbb{R}_2^+$, which is denoted by E^*. Then, using the Poincare-Bendixon theory, all solutions in $\mathbb{R}_2^+$ approach the nontrivial equilibrium point as $t \to \infty$. Thus, E^* is globally asymptotically stable.

To show the behavior of the solutions of the model, we use the following values of the parameters. $r_1 = 1, r_2 = 2, d_1 = 2, d_2 = 2, \alpha_1 = 0.2, \alpha_2 = 0.4, \beta_1 = 1, \beta_2 = 2, \gamma_1 = 0.2, \gamma_2 = 0.4, \delta_1 = 1, \delta_2 = 1, \eta_1 = 2, \eta_2 = .5, \theta_1 = 0.2, \theta_2 = 0.6$ with the initial conditions $(0.2, 0.2), (2, 1), (0.9, 0.5)$. Figure 4.3 shows that solutions converge to a global attractor denoted by E_3.

Example d. In model (4.7), the functions $f_1(x,y) = m_1 y e^{-\alpha_1 x}$ and $f_2(x,y) = m_2 x e^{-\alpha_2 y}$ describe a scenario in which the per capita benefit received from the interaction decreases exponentially with the density of the recipient species. To wit, the model describes a scenario in which benefits granted by mutualism are most pronounced at low recipient densities; see [3]. In contrast, the functions $g_1(x,y) = \frac{\delta_1 y}{\eta_1+\theta_1 y}$ and $g_2(x,y) = \frac{\delta_2 x}{\eta_2+\theta_2 x}$ describe a situation in which the costs involved in the interaction increase with the density of the associated species. All other parameters of the model are defined in the same way as in example c. Therefore, the model proposed is

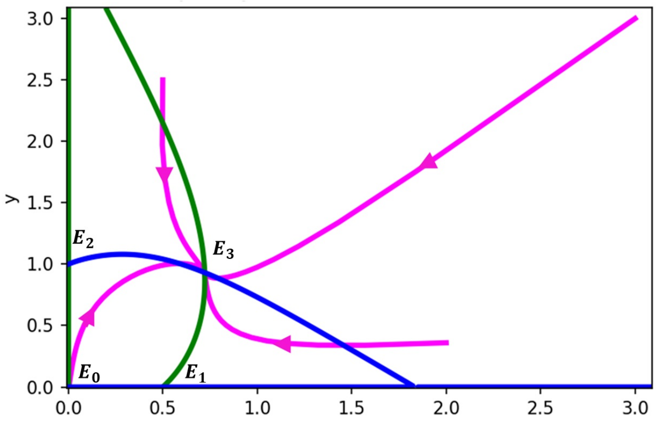

Figure 4.3: Solutions of model with different initial conditions go to a unique globally stable almost periodic solution.

$$\begin{aligned} \dot{x} &= x(r_1 - d_1x) + \left[m_1ye^{-\alpha_1 x} - \frac{\delta_1 y}{\eta_1+\theta_1 y}\right]xy, \\ \dot{y} &= y(r_2 - d_2y) + \left[m_2xe^{-\alpha_2 y} - \frac{\delta_2 x}{\eta_2+\theta_2 x}\right]xy. \end{aligned} \tag{4.7}$$

In this case, the function that leads to quickly solving the equation (3.3) is

$$C(x, y) = -xy\left(m_1y\alpha_1\mathrm{e}^{-\alpha_1 x} + m_2x\alpha_2\mathrm{e}^{-\alpha_2 y}\right) - d_1x - d_2y. \tag{4.8}$$

The model satisfies the conditions of theorem 3.2. Therefore, the model admits a Dulac function, which is given by $h(x, y) = \frac{1}{xy}$. For some values of the parameters, the model shows a bistability scenario between two coexistence equilibrium points, which are denoted by E_3 and E_5; see Figure 4.4. To show numerically this phenomenon, we use the values of the parameters: $r_1 = 0.5, r_2 = 2, d_1 = 2, d_2 = 2, \alpha_1 = 0.1, \alpha_2 = 0.4, m_1 = 10.51, m_2 = 0.5, \delta_1 = 1, \delta_2 = 1, \eta_1 = 2, \eta_2 = 0.5, \theta_1 = 0.2, \theta_2 = 0.6$. We also use the initial conditions $(2.5, 1.2)$, $(2, 0.08)$, $(6, 2)$ and $(14.8, 5.1)$.

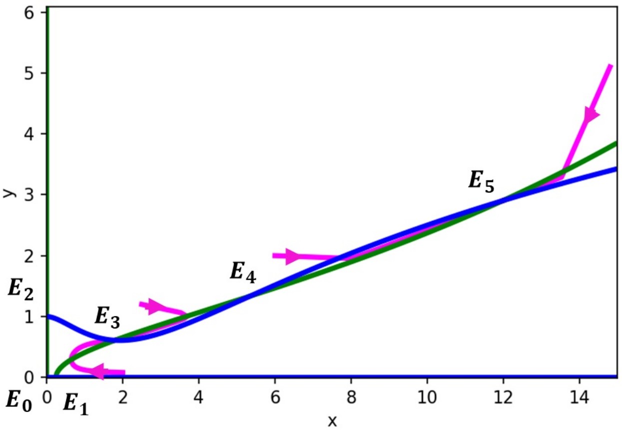

Figure 4.4: Model (4.7) shows a bistability scenario between two coexistence equilibrium points. To wit, solutions of the model go to different equilibrium point depending on the initial conditions.

4.3. Mutualistic models associated to the System Type III. The next examples describe the dynamics of two mutualistic species in which each species is subject to a weak Allee effect. That is, we assume that each population has a reduced per capita growth rate at a lower population density, but the per capita growth rate is positive for all population levels, unlike when a strong Allee effect is considered. Models (4.9) and (4.12) generalize the models given in [34] and [35].

Example e

In model (4.9), a_1 and b_1 denote the growth rate and the intraspecific competition rate for the species x, respectively. In a similar way, we define the parameters a_2 and b_2 for the species y. We assume that the per capita growth rates which are given by $(a_1 - b_1 x)$ for x, and $(a_2 - b_2 y)$ for y, are affected by the nonlinear functions $g_1(x) = \frac{\alpha_1 x}{\beta_1+\gamma_1 x}$ and $g_2(y) = \frac{\alpha_2 y}{\beta_2+\gamma_2 y}$, respectively. In the modeling process, the benefits received for the recipient species from the mutualistic relationship increase with the presence of the partner species with the rates $m_1(y) = \frac{\epsilon_1 y^{\delta_1}}{\beta_3+\gamma_3 y^{\delta_1}}$ and $m_2(x) = \frac{\epsilon_2 x^{\delta_2}}{\beta_4+\gamma_4 x^{\delta_2}}$. In this case, $h_1(x) = x$ and $h_2(y) = y$. The model proposed is

$$\begin{aligned} \dot{x} &= x\,(a_1 - b_1 x)\,\tfrac{\alpha_1 x}{\beta_1+\gamma_1 x} + \tfrac{\epsilon_1 y^{\delta_1}}{\beta_3+\gamma_3 y^{\delta_1}} x, \\ \dot{y} &= y\,(a_2 - b_2 y)\,\tfrac{\alpha_2 y}{\beta_2+\gamma_2 y} + \tfrac{\epsilon_2 x^{\delta_2}}{\beta_4+\gamma_4 x^{\delta_2}} y. \end{aligned} \tag{4.9}$$

To find a Dulac function, we propose the function

$$C(x,y) = -\left(\frac{\alpha_1 x^2(\gamma_1 a_2 + \beta_1 b_1)}{(\beta_1+\gamma_1 x)^2} + \frac{\alpha_2 y^2(\gamma_2 a_2 + \beta_2)}{(\beta_2+\gamma_2 y)^2} + \frac{\epsilon_1 y^{\delta_1} + \epsilon_2 x^{\delta_1}}{\beta_3 + \gamma_3 y^{\delta_1}} \right). \tag{4.10}$$

Since model (4.9) satisfied the conditions of theorem 3.3, we can conclude that the model admits the Dulac function $h(x,y) = \frac{1}{x^2 y^2}$. Therefore, the model does not admit periodic solutions.

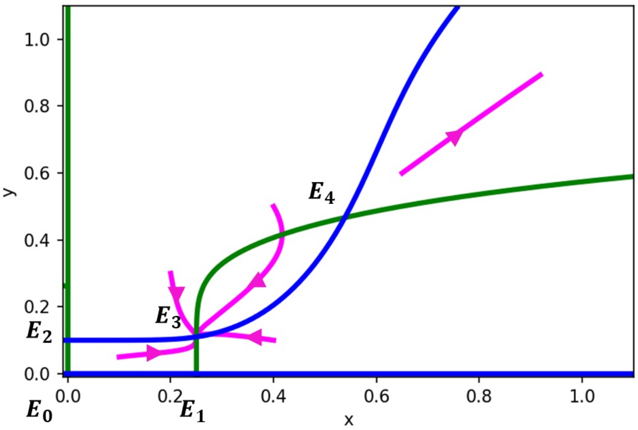

Figure 4.5: Solutions of model with different initial conditions go to E_3. The model presents unbounded solutions.

Figure 4.5 shows the behavior of the solutions of the model for the values of the parameters shown as follows. $a_1 = 0.05, a_2 = 0.02, b_1 = 2, b_2 = 2, \alpha_1 = 0.2, \alpha_2 = 0.4, \beta_1 = 0.4, \beta_2 = 0.4, \beta_3 = 0.9, \beta_4 = 0.9, \gamma_1 = 0.7, \gamma_2 = 0.7, \gamma_3 = 0.5, \gamma_4 = 0.5, \epsilon_1 = 0.7, \epsilon_2 = 0.7, \delta_1 = 6$ with the initial conditions $(0.4, 0.5), (0.4, 0.1), (0.2, 0.3), (0.1, 0.05)$ and $(0.65, 0.6)$. Notice that, the solution with the initial condition $(0.65, 0.6)$ increases when $t \to \infty$. In this case, the model presents unbounded solutions. This scenario is clearly unrealistic. The existence of unbounded solution occurs because the benefits due to mutualism outweigh the costs of the interaction.

Example f. In this scenario, the functions that reduce the per capita growth rates of the species x and y are given by $g_1(x) = \frac{\alpha_1 e^x}{1+e^x}$ and $g_2(y) = \frac{\alpha_2 e^y}{1+e^y}$. The benefits that species x receive from the interaction is the product of the functions $m_1(y) = \frac{\epsilon_1 y^{\delta_1}}{\beta_3+\gamma_3 y^{\delta_1}}$ and $h_1(x) = \frac{\theta_1 x}{\mu_1+\phi_1 x}$. In the same way, the benefits received for y from the interaction with x are given by the product of the functions $+m_2(x) = \frac{\epsilon_2 x^{\delta_2}}{\beta_4+\gamma_4 x^{\delta_2}}$ and $h_2(y) = \frac{\theta_2 y}{\mu_2+\phi_2 y}$. All other parameters are defined as in the example e. Then, the model proposed is given by

$$\begin{aligned} \dot{x} &= x\,(a_1 - b_1 x)\,\tfrac{\alpha_1 e^x}{1+e^x} + \tfrac{\epsilon_1 y^{\delta_1}}{\beta_3+\gamma_3 y^{\delta_1}}\,\tfrac{\theta_1 x}{\mu_1+\phi_1 x}, \\ \dot{y} &= y\,(a_2 - b_2 y)\,\tfrac{\alpha_2 e^y}{1+e^y} + \tfrac{\epsilon_2 x^{\delta_2}}{\beta_4+\gamma_4 x^{\delta_2}}\,\tfrac{\theta_2 y}{\mu_2+\phi_2 y}. \end{aligned} \tag{4.11}$$

Observe that model (4.12) satisfies the conditions in theorem 3.3, we can conclude that the model admits the Dulac function $h(x,y) = \frac{1}{x^2 y^2}$. Therefore, the model does not admit periodic solutions.

In this case, to solve the partial differential equation (3.3), we propose the function

$$\begin{aligned} C(x,y) \;=\; & -\frac{\alpha_1 \mathrm{e}^x(1+\mathrm{e}^x-x)a_1}{(1+\mathrm{e}^x)^2} - \frac{\alpha_2 \mathrm{e}^y(1+\mathrm{e}^y-y)a_2}{(1+\mathrm{e}^y)^2} - \frac{\epsilon_1 y^{\delta_1} x\theta_1\phi}{(\beta_3+g_3y^{\delta_1})(\mu_1+\phi\, x)^2} - \frac{\epsilon_2 x^{\delta_2} y\theta_2\phi_2}{(\beta_4+g_4x^{\delta_2})(\mu_2+\phi_2 y)^2} \\ & -\frac{x^2\alpha_1 \mathrm{e}^x b_1}{(1+\mathrm{e}^x)^2} - \frac{y^2\alpha_2 \mathrm{e}^y b_2}{(1+\mathrm{e}^y)^2} - \frac{\epsilon_1 y^{\delta_1}\theta_1}{(\beta_3+g_3y^{\delta_1})(\mu_1+\phi\, x)} - \frac{\epsilon_2 x^{\delta_2}\theta_2}{(\beta_4+g_4x^{\delta_2})(\mu_2+\phi_2 y)}. \end{aligned} \tag{4.12}$$

which is negative in the positive quadrant since $(1+e^x-x)$ and $(1+e^y-y)$ are positive functions for all values of x and y, respectively.

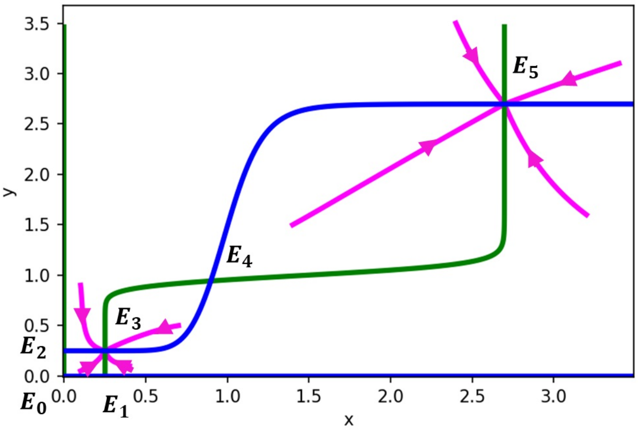

Figure 4.6: Model (4.11) shows a bistability scenario between the equilibrium points E_3 and E_5. In this scenario, solutions of the model tend to different coexistence scenarios depending on the initial conditions.

Figure 4.6 shows the behavior of the solutions of model (4.11) for the values of the parameters $a_1 = 0.05, a_2 = 0.05, b_1 = 0.2, b_2 = 0.2, \alpha_1 = 0.4, \alpha_2 = 0.4, \beta_1 = 0.4, \beta_2 = 0.4, \beta_3 = 0.9, \beta_4 = 0.9, \gamma_1 = 0.7, \gamma_2 = 0.7, \gamma_3 = 0.5, \gamma 4 = 0.5, \theta_1 = 0.2, \theta_2 = 0.2, \mu_1 = 0.5, \mu_2 = 0.5, \phi_1 = 0.2, \phi_2 = 0.2, \epsilon_1 = 0.7, \epsilon_2 = 0.7, \delta_1 = 20, \delta_2 = 10$. In the numerical simulations we use the initial conditions $(0.7, 0.5)$, $(1.4, 1.5)$, $(2.4, 3.5)$, $(3.4, 3.1)$, $(3.2, 1.6)$, $(0.4, 0.1)$, $(0.1, 0.9)$, $(0.1, 0.05)$. Observe that, depending on the initial conditions, solutions of the model converge to different coexistence scenarios, which are denoted by E_3 and E_5.

5. Discussion and Conclusions. The ecological relationships between species have been widely studied from a biological and a mathematical perspective. However, among all ecological relationships, mutualism has been biologically studied less often than other interactions such as predation-prey, competition and victim-exploiter relationships [1]. This lack of analysis from a biological perspective has been translated into a lack of analysis of mutualism through mathematical models.

A review of mutualistic models leads to conclude that these models can present a very complex dynamics. In particular, in these models, scenarios of exclusion of species are possible or multiple scenarios of coexistence of species can occur. These coexistence scenarios describe different ecological relationships as a result of varying some parameters of the model to simulate changes in the biotic or abiotic factors [5, 7, 1]. From a sustainability perspective, it is of paramount relevance to know if the coexistence scenarios are represented either by solutions that converge to an equilibrium point or by solutions converging to a periodic solution. In particular, populations with sustained oscillations are considered less stable because they are more vulnerable to extinction if the environment is disturbed.

The existence or the exclusion of periodic solutions of mutualistic models has been repeatedly discussed in the literature without a consensus about what type of ecological or demographic mechanisms lead to a oscillatory behavior. In such scenario, it is unknown if the population densities of the partner species present either sustained oscillations or the oscillations are transient and they tend to an equilibrium. This lack of qualitative information about the behavior of the solutions of the model can lead to the design of wrong strategies of intervention by conservationists.

Since the dynamic behavior of mutualism models has not yet been deeply characterized, we are interested in providing a criterion that can be used to respond, what type of ecological mechanisms do not produce sustained oscillations in the dynamics of mutualistic populations. To prove the nonexistence of periodic solutions, we construct an auxiliary function such that we construct and solve a partial differential equation whose solution is a Dulac function for each particular family of the models proposed. To do this, in a first case, we exclude periodic behavior of a wide variety of mutualistic models in which the mutualistic benefit (modeled by a function of the partner species) affects the intrinsic rate of increase and the carrying capacity of the partner species; see system type I. For example, the systems type I model conditioned interactions between species such as scenarios in which there is a cooperation relationship at low population densities and there is a competition relationship at high populations densities [5]. In a second case, we also prove a result about the nonexistence of periodic solutions of a family of consumer-resource models; see system type II. These type of models describe scenarios in which the benefits and the costs involved in the interaction depend on the population densities of both mutualistic species [7]. In a third case, we prove that sustained oscillations are not possible in a wide variety of mutualistic models when there is a weak Allee effect in the per capita growth rate of each species [12, 34]. We want to point out that, systems type I, II and III can describe either facultative mutualism or obligate one for some values of the parameters. The results obtained can also be applied to models describing a commensalist interaction between especies if the net change of benefits-costs received from the interaction with the partner species in one species is zero.

Finally, we classified as Systems Type I, II or III most of the models in a historical collection of mutualistic models made for Hale and Valdovinos in [1]. We conclude that most of these models have no periodic solutions; see Appendix. From this analysis, we can conclude that even though these models might have a very complex dynamics, they do not present sustained oscillations. So, when the solutions of the models oscillate, the oscillatory behaviors are transient.

Therefore, from the analysis of the systems type I, II and III, and the historical list given in [1], we can conclude that, in many cases, a mutualistic strategy offers an evolutive advantage for both species since the population dynamics of mutualistic species converge to an equilibrium point. In summary, the results shown in this work are a valuable contribution to the theoretical ecology literature because it substantially deepens our understanding of the dynamic behavior of a large set of population models of mutualism, including recent models that are relatively analytically intractable. The results can be used by decision makers to design strategies that lead to scenarios of conservation of mutualistic species.

Author contributions. Osuna Osvaldo: Conceptualization, Metodology, Formal Analysis, Writing –review & editing. Tapia-Santos Brenda: Formal Analysis, Writing –review & editing. Villavicencio-Pulido Jose Geiser: Conceptualization, Methodology, Formal analysis, Writing –review & editing.

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6. Appendix A. The mathematical results were applied to a part of the list of models proposed by Hale and Valdovinos; see [1]. The authors provided a semi-chronological list of the study of mutualistic models. We found a Dulac's function for the most of the cases mentioned by them.

Table 6.1 is a modified version of Table 2 proposed in [1]. We also added two mutualistic models with an Allee effect. In the third column appears what theorem was applied to constructing a Dulac's function to exclude periodic orbits of the model mentioned in the second column. The nomenclature N/A denotes that the model associated is a discrete model and the symbol X denotes that the model does not satisfy the conditions of the Theorems 3.1, 3.2 and 3.3. Finally the symbol **** denotes a case that was not explored in this work.

Reference	Cite	Model	Type of model
Gause & Witt 1935	[36]	$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i+\alpha_{ij}N_j-N_i}{K_i}\right)$	Theorem 3.1
Whittaker 1975	[37]	$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1+\alpha_{12}N_2-N_1}{K_1+\alpha_{12}N_2}\right)$ $\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2+\alpha_{21}N_1-N_2}{K_2}\right)$	Theorem 3.1
	X	$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{\alpha_{12}N_2-N_1}{\alpha_{12}N_2}\right)$ $\frac{dN_2}{dt} = \frac{r_2 N_2}{K_2} \left(K_2 + \frac{aDN_1}{D+N_2} - N_2\right)$	Theorem 3.1
May 1976	[38]	$\frac{dN_1}{dt} = N_1 \left(\frac{IN_2}{CD+CN_1+N_1N_2} - d_1\right)$ $\frac{dN_2}{dt} = r_2 N_2 \left(\frac{\alpha_{21}N_1-N_2}{\alpha_{21}N_1}\right)$	Theorem 3.2
Vandermeer & Boucher 1978	[39]	$\frac{dN_i}{dt} = N_i \left(r_i + \alpha_{ij}N_j - \alpha_{ii}N_i\right)$	Theorem 3.1
Addicott 1981	[40]	$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i-N_i}{K_i}\right)\left(1 + \frac{\alpha_{ij}N_j}{K_i}\right)$	Theorem 3.1
Soberón & Martinez del Rio 1981	[41]	$\frac{dN_i}{dt} = N_1 \left(\frac{k_1\sigma\mu N_2}{1+\sigma\phi\mu^2 N_1} - \gamma\right)$ $\frac{dN_i}{dt} = N_2 \left(\epsilon(K_2 - N_2) + \frac{k_2\sigma\mu^2 N_1}{1+\sigma\phi\mu^2 N_1}\right)$	Theorem 3.2
Dean 1983	[42]	$\frac{dN_i}{dt} = r_i N_i \left(\frac{k_i-N_i}{k_i}\right)$ $k_i = K_{i_{max}} \left(1 - e^{-(a_iN_j+C_i)/K_{i_{max}}}\right)$	Theorem 3.1
Wells 1983	[43]	$\frac{dN_i}{dt} = N_1 \left(\frac{bN_2}{aN_1+N_2+c} - dfN_1 - d\right)$ $\frac{dN_i}{dt} = N_2 \left(\frac{mN_1}{rN_2+N_1+h} - g\right)$	Theorem 3.2

Reference	Cite	Model	Type of model
Wolin & Lawlor 1984	[3]	$\frac{dN_i}{dt} = N_i\left(r_i - \frac{bN_i}{1+mN_j} - dN_i\right)$	Theorem 3.2
	X	$\frac{dN_i}{dt} = N_i\left(r_i - (b - mN_j + d)N_i\right)$	Theorem 3.1
		$\frac{dN_i}{dt} = N_i\left(r_i\left(1 - \frac{N_i}{K}\right) + mN_j e^{-\alpha N_i}\right)$	Theorem 3.2
Tonkyn 1986	[44]	$\frac{dN_i}{dt} = r_i N_i\left(1 - \left(\frac{N_i+\alpha_{ij}N_j-U_i}{K_i-U_i}\right)^2\right)$	Theorem 3.2
Pierce & Young 1986	[45]	$\frac{dN_i}{dt} = N_1\left(r_1(N_2) - \frac{N_1}{K_1}\right)$ $\frac{dN_i}{dt} = r_2 N_2\left(1 - \frac{N_2}{K_2(N_1)}\right)$	Theorem 3.1
Wright 1989	[33]	$\frac{dN_i}{dt} = N_i\left(r_i(1 - c_i N_i) + b_{ij}\frac{a_{ij}N_j}{1+a_{ij}h_{ij}N_j}\right)$	Theorem 3.2
		$\frac{dN_i}{dt} = N_i\left(r_i - c_i N_i + b_{ij}\frac{a_{ij}N_j}{1+a_{ij}h_{ij}N_j}\right)$	Theorem 3.2
Hernandez 1998	[4]	$\frac{dN_i}{dt} = r_i N_i\left(1 - \frac{N_i}{K_i} + \left(\frac{b_j N_j - c_i N_j^2}{1+d_j N_j^2}\right)\frac{N_j}{K_i}\right)$	Theorem 3.1
		$\frac{dN_i}{dt} = r_i N_i\left(-1 + \left(\frac{b_j N_j - c_i N_j^2}{1+d_j N_j^2}\right)\frac{N_j}{K_i}\right)$	Theorem 3.1
Holland et al. 2002	[6]	$\frac{dN_i}{dt} = N_1\left((1-\alpha)\alpha F\left(1 - e^{\left(-\frac{\gamma_1 N_2}{F N_1}\right)}\right)A_1\right)$ $\frac{dN_i}{dt} = (1-\alpha)\alpha F\left(1 - e^{\left(-\frac{\gamma_1 N_2}{F N_1}\right)}\right)A_2$ with $A_1 = \left(e^{\left(-\frac{\gamma_2 N_2}{F N_1}\right)}\right) - d_1 - gN_1$ and $A_2 = \left(e^{\left(-\frac{\gamma_2 N_2}{F N_1}\right)}\right) - d_2 N_2.$	Theorem 3.2

Reference	Model	Cite	Type of model
Zhang 2003	[46]	$\frac{dN_i}{dt} = R_i N_i \left(c_i - N_i - \alpha_i (N_j - b_i)^2\right)$	Theorem 3.1
Neuhauser & Fargione 2004	[47]	$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_1}{K_1+\gamma_{12}} - \alpha N_2\right)$ $\frac{dN_i}{dt} = r_2 N_2 \left(\frac{K_2+\alpha_{12}N_1-N_2}{K_2}\right)^{-1} - 1$	Theorem 3.1
Graves et al. 2006	[48]	$\frac{dN_i}{dt} = N_i \left(r_{i0} + (r_{i1} - r_{i0}) \left(1 - e^{-k_i N_j}\right)\right) - a_i N_i^2$	Theorem 3.1
Fishman & Hadany 2010	[49]	$\frac{dN_1}{dt} = N_1 \left(\frac{\eta\alpha N_2}{1+\alpha N_1+\alpha\beta N_2} - b - cN_1\right)$ $\frac{dN_i}{dt} = N_2 \left(\frac{\mu\alpha N_1}{1+\alpha N_1+\alpha\beta N_2} - d\right)$	Theorem 3.2
Kang et al. 2011	[50]	$\frac{dN_1}{dt} = N_1 \left(r_f \left(\frac{\alpha N_2^2}{b+\alpha N_2^2}\right) - r_c N_2 - d_1 N_1\right)$ $\frac{dN_2}{dt} = N - 2(r_\alpha N_1 - d_2 N_2)$	Theorem 3.1
Johnson & Amarasekare 2013	[51]	$\frac{dN_i}{dt} = N_i \left(r_i + \frac{m_{ij} N_j}{1+m_{ij}\tau_i N_j+\alpha_i N_i^2}\right)$	Theorem 3.2
García-Algarra et al. 2014	[52]	$\frac{dN_i}{dt} = N_i(r_i + b_{ij} N_j - (\alpha_i + c_i b_{ij} N_j) N_i)$	Theorem 3.2
Revilla 2015	[20]	$\frac{dN_i}{dt} = N_i \left(r_1 + \frac{\sigma_i \beta_i \alpha_j N_j}{\omega_j+\beta_i N_i} - c_i N_i\right)$	Theorem 3.2
		$\frac{dN_1}{dt} = N_1 \left(r_1 + \frac{\sigma_0\beta_0\alpha_0 N_0+\sigma_1\beta\alpha N_2}{\omega+\beta_0 N_0+\beta N_2} - c_1 N_1\right)$ $\frac{dN_2}{dt} = N_2 \left(r_1 + \frac{\sigma_2\beta\alpha N_1}{\omega+\beta_0 N_0+\beta N_2} - c_2 N_2\right)$	Theorem 3.2

Reference	Model	Cite	Type of model
Moore et al. 2018	[53]	$\frac{dN_i}{dt} = N_i\left(r_i + \beta_j N_j - \alpha_i N_i^{\theta_i}\right)$	Theorem 3.1
Cropp & Norbury 2019	[54]	$\frac{dN_i}{dt} = N_i\left(r_i\left(\frac{N_j}{\epsilon_j+N_j}\right)R + \alpha_{ij}N_j - \alpha_{ii}N_i\right)$ where $R = 1 - N - 1 - N_2$	Theorem 3.2
Martignoni et al. 2020	[55]	$\frac{dN_1}{dt} = N_1\left(r_p + \frac{q_{hp}\alpha N_2}{d+N_1} - q_{cp}\beta N_2 - \mu_p N_1\right)$ $\frac{dN_2}{dt} = N_2\left(q_{cm}\beta N_1 - \frac{q_{hm}\alpha N_1}{d+N_1} - \mu_m N_2\right)$	Theorem 3.2
Hale et al. 2021	[1]	$\frac{dN_2}{dt} = N_2\left(b_2 + \epsilon\frac{\alpha N_1}{1+\alpha h N_1} - s_2 N_2 - d_2\right)$ $\frac{dN_1}{dt} = N_1 b_p f\left(g + \gamma\frac{\alpha N_2}{1+\alpha h N_1+\alpha N_2}\right) - N_1\left(s_p N_1 + d_p\right)$	Theorem 3.2
Lin 2018	[34]	$\frac{dx}{dt} = x(b_1 - a_{11}x)\frac{x}{\beta+x} + a_{12}xy$ $\frac{dy}{dy} = y(b_2 - a_{22}y)$	Theorem 3.3
Wu et al. 2018	[35]	$\frac{dx}{dt} = x(a_1 - b_1 x) + x\frac{c_1 y^p}{1+y^p}$ $\frac{dy}{dy} = y(a_2 - b_2 y)\frac{y}{\beta+y}$	Theorem 3.3

Table 6.1: Mutualist models