Biodiversity and vulnerability in a 3D mutualistic system

G. Guerrero[1], J.A. Langa[2], A. Suárez[2]

1.- Universidad Central del Ecuador, Ciudadela Universitaria,
Av. América S/N, Quito - Ecuador.
2.- Dpto. Ecuaciones Diferenciales y Análisis Numérico
Seville University

April 16, 2013

Abstract

In this paper we study a three dimensional mutualistic model of two plants in competition and a pollinator with cooperative relation with plants. We compare the dynamical properties of this system with the associated one under absence of the pollinator. We observe how cooperation is a common fact to increase biodiversity, which it is known that, generically, holds for general mutualistic dynamical systems in Ecology as introduced in [4]. We also give mathematical evidence on how a cooperative species induces an increased biodiversity, even if the species is push to extinction. For this fact, we propose a necessary change in the model formulation which could explain this kind of phenomenon.

1   Introduction

A mathematical model for mutualistic networks in Ecology has been proposed in Bastolla et al. [4]. Basically, it is studied how interactions between groups of plants and pollinators affect to the whole network. In particular, the authors analyze the net of connections between groups of competitive species (the group of plants and the groups of animals) and the cooperative links between plants and pollinators (see also [1, 2, 3]). The mathematical model reads as follows: suppose P is the total number of plants and A the total number of animals. We suppose that plants (and animals) are in

1

competition and plants and animals have cooperation links. Then, we can write the following system of $P + A$ differential equations for S_{p_i} and S_{a_i} the species density populations for the i-th species of plant and of animal respectively:

$$
\begin{cases}
\dfrac{dS_{p_i}}{dt} & = \alpha_{p_i} S_{p_i} - \displaystyle\sum_{j=1}^{P} \beta_{p_{ij}} S_{p_i} S_{p_j} + \displaystyle\sum_{k=1}^{A} \dfrac{\gamma_{p_{ik}} S_{p_i} S_{a_k}}{1 + h_P \sum_{l=1}^{A} \gamma_{p_{il}} S_{a_l}} \\[4mm]
\dfrac{dS_{a_i}}{dt} & = \alpha_{a_i} S_{a_i} - \displaystyle\sum_{j=1}^{A} \beta_{a_{ij}} S_{a_i} S_{a_j} + \displaystyle\sum_{k=1}^{P} \dfrac{\gamma_{a_{ik}} S_{a_i} S_{p_k}}{1 + h_A \sum_{l=1}^{P} \gamma_{a_{il}} S_{p_l}} \\[2mm]
S_{p_i}(0) & = S_{p_{i0}} \\
S_{a_i}(0) & = S_{a_{i0}}
\end{cases}
\tag{1}
$$

for each p_i for $1 \leq i \leq P$ and a_i with $1 \leq i \leq A$. Here, the real numbers α_{p_i} and α_{a_i} represent the intrinsic growth rates in the absence of competition and cooperation for plants and animals, respectively, $\beta_{p_{ij}} \geq 0$ and $\beta_{a_{ij}} \geq 0$ denote the competitive interactions and $\gamma_{p_{ij}} \geq 0$ and $\gamma_{a_{ij}} \geq 0$ the mutualistic interactions. Finally, the parameters h_P and h_A represent the handling time.

For this model, the authors study in [4] how the architecture of a mutualistic network, i.e, the topology of connections between species increases biodiversity in the system. Indeed, it is observed that the more nestedness of the network, the more probability for a richer biodiversity. In particular, and from a dynamical system approach related to (1), this means that *the presence of highly linked cooperative species in the system produces coexistence of species that would go to extinction without them.* But the authors go even further, and explain how the more nestedness species (a topological property of the system), the more capacity of the network to increase biodiversity (a dynamical fact of the system). This is what we will refer to as:

Phenomenon 1: The presence of nested cooperative species contributes to increase biodiversity.

Very recently, the authors of [11] go further and reveal a very interesting and intriguing behaviour of mutualistic networks. They prove that it is a general fact not only in population dynamics, but also in economical systems. Essentially, it holds that *'although strong contributors to nestedness are more important for the persistence of the entire network, they are also more prone to extinction compared to those nodes that contribute proportionally less"* ([11], page 234). We will called it as:

Phenomenon 2: Strong contributors to biodiversity (i.e., species which presence induce an increased biodiversity) are more vulnerable to extinction.

In this paper we want to give mathematical evidence to both of these phenomena for a simplified model. Indeed, we will focus in the simplest case, i.e., a 3D mutualistic system in which we find two plants (u_1 and u_2) in competition and a pollinator (u_3) with cooperative relations with them

$$\begin{cases} u_1' = u_1(\alpha_1 - u_1 - \beta u_2 + \gamma_1 u_3) \\ u_2' = u_2(\alpha_2 - u_2 - \beta u_1 + \gamma_1 u_3) \\ u_3' = u_3(\alpha_3 - u_3 + \gamma_2 u_1 + \gamma_2 u_2), \\ (u_1(0), u_2(0), u_3(0)) = (u_1^0, u_2^0, u_3^0), \end{cases} \qquad (2)$$

where $\alpha_1, \alpha_2, \alpha_3 \in \mathbb{R}$, $0 < \beta < 1$, $\gamma_1, \gamma_2 > 0$ and we suppose positive initial data. Observe that in (2) we are assuming that the competition is of mean field type (see [4]) ($\beta_{a_{ij}} = \beta_{p_{ij}} = (\beta + (1 - \beta)\delta_{ij})$ where δ_{ij} is Kronecker's delta) and also mean field mutualist interactions $\gamma_{p_{ij}} = \gamma_1$ and $\gamma_{a_{ij}} = \gamma_2$ and $h_A = h_P = 0$. This last fact ($h_A = h_P = 0$) will made us to concentrate in the weak cooperation regime (see Theorem 2.3), which highly differs from the strong cooperation regime, and goes out of the aims for this work.

In absence of the pollinator, we get a 2D competitive Lotka-Volterra system, for which all its dynamical behaviour is well-known in the literature (see for instance [10], [14] and Lemma 2.1). However, less is known in the 3D system due mainly to the lack of order in the problem. Indeed, when u_1 and u_2 cooperate and u_3 compite with both of them, the system generates monotone flows, see [12] and [15], but this is not the situation in our case.

From a dynamical point of view, and following [4, 11], *Phenomenon 1* for (2) means that the presence of the cooperative species u_3 makes the coexistence of species u_1 and u_2 which (one of both of them) are lead to extinction in absence of u_3. We will study in detail regions in which *Phenomenon 1* holds, concluding the high generality of this behaviour.

Phenomenon 2 is more surprising (see [11]) and will not be observed with such a generality. We are looking for an increasing of biodiversity under the appearance of species u_3, i.e., coexistence of u_1 and/or u_2 which were extincted if u_3 is not present. But we also want u_3 is push to extinction as time is increased. We will prove that this phenomena is impossible. Indeed, we show that the asymptotic dynamical behaviour of (2) with $u_3 \to 0$ as $t \to \infty$ is the same as the associated competitive system for (u_1, u_2) with $u_3 = 0$, so that no increasing in coexistence species (and hence biodiversity) can be observed.

However, from [13, 4] we know that cooperative links in a network reduces competition. In particular, the rate of competition between two species is decreased if they have a common cooperative link with another species. This fact is crucial, and lead to a non-trivial modification of the general model (1) in order to take into account this behaviour. Mathematically, we find it as a possible explanation for *Phenomenon 2* to hold generically. Indeed, we give mathematical reason to this fact for our 3D model (2), by increasing the rate of competition to $\beta_0 > \beta$ if $u_3 = 0$. Indeed, we will study and compare the qualitative behaviour of systems (2) and

$$\begin{cases} u_1' = u_1(\alpha_1 - u_1 - \beta_0 u_2) \\ u_2' = u_2(\alpha_2 - u_2 - \beta_0 u_1) \end{cases} \tag{3}$$

with $\beta_0 > \beta$.

In this framework, we analyze all possible regions in which *Phenomenon 2* also holds. As a consequence, we conclude that the general model (1) has to be modified to include the fact of dependence of the rate of competition on mutualism links among species.

An outline of this work is as follows: in Section 2 we prove existence, uniqueness and extinction results for (2). Section 3 is devoted to study stationary points and their stability. Permanence of the model is shown in Section 4. In Sections 5 and 6 we discuss zones and simulations for Phenomena 1 and 2. In the last section, we suggest a possible modification for general model (1).

2   Existence and uniqueness of solutions

In this section, we show existence and uniqueness of positive solution for (2). Firstly, let us recall some important results. Consider the system:

$$\begin{cases} u' = u(\lambda - Au - Bv) \\ v' = v(\mu - Dv - Cu) \\ (u(0), v(0)) = (u_0, v_0), \end{cases} \tag{4}$$

with $\lambda, \mu \in \mathbb{R}$, $A, D > 0$ and $B, C \in \mathbb{R}$. It holds (see, for instance, [10] and [14]):

Lemma 2.1.   *a) Assume that $B, C > 0$ (**competitive case**) and $BC < AD$.*

   (a) If $\lambda, \mu < 0$ then $(u, v) \to (0, 0)$ as $t \to \infty$.

4

(b) *If* $\lambda > 0$ *and* $\mu < \lambda \frac{C}{A}$ *then* $(u, v) \to (\lambda/A, 0)$ *as* $t \to \infty$.

(c) *If* $\mu > 0$ *and* $\lambda < \mu \frac{B}{D}$ *then* $(u, v) \to (0, \mu/D)$ *as* $t \to \infty$.

(d) *If* $\mu > \lambda \frac{C}{A}$ *and* $\lambda > \mu \frac{B}{D}$ *then* $(u, v) \to (\frac{\lambda D - B\mu}{AD - BC}, \frac{\mu A - C\lambda}{AD - BC})$ *as* $t \to \infty$.

b) *Assume now that* $B, C < 0$ (**cooperative case**):

(a) *If* $BC > AD$, *then for* $\lambda, \mu > 0$ *there exists a blow-up in finite time*.

(b) *Assume that* $BC < AD$.

    i. *If* $\lambda, \mu < 0$ *then* $(u, v) \to (0, 0)$ *as* $t \to \infty$.

    ii. *If* $\lambda > 0$ *and* $\mu < \lambda \frac{C}{A}$ *then* $(u, v) \to (\lambda/A, 0)$ *as* $t \to \infty$.

    iii. *If* $\mu > 0$ *and* $\lambda < \mu \frac{B}{D}$ *then* $(u, v) \to (0, \mu/D)$ *as* $t \to \infty$.

    iv. *If* $\mu > \lambda \frac{C}{A}$ *and* $\lambda > \mu \frac{B}{D}$ *then* $(u, v) \to (\frac{\lambda D - B\mu}{AD - BC}, \frac{\mu A - C\lambda}{AD - BC})$ *as* $t \to \infty$.

As consequence of the above results, we obtain:

Corollary 2.2. *Assume that* $B, C < 0$, $BC < AD$, $\mu > \lambda \frac{C}{A}$ *and* $\lambda > \mu \frac{B}{D}$. *Then, for any* $\varepsilon > 0$ *there exists* $t_0 > 0$ *such that for* $t \geq t_0$ *we have that*

$$u \leq \frac{\lambda D - B\mu}{AD - BC} + \varepsilon, \qquad v \leq \frac{\mu A - C\lambda}{AD - BC} + \varepsilon.$$

In the following result we show existence and uniqueness of positive solution for (2) under the condition

$$\gamma_1 \gamma_2 < \frac{1 + \beta}{2}.$$

Moreover, the result shows that this condition is optimal in some way.

Theorem 2.3.   a) *Assume that* (**weak cooperation regime**)

(H1) $\gamma_1 \gamma_2 < \dfrac{1 + \beta}{2}.$

Then, there exists a unique positive bounded solution of (2) *for all* $t > 0$.

b) *Assume that* (**strong cooperation regime**)

(H2) $\gamma_1 \gamma_2 > \dfrac{1 + \beta}{2}.$

Then, if $\alpha_1 = \alpha_2 > 0$ *and* $\alpha_3 > 0$, *then the unique solution of* (2) *blows up in finite time*.

Proof. a) It is well-known the existence and uniqueness of positive solution for small time $t > 0$. We are going to prove that the solutions are bounded for all $t > 0$. Denote by

$$w := u_1 + u_2.$$

Assume for instance that $\alpha_1 \leq \alpha_2$. Then,

$$w' \leq \alpha_2 w - u_1^2 - u_2^2 - 2\beta u_1 u_2 + \gamma_1 w u_3.$$

Then, using that

$$-u_1^2 - u_2^2 - 2\beta u_1 u_2 \leq -\frac{1+\beta}{2} w^2$$

we obtain that

$$\begin{cases} w' \leq w(\alpha_2 - \dfrac{1+\beta}{2} w + \gamma_1 u_3) \\ u_3' = u_3(\alpha_3 - u_3 + \gamma_2 w), \end{cases}$$

that is, (w, u_3) is a subsolution of the system.

$$\begin{cases} w' = w(\alpha_2 - \dfrac{1+\beta}{2} w + \gamma_1 u_3) \\ u_3' = u_3(\alpha_3 - u_3 + \gamma_2 w), \\ w(0) = u_1^0 + u_2^0, \ u_3(0) = u_3^0. \end{cases} \tag{5}$$

Thus, by (H1) and using Corollary 2.2, (w, u_3) is bounded for all $t > 0$.

b) Assume now (H2). Denote by (w_1, w_2) the solution of

$$\begin{cases} w_1' = w_1(\alpha_1 - \dfrac{1+\beta}{2} w_1 + \gamma_1 w_2) \\ w_2' = w_2(\alpha_3 - w_2 + \gamma_2 w_1). \end{cases} \tag{6}$$

Observe that since $\alpha_1 = \alpha_2$, $((1/2)w_1, (1/2)w_1, w_2)$ is a solution of (2). By (H2) and Lemma 2.1 the solution blows up in finite time. This concludes the proof. ∎

From now on we assume (H1). In the rest of this section, we show regions where some of the species goes to the extinction. We firstly need the following lemma:

Lemma 2.4. *Denote by* $w = u_1 + u_2$. *Then, for t large enough,*

$$w \leq \frac{\max\{\alpha_1, \alpha_2\} + \gamma_1 \alpha_3}{\dfrac{1+\beta}{2} - \gamma_1 \gamma_2},$$

$$\alpha_3 \leq u_3 \leq \frac{\alpha_3 \dfrac{1+\beta}{2} + \gamma_2 \max\{\alpha_1, \alpha_2\}}{\dfrac{1+\beta}{2} - \gamma_1 \gamma_2}. \tag{7}$$

Proof. Assume $\alpha_1 \leq \alpha_2$, then (w, u_3) is sub-solution of (5). Now, the upper bounds of (7) follow by Corollary 2.2.

On the other hand,

$$u_3' \geq u_3(\alpha_3 - u_3)$$

and so $u_3 \geq \alpha_3$ for large t. ∎

Lemma 2.5. *Assume that* $\alpha_1 \leq \alpha_2$.

    a) If $\alpha_2, \alpha_3 < 0$, *then,* $(u_1, u_2, u_3) \to (0, 0, 0)$ *as* $t \to \infty$.

    b) Assume that $\alpha_2 > 0$ *and* $\alpha_3 < 0$ *with*

$$\alpha_3 < -\alpha_2 \frac{2\gamma_2}{1 + \beta},$$

    then $u_3 \to 0$.

    c) Assume that $\alpha_3 > 0$ *and* $\alpha_2 < 0$ *with*

$$\alpha_3 < -\frac{\alpha_2}{\gamma_1},$$

    then $(u_1, u_2, u_3) \to (0, 0, \alpha_3)$ *as* $t \to \infty$.

Proof. The result follows using again that (w, u_3) is subsolution of (5) and Lemma 2.1. ∎

Remark 2.6. *In the case when* $u_3 \to 0$, *then* (u_1, u_2) *behaves as the competitive system (4), see Lemma 6.1.*

3   Analysis of stability

From the result in the last section, we can suppose from now on that for (2) and (3) it holds that

$$(H) \qquad 0 < \beta < \beta_0 < 1, \quad \gamma_1 \gamma_2 < \frac{1 + \beta}{2}(< 1).$$

7

3.1 Stationary points and stability for the 2D model

Firstly we rewrite part a) in Lemma 2.1 for our 2D Lotka-Volterra system (3):

Lemma 3.1.   *a) If $\alpha_1, \alpha_2 < 0$, then solution $(0,0)$ is globally stable.*

b) If $\alpha_1 > 0$ and $\alpha_2 < \beta_0\alpha_1$, then the solution $E_{10} = (\alpha_1, 0)$ is globally stable.

c) If $\alpha_2 > 0$ and $\alpha_1 < \beta_0\alpha_2$, then the solution $E_{01} = (0, \alpha_2)$ is globally stable.

d) If $\alpha_1 > \beta_0\alpha_2$ and $\alpha_2 > \beta_0\alpha_1$, then the solution

$$E_{11} = \left(\frac{\alpha_1 - \beta_0\alpha_2}{1 - \beta_0^2}, \frac{\alpha_2 - \beta_0\alpha_1}{1 - \beta_0^2} \right)$$

is globally stable.

3.2 Stationary points and stability for the 3D model

Note that we can get the stationary points of (2) explicitly:

$$E_0 = (0,0,0), \; E_{100} = (\alpha_1, 0, 0), \; E_{010} = (0, \alpha_2, 0), \; E_{001} = (0, 0, \alpha_3),$$

$$E_{011} = \left(0, \frac{\alpha_2 + \gamma_1\alpha_3}{1 - \gamma_1\gamma_2}, \frac{\alpha_3 + \gamma_2\alpha_2}{1 - \gamma_1\gamma_2} \right),$$

$$E_{101} = \left(\frac{\alpha_1 + \gamma_1\alpha_3}{1 - \gamma_1\gamma_2}, 0, \frac{\alpha_3 + \gamma_2\alpha_1}{1 - \gamma_1\gamma_2} \right),$$

$$E_{110} = \left(\frac{\alpha_1 - \beta\alpha_2}{1 - \beta^2}, \frac{\alpha_2 - \beta\alpha_1}{1 - \beta^2}, 0 \right),$$

$$E_{111} = \begin{pmatrix} \dfrac{\alpha_1(1 - \gamma_1\gamma_2) + \alpha_2(\gamma_1\gamma_2 - \beta) + \alpha_3\gamma_1(1 - \beta)}{(1 - \beta)(1 + \beta - 2\gamma_1\gamma_2)} \\[2ex] \dfrac{\alpha_1(\gamma_1\gamma_2 - \beta) + \alpha_2(1 - \gamma_1\gamma_2) + \alpha_3\gamma_1(1 - \beta)}{(1 - \beta)(1 + \beta - 2\gamma_1\gamma_2)} \\[2ex] \dfrac{(\alpha_1 + \alpha_2)\gamma_2 + \alpha_3(1 + \beta)}{1 + \beta - 2\gamma_1\gamma_2} \end{pmatrix}^t .$$

To analyze the stability of these points, we calculate the eigenvalues of the Jacobian. Denote by $J(u_1, u_2, u_3)$ the Jacobian matrix in a stationary point (u_1, u_2, u_3). We have:

$$J(u_1, u_2, u_3) =$$

$$\begin{pmatrix} \alpha_1 - 2u_1 - \beta u_2 + \gamma_1 u_3 & -\beta u_1 & \gamma_1 u_1 \\ -\beta u_2 & \alpha_2 - 2u_2 - \beta u_1 + \gamma_1 u_3 & \gamma_1 u_2 \\ \gamma_2 u_3 & \gamma_2 u_3 & \alpha_3 - 2u_3 + \gamma_2(u_1 + u_2) \end{pmatrix}.$$

Proposition 3.2. *a) The eigenvalues of $J(E_0)$ are $\alpha_1, \alpha_2, \alpha_3$.*

b) The eigenvalues of $J(E_{100})$ are $-\alpha_1, \alpha_2 - \beta\alpha_1, \alpha_3 + \gamma_2\alpha_1$.

c) The eigenvalues of $J(E_{010})$ are $\alpha_1 - \beta\alpha_2, -\alpha_2, \alpha_3 + \gamma_2\alpha_2$.

d) The eigenvalues of $J(E_{001})$ are $\alpha_1 + \gamma_1\alpha_3, \alpha_2 + \gamma_1\alpha_3, -\alpha_3$.

e) Then $J(E_{011})$ has three real eigenvalues, two of them are negative and the other one is:

$$\lambda_{011} = \frac{\alpha_1(1 - \gamma_1\gamma_2) + \alpha_2(\gamma_1\gamma_2 - \beta) + \alpha_3\gamma_1(1 - \beta)}{1 - \gamma_1\gamma_2}.$$

f) $J(E_{101})$ has three real eigenvalues, two of them are negative and the other one is:

$$\lambda_{101} = \frac{\alpha_1(\gamma_2\gamma_1 - \beta) + \alpha_2(1 - \gamma_1\gamma_2) + \alpha_3\gamma_1(1 - \beta)}{1 - \gamma_2\gamma_1}.$$

g) $J(E_{110})$ has three real eigenvalues, two of them are negative and the other one is:

$$\lambda_{110} = \frac{(\alpha_1 + \alpha_2)\gamma_2 + \alpha_3(1 + \beta)}{1 + \beta}.$$

h) Assume that the three components of E_{111} are positive. If $\gamma_1\gamma_2 < (1 + \beta)/2$ then E_{111} is locally stable.

Proof. Paragraphs a)-d) are direct. Let us prove e); f) and g) follow similarly. Recall that

$$E_{011} = (0, u_2^*, u_3^*) := \left(0, \frac{\alpha_2 + \gamma_1\alpha_3}{1 - \gamma_1\gamma_2}, \frac{\alpha_3 + \gamma_2\alpha_2}{1 - \gamma_1\gamma_2}\right).$$

Then, denoting by I the identity matrix, we have

$$det(\lambda I - J(E_{011})) = (\lambda - \alpha_1 + \beta u_2^* - \gamma_1 u_3^*)(\lambda^2 + \lambda(u_2^* + u_3^*) + (1 - \gamma_1\gamma_2)u_2^* u_3^*).$$

9

Now, since $\gamma_1\gamma_2 < 1$, it is clear that $\lambda^2 + \lambda(u_2^* + u_3^*) + (1 - \gamma_1\gamma_2)u_2^*u_3^* = 0$ has two real negative roots. The other eigenvalue is given by

$$\lambda_{011} = \alpha_1 - \beta u_2^* + \gamma_1 u_3^* = \frac{\alpha_1(1 - \gamma_1\gamma_2) + \alpha_2(\gamma_1\gamma_2 - \beta) + \alpha_3\gamma_1(1 - \beta)}{1 - \gamma_1\gamma_2}.$$

h) Denote by $E_{111} = (u_1^*, u_2^*, u_3^*)$ and assume that $u_i^* > 0$, $i = 1, 2, 3$. We have that

$$J(E_{111}) = -diag(u_1^*, u_2^*, u_3^*)B$$

where

$$B = \begin{pmatrix} 1 & \beta & -\gamma_1 \\ \beta & 1 & -\gamma_1 \\ -\gamma_2 & -\gamma_2 & 1 \end{pmatrix}.$$

Observe that since $\beta < 1$, we have that $\gamma_1\gamma_2 < 1$ and then B is quasi weakly diagonally dominant (see [6]). Thus, by Theorem 3 in [6] it follows that E_{111} is stable if $det(B) = 1 + 2\gamma_1\gamma_2(\beta - 1) - \beta^2 > 0$, or equivalently, if $\gamma_1\gamma_2 < (1 + \beta)/2$. ∎

From this last result, now it is clear that existence and stability of equilibria for systems (2) and (3) depend on positions of the following seven straight lines in the (α_1, α_2)-plane:

$$\begin{cases} r_1 \equiv & \alpha_2 = \beta_0\alpha_1, \\ r_2 \equiv & \alpha_2 = \dfrac{1}{\beta_0}\alpha_1, \\ r_3 \equiv & \alpha_2(\gamma_1\gamma_2 - \beta) = -\alpha_1(1 - \gamma_1\gamma_2) - \alpha_3\gamma_1(1 - \beta), \\ r_4 \equiv & \alpha_2(1 - \gamma_1\gamma_2) = -\alpha_1(\gamma_1\gamma_2 - \beta) - \alpha_3\gamma_1(1 - \beta), \\ r_5 \equiv & \alpha_2 = -\alpha_1 - \alpha_3\dfrac{1 + \beta}{\gamma_2}, \\ r_6 \equiv & \alpha_2 = \beta\alpha_1, \\ r_7 \equiv & \alpha_2 = \dfrac{1}{\beta}\alpha_1, \end{cases}$$

We would like to point out that, thanks to Proposition 3.2, when the components of E_{111} are positive then the semi-trivial points E_{011}, E_{101} and E_{110} are unstable. Indeed, observe that the components of E_{111} are positive if:

$$\begin{aligned} &\alpha_1(1 - \gamma_1\gamma_2) + \alpha_2(\gamma_1\gamma_2 - \beta) + \alpha_3\gamma_1(1 - \beta) > 0, \\ &\alpha_1(\gamma_1\gamma_2 - \beta) + \alpha_2(1 - \gamma_1\gamma_2) + \alpha_3\gamma_1(1 - \beta) > 0, \qquad (8) \\ &(\alpha_1 + \alpha_2)\gamma_2 + \alpha_3(1 + \beta) > 0. \end{aligned}$$

Fix α_3. Let us analyze (8) in the (α_1, α_2)-plane. The region defined by (8) depends on the size of $\gamma_1\gamma_2$ with respect to β.

3.3 Case $\gamma_1\gamma_2 < \beta$.

In this case, conditions in (8) are equivalent to

$$\begin{aligned}
\alpha_2 &< \alpha_1 \left(\frac{1 - \gamma_1\gamma_2}{\beta - \gamma_1\gamma_2}\right) + \alpha_3\gamma_1 \left(\frac{1 - \beta}{\beta - \gamma_1\gamma_2}\right), \\
\alpha_2 &> \alpha_1 \left(\frac{\beta - \gamma_1\gamma_2}{1 - \gamma_1\gamma_2}\right) - \alpha_3\gamma_1 \left(\frac{1 - \beta}{1 - \gamma_1\gamma_2}\right), \\
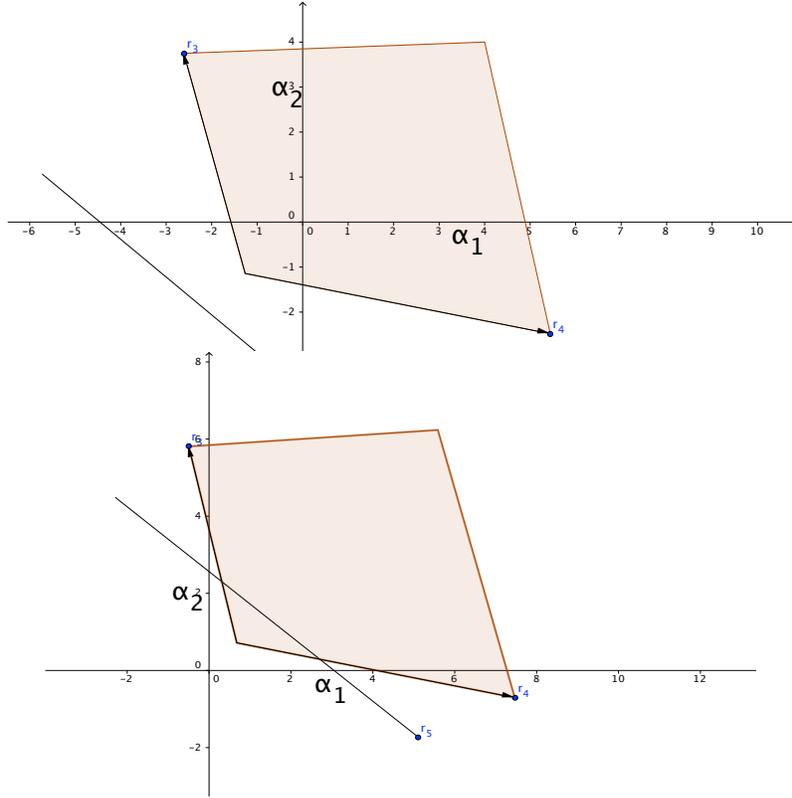\alpha_2 &> -\alpha_1 - \frac{\alpha_3}{\gamma_2}(1 + \beta).
\end{aligned} \tag{9}$$

Observe that

$$r_3 \cap r_4 = (-\alpha_3\gamma_1, -\alpha_3\gamma_1), \ r_3 \cap r_5 = (-\frac{\beta\alpha_3}{\gamma_2}, -\frac{\alpha_3}{\gamma_2}), \ r_4 \cap r_5 = (-\frac{\alpha_3}{\gamma_2}, -\frac{\beta\alpha_3}{\gamma_2}). \tag{10}$$

It is not hard to show that this region is not empty, see Figure 1. Observe that in the case $\alpha_3 > 0$, r_5 does not impose any restriction.

11
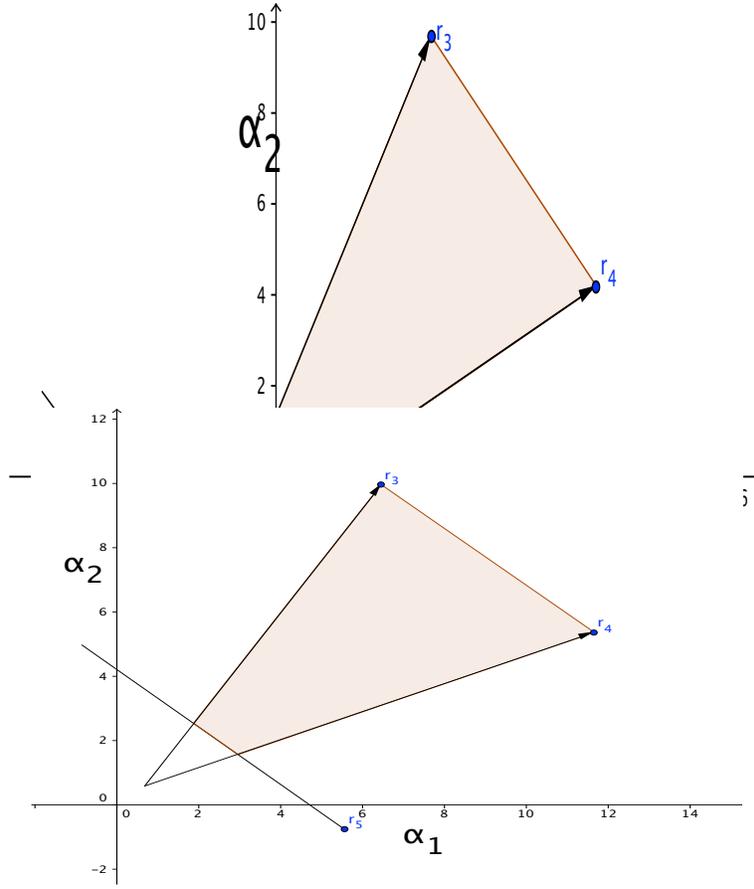
Figure 1: Weak cooperation areas for $\alpha_3 > 0$ and $\alpha_3 < 0$ respectively, where the positive equilibrium E_{111} exists.

3.4 Case $\beta < \gamma_1\gamma_2$.

In this case, conditions (8) are equivalent to

$$
\begin{aligned}
\alpha_2 &> -\alpha_1 \left(\frac{1 - \gamma_1\gamma_2}{\gamma_1\gamma_2 - \beta} \right) - \alpha_3\gamma_1 \left(\frac{1 - \beta}{\gamma_1\gamma_2 - \beta} \right), \\
\alpha_2 &> -\alpha_1 \left(\frac{\gamma_1\gamma_2 - \beta}{1 - \gamma_1\gamma_2} \right) - \alpha_3\gamma_1 \left(\frac{1 - \beta}{1 - \gamma_1\gamma_2} \right), \\
\alpha_2 &> -\alpha_1 - \frac{\alpha_3}{\gamma_2}(1 + \beta).
\end{aligned}
\tag{11}
$$

Figure 2: Strong cooperation areas for $\alpha_3 > 0$ and $\alpha_3 < 0$ respectively, where the positive equilibrium E_{111} exists.

Remark 3.3. *In the particular case $\beta = \gamma_1 \gamma_2$, (8) is equivalent to*

$$
\begin{aligned}
&\alpha_1 > -\alpha_3 \gamma_1, \\
&\alpha_2 > -\alpha_3 \gamma_1, \\
&\alpha_2 > -\alpha_1 - \frac{\alpha_3}{\gamma_2}(1 + \beta).
\end{aligned}
\tag{12}
$$

4 Permanence and global stability

In this section we give global results on the asymptotic behaviour of solutions for our model (2). Observe that the analysis in the previous section only gives local stability or unstability properties of equilibria. In this section we firstly prove the global property that (2) is permanent under some conditions on the data of the problem. For that, we are going to use average Lyapunov

13

function approach, (see [9] or [5]). Then, we prove that, in fact, the positive equilibrium E_{111} is globally stable, by the existence of a Lyapunov function. As this last result is, in general, more restrictive, we have decided to keep both approaches in order to take them into account when studying more general systems as (1).

4.1   Permanence

In order to formalize a global result on permanence for model (2), we need some notation. Define the map

$$\pi : \mathcal{K} \times [0, \infty) \mapsto \mathcal{K}, \quad \pi((u_1^0, u_2^0, u_3^0), t) := (u_1, u_2, u_3)$$

where (u_1, u_2, u_3) is the unique solution of (2) in t initially in (u_1^0, u_2^0, u_3^0) and $\mathcal{K} = \mathbb{R}_+^3$. We will show some properties of π later.

Definition 4.1. *We say that (2) is permanent if there exists a bounded set $U \subset \mathcal{K}$ such that*

a) $\inf_{u \in U} d(u, \partial \mathcal{K}) > 0$, *where* $d(u, \partial \mathcal{K}) = \inf_{v \in \partial \mathcal{K}} d(u, v)$, *and*

b) $\lim_{t \to \infty} d(\pi((u_1^0, u_2^0, u_3^0), t), U) = 0$ *for all* $(u_1^0, u_2^0, u_3^0) \in int(\mathcal{K})$.

Our main result reads as follows

Theorem 4.2. *Assume (8). Then system (2) is permanent.*

For that, we use the following result (see Corollary 2.3 of [9] or Theorems 4.1 and 4.2 in [5]).

Theorem 4.3. *Assume that π is dissipative and $\pi(\cdot, t)$ is compact for $t \geq t_0$ for some $t_0 > 0$. Let $\mathcal{A}$ denote the global attractor for π and*

$$X' := \overline{\pi(B(\mathcal{A}, \varepsilon), [t_0, \infty))} \quad and \quad X'' := \pi(X', t')$$

for some t' large, with $B(\mathcal{A}, \varepsilon)$ is an ε-neighbourhood of $\mathcal{A}$. Finally, let

$$S := X'' \cap \partial \mathcal{K}.$$

Assume that there exists a continuous function $P : X'' \mapsto [0, +\infty)$ with $P(u_1, u_2, u_3) = 0$ if and only if $(u_1, u_2, u_3) \in S$, and define

$$a(t, (z_1, z_2, z_3)) = \liminf_{(U_1, U_2, U_3,) \to (z_1, z_2, z_3)} \left(\frac{P(\pi(U_1, U_2, U_3, t))}{P(U_1, U_2, U_3)} \right), \tag{13}$$

14

with $(U_1, U_2, U_3) \in X'' \setminus S$. Then, (2) is permanent if

$$\sup_{t>0} a(t, (z_1, z_2, z_3)) > \begin{cases} 1 & (z_1, z_2, z_3) \in \omega(S), \\ 0 & (z_1, z_2, z_3) \in S, \end{cases}$$

where $\omega(S) = \bigcup_{s \in S} \omega(s)$ with $\omega(s)$ the omega-limit set of s.

Proof of Theorem 4.2. Since π arises from an ODE, and from Theorem 2.3 and Lemma 2.4, $\pi(\cdot, t)$ is a compact map from $\mathcal{K}$ to $\mathcal{K}$ and also π is dissipative for $t > t_0$ for some $t_0 \geq 0$, and so π has a global attractor $\mathcal{A}$. Now we need to build a continuous function P verifying the hypotheses of Theorem 4.3. It is clear that

$$S \subset \{(u_1, u_2, u_3) \in \mathcal{K} : u_1 = 0 \quad \text{or} \quad u_2 = 0 \quad \text{or} \quad u_3 = 0\},$$

and so

$$\omega(S) = \{E_0, E_{100}, E_{010}, E_{001}, E_{110}, E_{011}, E_{010}\}.$$

Define

$$P(u_1, u_2, u_3) := u_1^{\beta_1} u_2^{\beta_2} u_3^{\beta_3}$$

or equivalently written as

$$P(u_1, u_2, u_3) = exp\left(\beta_1 log(u_1) + \beta_2 log(u_2) + \beta_3 log(u_3)\right), \qquad (14)$$

with β_1, β_2 and β_3 positive constants to be chosen.

Denoting by $(u_1, u_2, u_3) = \pi(U_1, U_2, U_3, t)$, we have that

$$\frac{P(\pi(U_1, U_2, U_3, t))}{P(U_1, U_2, U_3)} = exp\left(\beta_1(log(u_1(t)) - log(U_1)) + \right.$$

$$\left. + \beta_2(log(u_2(t)) - log(U_2)) + \beta_3(log(u_3(t)) - log(U_3))\right),$$

and using the fact that $log(f(t)) - log(f(0)) = \int_0^t f'(s)/f(s)ds$ for a positive and regular function f, we get

$$\frac{P(\pi(U_1, U_2, U_3, t))}{P(U_1, U_2, U_3)} = exp\left(\beta_1 \int_0^t (\alpha_1 - u_1 - \beta u_2 + \gamma_1 u_3)ds + \right.$$
$$\left. \beta_2 \int_0^t (\alpha_2 - u_2 - \beta u_1 + \gamma_1 u_3)ds + \beta_3 \int_0^t (\alpha_3 - u_3 + \gamma_2(u_1 + u_2))ds\right).$$
$$(15)$$

Now, since u_1, u_2 and u_3 are bounded, there exist $d_1, d_2, d_3 \in \mathbb{R}$ such that

$$\frac{P(\pi(U_1, U_2, U_3, t))}{P(U_1, U_2, U_3)} \geq exp\left\{((\beta_1 d_1 + \beta_2 d_2 + \beta_3 d_3)t\right\},$$

15

and so $a(t, (z_1, z_2, z_3)) > 0$ for some t.

It remains to show that $a(t, (z_1, z_2, z_3)) > 1$ for some $t > 0$ if $(z_1, z_2, z_3) \in \omega(S)$. Take $(z_1, z_2, z_3) \in \omega(S)$ and $(U_1, U_2, U_3) \to (z_1, z_2, z_3)$.

Recall that $\pi : \mathcal{K} \times [0, 1] \mapsto \mathcal{K}$ is uniformly continuous. Then, if $(z_1, z_2, z_3) \in \omega(S)$ and $(U_1, U_2, U_3) \to (z_1, z_2, z_3)$, then the solution $(u_1(t), u_2(t), u_3(t))$ is near (z_1, z_2, z_3) for $t \in [0, 1]$ because (z_1, z_2, z_3) is the solution of (2) with initial data (z_1, z_2, z_3).

We distinguish different cases:

<u>Case 1</u>: $(z_1, z_2, z_3) = E_0$. Observe that, using (15), we conclude that for all $s \in [0, 1]$

$$\frac{P(\pi(U_1, U_2, U_3, s))}{P(U_1, U_2, U_3)} \to exp\{(\beta_1\alpha_1 + \beta_2\alpha_2 + \beta_3\alpha_3)s\}, \quad \text{as } (U_1, U_2, U_3) \to E_0.$$

<u>Case 2</u>: $(z_1, z_2, z_3) \in \{E_{100}, E_{010}, E_{001}\}$. We argue with the case $(z_1, z_2, z_3) = E_{100}$, similar argument works for the other cases. Observe that in this case we conclude that for all $s \in [0, 1]$

$$\frac{P(\pi(U_1, U_2, U_3, s))}{P(U_1, U_2, U_3)} \to exp\left((\beta_2(\alpha_2 - \beta\alpha_1) + \beta_3(\alpha_3 + \gamma_2\alpha_1))s\right),$$

as $(U_1, U_2, U_3) \to E_{100}$.

With a similar argument, we can prove that

$$\frac{P(\pi(U_1, U_2, U_3, s))}{P(U_1, U_2, U_3)} \to exp\left((\beta_1(\alpha_1 - \beta\alpha_2) + \beta_3(\alpha_3 + \gamma_2\alpha_2))s\right),$$

as $(U_1, U_2, U_3) \to E_{010}$ and when $(U_1, U_2, U_3) \to E_{001}$

$$\frac{P(\pi(U_1, U_2, U_3, s))}{P(U_1, U_2, U_3)} \to exp\left((\beta_1(\alpha_1 + \gamma_1\alpha_3) + \beta_2(\alpha_2 + \gamma_1\alpha_3))s\right).$$

<u>Case 3</u>: $(z_1, z_2, z_3) \in \{E_{110}, E_{011}, E_{101}\}$. Again, we argue with the case $(z_1, z_2, z_3) = E_{110}$, similar argument works for the other cases. We conclude that for all $s \in [0, 1]$

$$\frac{P(\pi(U_1, U_2, U_3, s))}{P(U_1, U_2, U_3)} \to exp\left(\beta_3\left(\frac{\alpha_3(1 + \beta) + \gamma_2(\alpha_1 + \alpha_2)}{1 + \beta}\right)s\right),$$

as $(U_1, U_2, U_3) \to E_{110}$. In a similar way,

$$\frac{P(\pi(U_1, U_2, U_3, s))}{P(U_1, U_2, U_3)} \to exp\left(\beta_1\left(\frac{\alpha_1(1 - \gamma_1\gamma_2) + \alpha_2(\gamma_1\gamma_2 - \beta) + \alpha_3\gamma_1(1 - \beta)}{1 - \gamma_1\gamma_2}\right)s\right),$$

16

as $(U_1, U_2, U_3) \to E_{011}$ and when $(U_1, U_2, U_3) \to E_{101}$

$$\frac{P(\pi(U_1, U_2, U_3, s))}{P(U_1, U_2, U_3)} \to exp\left(\beta_2\left(\frac{\alpha_1(\gamma_1\gamma_2 - \beta) + \alpha_2(1 - \gamma_1\gamma_2) + \alpha_3\gamma_1(1 - \beta)}{1 - \gamma_1\gamma_2}\right)s\right).$$

Now, assume that $(\alpha_1, \alpha_2, \alpha_3)$ satisfies (8). Then, taking β_1, β_2 and β_3 positive, we have that

$$a(1, E_{110}), a(1, E_{101}), a(1, E_{011}) > 1.$$

On the other hand, since $(\alpha_1, \alpha_2, \alpha_3)$ satisfies (8), then $\alpha_2 - \beta\alpha_1 > 0$ and $\alpha_1 - \beta\alpha_2 > 0$. Moreover, or $\alpha_1 + \gamma_1\alpha_3 > 0$ or $\alpha_1 + \gamma_1\alpha_3 > 0$ (or both of them in the case $\gamma_1\gamma_2 < \beta$, see Figures 1 and 2). Finally, at least one $\alpha_i > 0$. So, we can choose $\beta_1 > 0$, $\beta_2 > 0$ and $\beta_3 > 0$ such that

$$a(1, E_0), a(1, E_{100}), a(1, E_{001}), a(1, E_{010}) > 1.$$

This completes the proof.

4.2   Global stability of positive equilibria

Goh in [7] (see also [8]) proves a general criteria for the existence of a Lyapunov functional of m-dimensional Lotka-Volterra models which can be applied to our 3D mutualistic system. Indeed, Goh's results reads as follows ([7], Theorem in page 138 and Lemma in Appendix, page 142): Consider

$$\frac{dN_i}{dt} = N_i(b_i + \sum_{j=1}^{m} a_{ij}N_j), \quad j = 1, \ldots, m, \tag{16}$$

with $A = (a_{ij})$ and $N^* = (N_1^*, \ldots, N_m^*)$ its associated positive nontrivial equilibrium. Then

Theorem 4.4. *If the nontrivial equilibrium N^* of model (16) is feasible and there exists a constant positive diagonal matrix C such that $CA + A^T C$ is negative definite, then (16) is globally stable in the feasible region. In particular, this condition holds if every principal minor of $-A$ is nonnegative.*

Note that, in our case for model (2) we have

$$A = \begin{pmatrix} -1 & -\beta & \gamma_1 \\ -\beta & -1 & \gamma_1 \\ \gamma_2 & \gamma_2 & -1 \end{pmatrix}.$$

and $E_{111} = (u_1^*, u_2^*, u_3^*)$. Assume that $u_i^* > 0$, $i = 1, 2, 3$. Since $\beta < 1$ and $\gamma_1 \gamma_2 < (1 + \beta)/2$, we have that every principal minor of $-A$ is nonnegative, so that Theorem 4.4 applies and E_{111} is globally stable in the regions defined in the feasible region where it exits (see Figure 1).

In the following sections we discuss Phenomena 1 and 2. We will study regions in the (α_1, α_2)-plane depending on the parameter α_3. Some simulations will complement our results.

5 Phenomenon 1. Case $\alpha_3 > 0$: increasing of biodiversity

We assume that $\gamma_1 \gamma_2 < \beta$, but we would like to remark that similar results are obtained in the case $\gamma_1 \gamma_2 \geq \beta$. In the case $\alpha_3 > 0$, biodiversity is enriched, in the sense that there are regions in (3) for which one or both species goes to extinction but the presence of u_3 in (2) makes the species to keep (coexistence).

Remark 5.1. *Observe that, since $\alpha_3 > 0$, and using Lemma 2.4, we conclude that u_3 can not extinguish.*

Observe Figure 1, for which intersection point with axis are $(\frac{\alpha_3 \gamma_1 (1-\beta)}{\beta - \gamma_1 \gamma_2}, 0)$ and $(0, \frac{\alpha_3 \gamma_1 (1-\beta)}{\beta - \gamma_1 \gamma_2})$. If we fix values $\gamma_1, \gamma_2, \beta, \beta_0$ satisfying (H) and $\alpha_3 > 0$, we observe the following dynamical behaviour for systems (3) and (2):

a) $(\alpha_1, \alpha_2) \in A_1$ implies that solutions of (3) go to E_{10} and solutions of (2) to E_{111}.

b) $(\alpha_1, \alpha_2) \in A_2$ implies that solutions of (3) go to E_{01} and solutions of (2) to E_{111}.

c) $(\alpha_1, \alpha_2) \in B$ implies that solutions of (3) go to E_{11} and solutions of (2) to E_{111}.
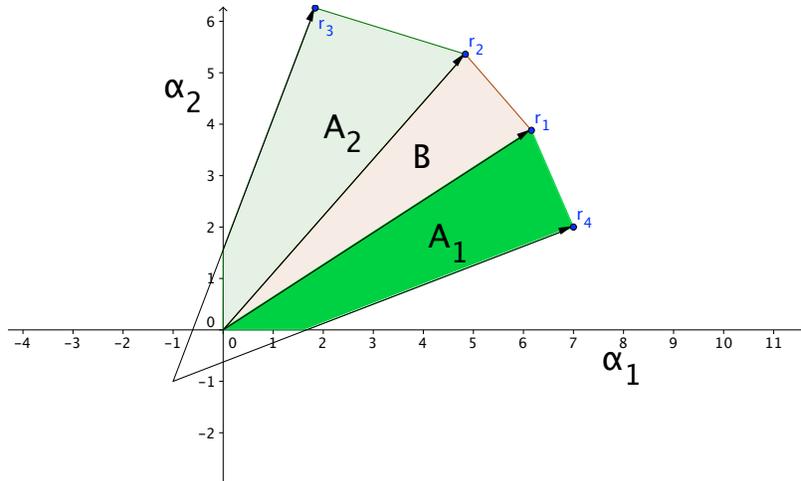
Figure 3: Regions in the first quadrant of coexistence of the three species. Phenomenon 1 holds in all pairs (α_1, α_2) of regions A_1 and A_2. In region B the coexistence of u_1, u_2 is kept after appearance of u_3.
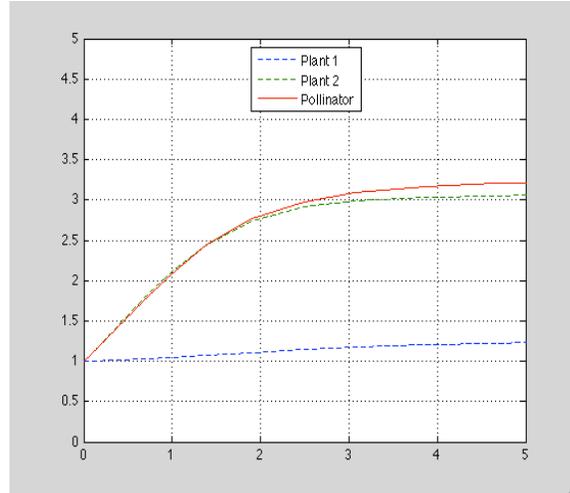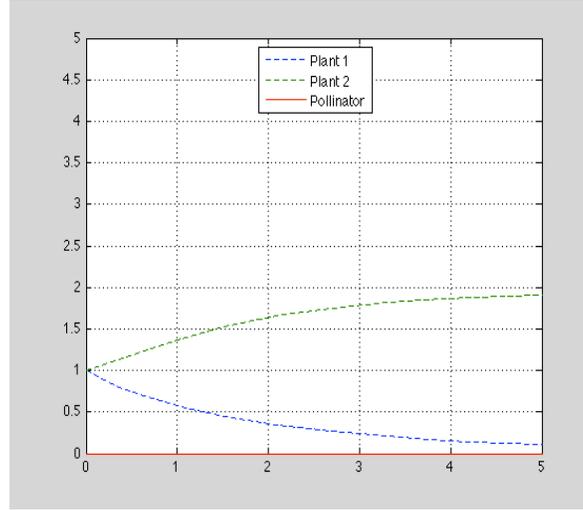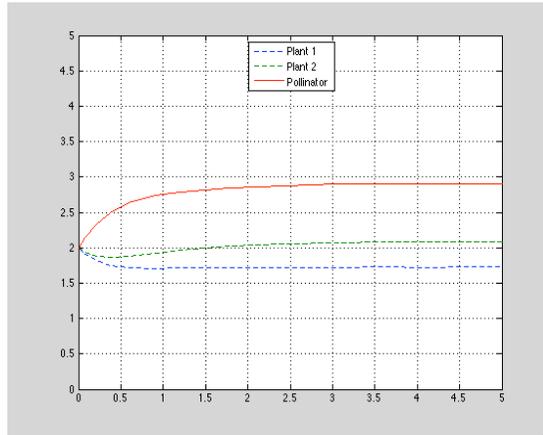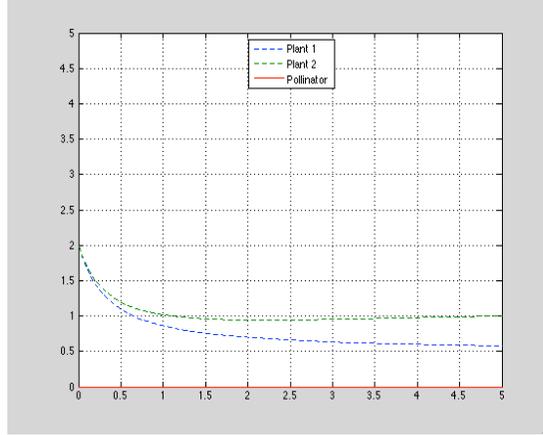
Figure 4: Phenomenon 1 holds for a pair (α_1, α_2) of region A_2, $\alpha_3 > 0$. $\beta_0 = 2/3, \beta = \beta_0/(1 + \gamma_1) = 4/9, \gamma_1 = \gamma_2 = 1/2, \alpha_3 = 1, \alpha_2 = 2, \alpha_1 = 1$; initial data $(1, 1)$ and $(1, 1, 1)$ respectively. The presence of u_3 makes u_1 to survive.

20

Figure 5: Simulation for region B, $\alpha_3 > 0$. $\beta_0 = 2/3, \beta = \beta_0/(1 + \gamma_1) = 4/9, \gamma_1 = \gamma_2 = 0.5, \alpha_3 = 1, \alpha_2 = 1.4, \alpha_1 = 1$; initial data $(2, 2)$ and $(2, 2, 2)$ respectively. Coexistence of u_1, u_2 is kept and increased after appearance of u_3.

6 Phenomena 1 and 2. Case $\alpha_3 < 0$: biodiversity and vulnerability of cooperative species

First, we are going to show that in the original system (2) we can not increase biodiversity if $u_3 \to 0$.

Lemma 6.1. *Assume that $u_3 \to 0$ as $t \to \infty$.*

a) *If $\alpha_1, \alpha_2 < 0$, then solution E_0 is globally stable.*

b) *If $\alpha_1 > 0$ and $\alpha_2 < \beta\alpha_1$, then the solution E_{100} is globally stable.*

c) *If $\alpha_2 > 0$ and $\alpha_1 < \beta\alpha_2$, then the solution E_{010} is globally stable.*

d) *If $\alpha_1 > \beta\alpha_2$ and $\alpha_2 > \beta\alpha_1$, then the solution E_{110} is globally stable.*

Proof. Assume that $u_3 \to 0$ as $t \to \infty$, then

$$u_3 \le \varepsilon, \qquad \text{for } t \ge t_0.$$

Then,

$$u_1' \le u_1(\alpha_1 + \gamma_1\varepsilon - u_1 - \beta u_2), \quad u_2' \ge u_2(\alpha_2 - u_2 - \beta u_1)$$

and then the pair $(\underline{u}, \underline{v}) = (u_1, 0)$, $(\overline{u}, \overline{v}) = (M, u_2)$, for $M > 0$ large, is a pair of sub-supersolution of the system

$$\begin{cases} u_1' = u_1(\alpha_1 + \gamma_1\varepsilon - u_1 - \beta u_2) \\ u_2' = u_2(\alpha_2 - u_2 - \beta u_1), \end{cases}$$

If we denote by $(U_{\lambda,\mu}, V_{\lambda,\mu})$ the solution of (3), we have shown that

$$u_1 \le U_{\alpha_1+\gamma_1\varepsilon,\alpha_2}, \quad V_{\alpha_1+\gamma_1\varepsilon,\alpha_2} \le u_2 \quad \text{for } t \text{ large.}$$

Repeating this argument, we arrive at

$$U_{\alpha_1,\alpha_2+\gamma_1\varepsilon} \le u_1 \le U_{\alpha_1+\gamma_1\varepsilon,\alpha_2}, \qquad V_{\alpha_1+\gamma_1\varepsilon,\alpha_2} \le u_2 \le V_{\alpha_1,\alpha_2+\gamma_1\varepsilon}.$$

Now, applying Lemma 3.1 we conclude the result. ∎

We show now that in the case $\alpha_3 < 0$ biodiversity is also enriched, in the sense of Phenomenon 1. Firstly, in Figure 6 we show the zone A for which E_{111} exists (recall that existence of E_{111} implies its local stability).
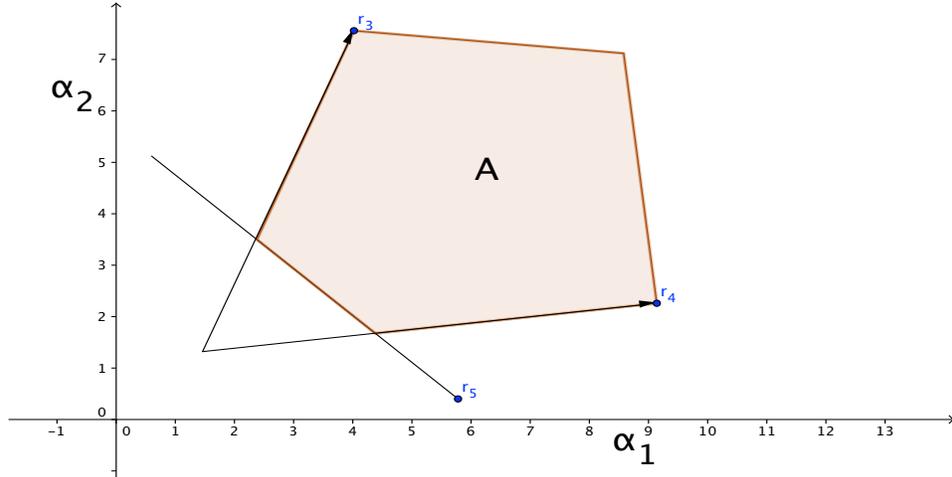
Figure 6: Region A of existence of equilibria E_{111}. The existence of E_{111} implies that this point is locally stable and the rest of equilibria are unstable. Moreover, region A implies coexistence of the three species.

6.1 Case $\alpha_3 < 0$: phenomenon 1 generically holds

If we fix values for $\gamma_1, \gamma_2, \beta, \beta_0$ satisfying (H), $\alpha_3 < 0$ we get the following simulations for Figure 7:

a) $(\alpha_1, \alpha_2) \in A_1$ for which solutions of (3) go to E_{10} and solutions of (2) to E_{111}.

b) $(\alpha_1, \alpha_2) \in A_2$ for which solutions of (3) go to E_{01} and solutions of (2) to E_{111}.

c) $(\alpha_1, \alpha_2) \in B$ for which solutions of (3) go to E_{11} and solutions of (2) to E_{111}.
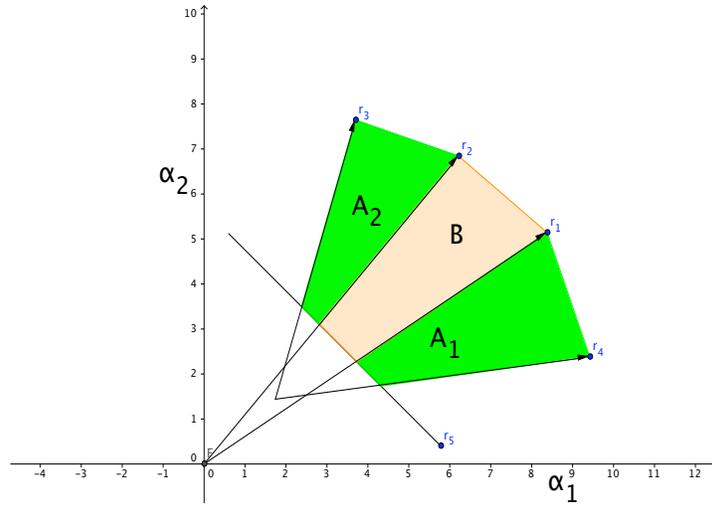
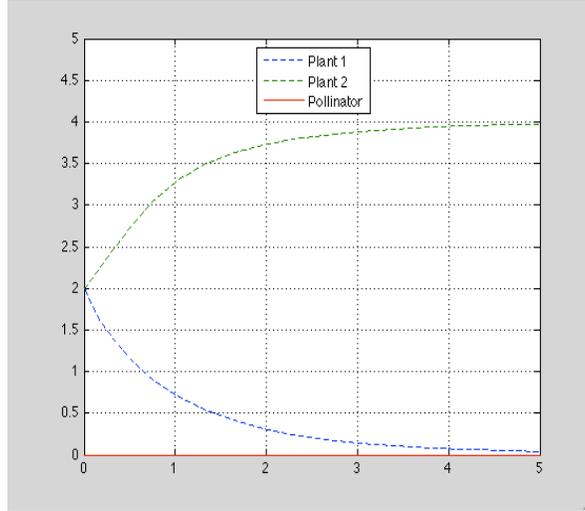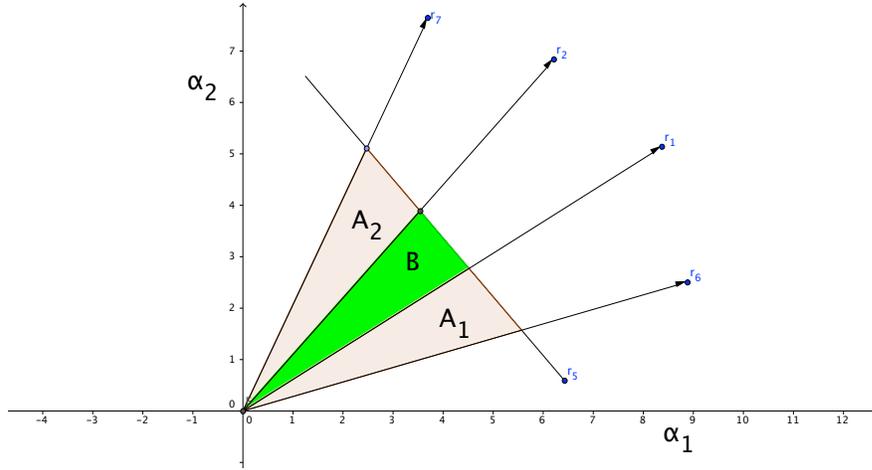Figure 7: Regions A_1 and A_2, above r_5, in which phenomenon 1 holds for $\alpha_3 < 0$.
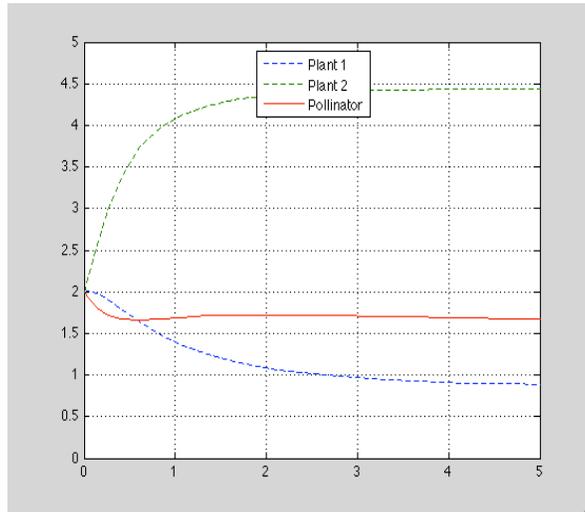
Figure 8: Phenomenon 1 holds for a pair (α_1, α_2) of region A_2, $\alpha_3 < 0$. $\beta_0 = 2/3, \beta = \beta_0/(1 + \gamma_1) = 4/9, \gamma_1 = \gamma_2 = 0.5, \alpha_3 = -1, \alpha_2 = 4, \alpha_1 = 2$; initial data $(2, 2)$ and $(2, 2, 2)$ respectively.The presence of u_3 makes u_1 to survive.

25

6.2 Case $\alpha_3 < 0$: phenomenon 2 also holds

In Figure 9 we show zones for vulnerability of u_3. Indeed, we show zones in which some of the species of system (3) goes to extinction, but coexists in system (2) after appearance of u_3, even when u_3 is push to extinction.

Simulations of zones in Figure 9 will produce:

a) $(\alpha_1, \alpha_2) \in A_1$ for which solutions of (3) go to E_{10} and solutions of (2) to E_{110}.

b) $(\alpha_1, \alpha_2) \in A_2$ for which solutions of (3) go to E_{01} and solutions of (2) to E_{110}.

c) $(\alpha_1, \alpha_2) \in B$ for which solutions of (3) go to E_{11} and solutions of (2) to E_{110}.

Figure 9: Regions A_1 and A_2, below r_5, in which phenomenon 2 holds for $\alpha_3 < 0$. In region B the two species u_1 and u_2 are kept after appearance of u_3, which goes to extintion.
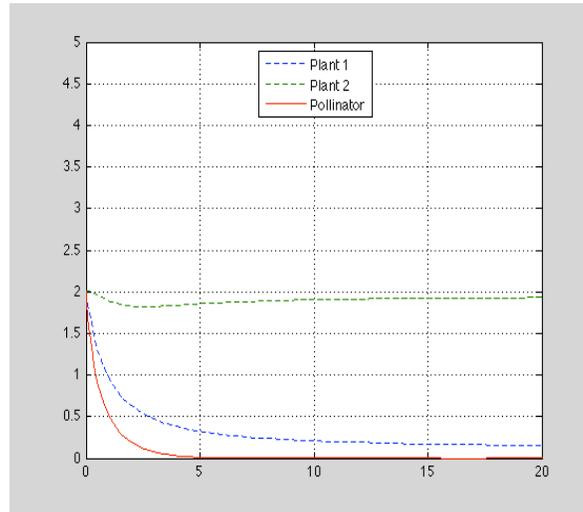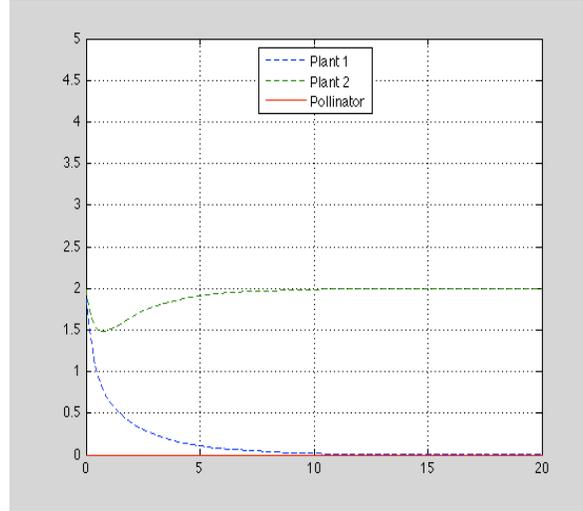
Figure 10: Phenomenon 2 holds for a pair (α_1, α_2) of region A_2, $\alpha_3 < 0$. $\beta_0 = 2/3, \beta = \beta_0/(1 + \gamma_1) = 4/9, \gamma_1 = \gamma_2 = 0.5, \alpha_3 = -2, \alpha_2 = 2, \alpha_1 = 1$; initial data $(2, 2)$ and $(2, 2, 2)$ respectively. The presence of u_3 makes u_1 to survive, although u_3 goes to extinction.

7   A more realistic general model

As we have seen in our simplest 3D case, phenomenon 2 (i.e., the cooperative specie increases biodiversity but goes to exctintion) is only possible if we add a non-trivial modification to system (1) so that the model is able to take into account the relationship between the rate of competition and associated cooperative links. The following modification to system (1) tries to take into account some realistic facts in Ecology, following [13] and [4]:

$$
\begin{cases}
\dfrac{dS_{p_i}}{dt} = \alpha_{p_i} S_{p_i} - \sum_{j=1}^{P} \beta_{p_{ij}} \left(\dfrac{1}{1 + \sum_{k=1}^{A} \gamma_{p_{ik}}} \right) S_{p_i} S_{p_j} + \sum_{k=1}^{A} \dfrac{\gamma_{p_{ik}} S_{p_i} S_{a_k}}{1 + h_P \sum_{l=1}^{A} \gamma_{p_{il}} S_{a_l}} \\
\dfrac{dS_{a_i}}{dt} = \alpha_{a_i} S_{a_i} - \sum_{j=1}^{A} \beta_{a_{ij}} \left(\dfrac{1}{1 + \sum_{k=1}^{P} \gamma_{a_{ik}}} \right) S_{a_i} S_{a_j} + \sum_{k=1}^{P} \dfrac{\gamma_{a_{ik}} S_{a_i} S_{p_k}}{1 + h_A \sum_{l=1}^{P} \gamma_{a_{il}} S_{p_l}} \\
S_{p_i}(0) = S_{p_{i0}} \\
S_{a_i}(0) = S_{a_{i0}}
\end{cases}
\tag{17}
$$

Observe that, if no cooperation is present, we get a competitive system without variation on the rate of competition. On the other hand, a very large cooperation rates would lead to small weights in the competitive constants. Other possible modifications of the model are possibly needed. For instance, to take into account asymmetries in cooperation associations (see [4]), we should have to modify parameter γ in relation with its number of links. Moreover, to avoid blow-up in the strong cooperation regime (see Theorem 2.3) we have to consider the model with the handling times $h_P, h_A > 0$ as in (1) or (17). It is not clear at all in the strong cooperation regime on which zones are where phenomena 1 and 2 happen.

   In a next future research, we plan to follow studying these general models (1) and (17) with the pointed modifications. The results obtained in this paper should serve as a guide for the development of the study of dynamical properties of these mutualistic networks, which structure of connections are on the base of biodiversity for complex systems in Ecology.

Acknowledgements

and references, specifically Goh's papers on global stability of the positive equilibria at Section 4.2.

References

[1] J. Bascompte, P. Jordano, C.J. Melián, J.M. Olesen, The nested assembly of plant-animal mutualistic networks. Proc. Natl Acad. Sci. USA 100 (2003), 93839387.

[2] J. Bascompte, P. Jordano, J.M. Olesen, Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312 (2006), 431433.

[3] J. Bascompte, P. Jordano, The structure of plant-animal mutualistic networks: the architecture of biodiversity. Annu. Rev. Ecol. Evol. Syst. 38 (2007), 567593.

[4] U. Bastolla, M.A. Fortuna, A. Pascual-García, A. Ferrera, B. Luque, and J. Bascompte (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature, 458: 1018-1020.

[5] R. S. Cantrell, and C. Cosner, Spatial ecology via reaction-diffusion equations, Wiley Series in Mathematical and Computational Biology. John Wiley & Sons, Ltd., Chichester, 2003.

[6] C. E. Clark and T. G. Hallam, The community matrix in three species community models, J. Math. Biology **16** (1982) 25-31.

[7] B. S. Goh, Stability in Models of Mutualism, The American Naturalist, Vol. 111, No. 977 (1977), 135-143.

[8] B. S. Goh, Stability in Models of Mutualism, The American Naturalist, Vol. 113, No. 2 (1979), 261-275.

[9] V. Hutson, A theorem on average Lyapunov functions, Monatsch. Math. **98** (1984), 267–275.

[10] J. D. Murray, Mathematical Biology, 1993 (New York: Springer).

[11] S. Saavedra, D.B. Stouffer, B. Uzzi, and J. Bascompte (2011), Strong contributors to network persistence are the most vulnerable to extinction. Nature, 478: 233-235.

[12] H. L. Smith, Competing subcommunities of mutualists and a generalized Kamke theorem, SIAM J. Appl. Math., 46 (1986) 856–874.

[13] G. Sugihara and Hao Ye (2009). Cooperative network dynamics, Nature (News and View) 458: 979-980.

[14] Y. Takeuchi, Global dynamical properties of Lotka-Volterra systems, World Scientific Publishing Co., Inc., River Edge, NJ, 1996.

[15] Y. Wang and H. Wu, Dynamics of a cooperation-competition model for the WWW market, Physica A, 339 (2004) 609–620.