

Architecture of attractor determines dynamics on mutualistic complex networks



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ABSTRACT

A mathematical system of differential equations for the modelization of mutualistic networks in Ecology has been proposed in Bastolla et al. (2007). Basically, it is studied how the complex structure of cooperation interactions between groups of plants and pollinators or seed dispersals affects to the whole network. In this paper we prove existence and characterization of the global attractor associated to the model. The description of the geometrical internal structure of the attractor becomes the proper complex network describing all the possible future scenarios of the phenomena. The arguments show a Morse Decomposition of the attractors, leading to the existence of a global Lyapunov function for the associated gradient semigroup. In particular, we are able to prove topological structural stability of the system, i.e., the associated attracting complex networks are robust under (autonomous and non-autonomous) perturbation of parameters.

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1. Introduction

Complex networks driven by mutualistic (or cooperative) relations among nodes are very common in different areas of Science as Ecology, Sociology and Economy. It is probably in Theoretical Ecology where a more abstract formulation of these systems has been reached. In this line, the authors in [1] analyze the net of connections between bipartite graphs representing two kind of species (classified into two sets, plants and animals) and the cooperative links between the differentiated groups (see also [2–5]) (see Fig. 1).

For the analysis of the dynamical properties of the networks, a mathematical model of differential equations has been proposed, which 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 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}

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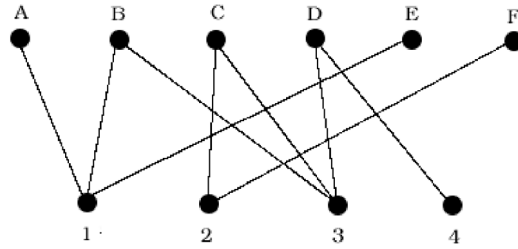


Fig. 1. Typical bipartite graph representing a complex network of mutualistic type. The two sets in the graph represent respectively groups of plants and animals. Each group has competition relations between every two nodes in the same group. The links in the graph represent cooperative relations of nodes between plants and animals of each different group.

the species density populations for the i th species of plant and of animal respectively:

$$\begin{cases} \frac{dS_{p_i}}{dt} = S_{p_i} \left(\alpha_{p_i} - \sum_{j=1}^P \beta_{p_{ij}} S_{p_j} + \sum_{k=1}^A \gamma_{p_{ik}} S_{a_k} \right) \\ \frac{dS_{a_i}}{dt} = S_{a_i} \left(\alpha_{a_i} - \sum_{j=1}^A \beta_{a_{ij}} S_{a_j} + \sum_{k=1}^P \gamma_{a_{ik}} S_{p_k} \right) \\ S_{p_i}(0) = S_{p_{i0}} \\ S_{a_i}(0) = S_{a_{i0}} \end{cases} \quad (1)$$

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 strengths. For this model, the authors study in [1] (see also [2–6]) 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 it).

In this paper we make a full mathematical study of system (1). This will need a careful treatment of parameters in order to avoid blow-up of solutions (see Theorem 2), although, from a dynamical point of view, will not introduce artificial facts into the model. In particular, after a sufficient condition for existence and uniqueness of solutions, which allows us to define a dynamical system $\{T(t)\}_{t \geq 0}$ for (1), we prove that the system possesses a global attractor, \mathcal{A} , i.e., a compact invariant set of the phase space determining all the asymptotic behavior of solutions, uniformly on bounded sets (Definition 3). We study the geometrical characterization of this global attractor, which can be described by the union of the unstable manifolds associated to the stationary points for (1). This is a consequence of the two main results of this paper: the dynamical system $T(t)$ is gradient (Theorem 21), which we prove as a consequence of the system to possess a unique stationary solution which is globally asymptotically stable in the positive cone of solutions (see Theorem 11).

It is important to realize that each equilibrium W^* is a vector in \mathbb{R}^{P+A} and that its $P + A$ components correspond to the $P + A$ nodes of the phenomenological complex network. In this sense, it is remarkable that each of the stationary points is highlighting a subnet of the former complex network. Indeed, the strictly positive components of each equilibrium point out a subset of nodes and connections of the original network. In particular, the globally stable equilibrium is indeed the complex network of the phenomena showing the future biodiversity of the Ecological system. This is the fact that makes crucial the study of global attractors and its geometrical description for our model. Indeed, for a gradient system, given a finite

set $\mathbf{E} = \{E_1, \dots, E_m\}$ of invariant sets, we have the following characterization for the global attractor

$$\mathcal{A} = \bigcup_{i=1}^m W^u(E_i), \quad (2)$$

where $W^u(E_i)$ denotes the unstable manifold of the set E_i , see [Definition 13](#).

Note that (2) is not only saying that all the asymptotic behavior of the system is concentrated around \mathcal{A} , but it is describing the way in which the attraction takes place. In particular, it is not only showing that there exists a unique globally stable equilibrium in the positive cone \mathbb{R}_+^n , but how this stationary point is connected to any other, building some energy levels which organize the attraction rates. In summary, all the equilibria are ordered and oriented connected, i.e., the connections are just in one direction, determined by the forwards dynamical of the system. In this sense, it is the structure of the global attractor what is showing a complex network with a natural intrinsic dynamics. In fact, as each node of this attracting network is a subnet of the former network, the global attractor in this case can be understood as a network of subnetworks of the original one, which, moreover, is dynamically organized to describe all the possible future scenarios of the phenomena.

An outline of the paper is as follows: Section 2 is devoted to prove the existence and uniqueness of solution of (1) and its global attractor. In Section 3 we study the stability of the equilibria and we prove the existence of a globally stable equilibrium. In Section 4 and 5 we describe the geometrical structure of the global attractor. In the last section we apply our results to the specific case $P = 2$ and $A = 1$.

2. Existence and uniqueness of solutions and global attractor

From now on we study a simplified model of (1), specifically

$$\begin{cases} \frac{du_i}{dt} = u_i \left(\alpha_{p_i} - u_i - \sum_{j \neq i}^P \beta u_j + \sum_{k=1}^A \gamma_1 v_k \right) & i = 1, \dots, P, \\ \frac{dv_i}{dt} = v_i \left(\alpha_{a_i} - v_i - \sum_{j \neq i}^A \beta v_j + \sum_{k=1}^P \gamma_2 u_k \right) & i = 1, \dots, A, \\ u_i(0) = u_{i0} & i = 1, \dots, P, \\ v_j(0) = v_{j0} & j = 1, \dots, A, \end{cases} \quad (3)$$

where u_i and v_i represent plants and animals, respectively, $\alpha_{p_i}, \alpha_{a_i} \in \mathbb{R}$, $\beta \geq 0$ and $\gamma_1, \gamma_2 \geq 0$.

Observe that if $u_{i0} = 0$ for some i (or $v_{j0} = 0$ for some j) then $u_i(t) = 0$ ($v_j(t) = 0$) for all $t \geq 0$. So, suppose that $u_{i0}, v_{i0} > 0$ for all i .

We introduce the following notation. Let P and A the number of plants and animals, respectively. We denote $n = P + A$ the total number of species, $w := (u, v) = (u_1, \dots, u_P, v_1, \dots, v_A)$ and so $w_0 = (u_{10}, \dots, u_{P0}, v_{10}, \dots, v_{A0})$.

It is clear that the natural phase space of (3) is the positive cone given by

$$\mathbb{R}_+^n = \{w = (w_1, w_2, \dots, w_n) \in \mathbb{R}^n \mid w_i \geq 0 \text{ for } i = 1, \dots, n\}. \quad (4)$$

We know that this set is invariant. We define the sets

$$\begin{aligned} C^+ &= \{w \in \mathbb{R}^n : w_i > 0, \forall i \in D\}, \\ \bar{C}^+ &= \{w \in \mathbb{R}^n : w_i \geq 0, \forall i \in D\}, \end{aligned}$$

where $D = \{1, \dots, n\}$.

2.1. Existence and uniqueness of solutions

In this section we give sufficient condition for the existence and uniqueness of solutions to (3). Firstly we need the following technical result:

Lemma 1. Suppose $\beta < 1$. Then,

$$\sum_{i=1}^n u_i^2 + 2\beta \sum_{i<j} u_i u_j \geq \frac{1 + \beta(n-1)}{n} \left(\sum_{i=1}^n u_i \right)^2. \quad (5)$$

Proof. Before proving (5), we claim that

$$\frac{2}{n-1} \sum_{i<j} u_i u_j \leq \sum_{i=1}^n u_i^2. \quad (6)$$

Indeed, it is clear that

$$\sum_{i<j}^n (u_i - u_j)^2 \geq 0,$$

and then,

$$(u_1 - u_2)^2 + \cdots + (u_1 - u_n)^2 + (u_2 - u_3)^2 + \cdots + (u_2 - u_n)^2 + \cdots + (u_{n-1} - u_n)^2 \geq 0,$$

whence

$$(n-1)(u_1^2 + \cdots + u_n^2) - 2(u_1 u_2 + \cdots + u_1 u_n + u_2 u_3 + \cdots + u_2 u_n + \cdots + u_{n-1} u_n) \geq 0.$$

This proves (6).

We show now (5). Observe that (5) is equivalent to

$$\begin{aligned} & \left(1 - \frac{1 + \beta(n-1)}{n} \right) \sum_{i=1}^n u_i^2 + 2 \left(\beta - \frac{1 + \beta(n-1)}{n} \right) \sum_{i<j} u_i u_j \geq 0 \\ & \Leftrightarrow \frac{(1-\beta)(n-1)}{n} \sum_{i=1}^n u_i^2 + \frac{2}{n} (\beta-1) \sum_{i<j} u_i u_j \geq 0, \end{aligned}$$

which is equivalent to (6) because $\beta < 1$. \square

We are ready to write the main result on existence and uniqueness of positive solution for (3). We prove in (a) a sufficient condition for the existence of global solutions, and (b) shows blow-up of solutions in finite time.

Theorem 2. (a) Assume that $\beta < 1$, and

$$\gamma_1 \gamma_2 < \frac{1 + \beta(P-1)}{P} \frac{1 + \beta(A-1)}{A}. \quad (7)$$

Then, there exists a unique positive solution of (3), for all $t > 0$.

(b) Assume that $\alpha = \alpha_{p_i} = \alpha_{a_i} > 0$ for all i, j and

$$\gamma_1 \gamma_2 > \frac{1 + \beta(P-1)}{P} \frac{1 + \beta(A-1)}{A}. \quad (8)$$

Then, any positive solution of (3) blows up in finite time.

Proof. Denote by

$$w := \sum_{i=1}^P u_i, \quad z := \sum_{i=1}^A v_i.$$

We get

$$\begin{aligned} w' &\leq \alpha w - (u_1^2 + u_2^2 + \cdots + u_P^2 + 2\beta(u_1 u_2 + u_1 u_3 + \cdots + u_{P-1} u_P)) + \gamma_1 w z, \\ z' &\leq \alpha z - (v_1^2 + v_2^2 + \cdots + v_A^2 + 2\beta(v_1 v_2 + v_1 v_3 + \cdots + v_{A-1} v_A)) + \gamma_2 w z, \end{aligned}$$

where $\alpha = \max\{\alpha_{p_i}, \alpha_{a_i}\}$, or equivalently,

$$\begin{aligned} w' &\leq \alpha w - \left(\sum_{i=1}^P u_i^2 + 2\beta \sum_{i<j}^P u_i u_j \right) + \gamma_1 w z, \\ z' &\leq \alpha z - \left(\sum_{i=1}^A v_i^2 + 2\beta \sum_{i<j}^A v_i v_j \right) + \gamma_2 w z. \end{aligned}$$

Using (5), we conclude that

$$\begin{aligned} w' &\leq \alpha w - \frac{1 + \beta(P-1)}{P} w^2 + \gamma_1 w z, \\ z' &\leq \alpha z - \frac{1 + \beta(A-1)}{A} z^2 + \gamma_2 w z. \end{aligned}$$

We consider now the system

$$\begin{cases} p' = p \left(\alpha - \frac{1 + \beta(P-1)}{P} p + \gamma_1 q \right), \\ q' = q \left(\alpha - \frac{1 + \beta(A-1)}{A} q + \gamma_2 p \right), \\ p(0) = p_0, \quad q(0) = q_0, \end{cases} \quad (9)$$

where p_0, q_0 are positive numbers to be chosen later.

Taking

$$p_0 = \sum_{i=1}^P u_{i0}, \quad q_0 = \sum_{i=1}^A v_{i0}$$

it is clear that (w, z) is a sub-solution of (9) and hence,

$$(w, z) \leq (p, q). \quad (10)$$

Finally observe that, thanks to (7), the solution (p, q) is bounded for all $t > 0$ (see [7]). This proves the first paragraph.

Assume now (8) and that $\alpha_{p_i} = \alpha_{a_i} = \alpha > 0$. Denote by (p, q) the unique positive solution of (9). It is well-known (see [7]) that, assuming (8), (p, q) blows up in finite time.

We claim that

$$\left(\frac{p}{P}, \dots, \frac{p}{P}, \frac{q}{A}, \dots, \frac{q}{A} \right)$$

is solution of (3) with $u_{i0} = p_0/P$, $i = 1, \dots, P$ and $v_{j0} = q_0/A$, $j = 1, \dots, A$. Then, the positive solution of (3) blows up in finite time.

Now, we show the claim. Observe that $(\frac{p}{P}, \dots, \frac{p}{P}, \frac{q}{A}, \dots, \frac{q}{A})$ is solution of (3) if

$$\begin{aligned} \frac{p'}{P} &= \frac{p}{P} \left(\alpha - \frac{p}{P} - \beta \left(\frac{p}{P} + \dots + \frac{p}{P} \right) + \gamma_1 \left(\frac{q}{A} + \dots + \frac{q}{A} \right) \right) \\ &\Leftrightarrow p' = p \left(\alpha - p \left(\frac{1 + \beta(P-1)}{P} \right) + \gamma_1 q \right), \end{aligned}$$

which is true. We can argue in a similar way with q/A . This concludes the proof. \square

2.2. Existence of the global attractor

We want to study (3) as a dynamical system. In this framework, the key concept is that of the global attractor, which determines the long time behavior of all solutions. Then we write some of the main results related to the internal structure of the attractor, in particular the case in which we can show its gradient structure that allows us to describe the attractor as a directed graph with nodes the stationary solutions and links the stable and unstable manifolds joining them.

We first recall the definition of a global attractor for a nonlinear semigroup $T(\cdot)$ [8–14]. Throughout this paper, unless mentioned otherwise, (X, d) is a metric space.

A family $\{T(t) : t \geq 0\}$ is called a *continuous semigroup* if

- (a) $T(0) = I_X$, with I_X being the identity in X ,
- (b) $T(t+s) = T(t)T(s)$, for all $t, s \in \mathbb{R}^+$ and
- (c) the map $\mathbb{R}^+ \times X \ni (t, x) \mapsto T(t)x \in X$ is continuous.

Here, $\text{dist}(A, B)$ denotes the Hausdorff semidistance between A and B defined as

$$\text{dist}(A, B) = \sup_{a \in A} \inf_{b \in B} d(a, b).$$

We can now define an attractor for a semigroup.

Definition 3. A set $\mathcal{A} \subseteq X$ is the *global attractor* for a semigroup $T(\cdot)$ if

- (i) \mathcal{A} is compact;
- (ii) \mathcal{A} is invariant; that is, $T(t)\mathcal{A} = \mathcal{A}$ for any $t \geq 0$.
- (iii) \mathcal{A} attracts each bounded subset of X ; that is, $\text{dist}(T(t)B, \mathcal{A}) \rightarrow 0$ as $t \rightarrow +\infty$, for any B bounded subset of X .

This definition yields the minimal compact set that attracts each bounded subset of X and the maximal closed and bounded invariant set.

A *global solution* for a semigroup $\{T(t) : t \geq 0\}$ is a continuous function $\xi : \mathbb{R} \rightarrow X$ such that $T(t)\xi(s) = \xi(t+s)$ for all $s \in \mathbb{R}$ and all $t \in \mathbb{R}^+$. We say that $\xi : \mathbb{R} \rightarrow X$ is a *global solution through* $z \in X$ if it is a global solution with $\xi(0) = z$.

Lemma 4. If a semigroup $T(\cdot)$ has a global attractor \mathcal{A} , then

$$\mathcal{A} = \{z \in X : \text{there is a bounded global solution through } z\}.$$

It is well known that global attractors for semigroups are unique. For the existence, we have the following general result (see [15,16] or equivalent results in [8,9,11–13]).

Theorem 5. *There exists a global attractor for a semigroup $T(\cdot)$ if and only if there exists a compact attracting set of bounded sets, i.e., a compact set $K \subset X$ such that $\text{dist}(T(t)C, K) \rightarrow 0$ as $t \rightarrow +\infty$, for all $C \subset X$ bounded.*

The global attractor is the maximal bounded invariant set of a semigroup, and the minimal compact attracting set (see [11,13]).

Proposition 6. *Suppose we have model (3), and assume condition (7). Then, it holds that (3) has a global attractor $\mathcal{A} \subset \mathbb{R}^{P+A}$.*

Proof. Let $(u_1, \dots, u_P, v_1, \dots, v_A)$ be a positive solution of (3) and define

$$w = \sum_{i=1}^P u_i, \quad z = \sum_{i=1}^A v_i.$$

Then, by (10) we have that $(w, z) \leq (p, q)$, where (p, q) is the global solution of the 2D cooperative Lotka–Volterra system (9). On the other hand, by (7), it is well-known that (9) has a compact attracting set, and hence the same is true for the pair (w, z) , so that we can apply Theorem 5. \square

3. Stability of equilibria

In this section we analyze local and global stability of stationary solutions (or equilibria) for (3). Note that every equilibrium point belongs to the attractor \mathcal{A} so that, actually, we start the description of the internal structure and dynamics inside the attractor.

For a general Lotka–Volterra model for n species, the system of differential equation is given by:

$$\dot{y}_i = y_i \left(b_i + \sum_{j=1}^n c_{ij} y_j \right), \quad i = 1, \dots, n, \quad (11)$$

where the matrix $C = (c_{ij})$ is called interaction-matrix. On the other hand, we say that $Y^* = (y_i^*) \in \mathbb{R}^n$ is a equilibrium point of (11) if

$$y_i^* \left(b_i + \sum_{j=1}^n c_{ij} y_j^* \right) = 0, \quad i = 1, \dots, n. \quad (12)$$

Of course, if Y^* is in the interior of \mathbb{R}_+^n , then (12) is equivalent to

$$b_i + \sum_{j=1}^n c_{ij} y_j^* = 0, \quad i = 1, \dots, n. \quad (13)$$

Let $E := \{Y_1^*, \dots, Y_m^*\}$ the set of stationary points for (11).

3.1. Local stability

It is well-known that a equilibrium point $Y^* = (y_i^*)$ is locally stable if the real parts of the eigenvalues of the Jacobian $J(Y^*)$ are negative, where

$$J(Y^*) = \begin{pmatrix} C_{11}^* & y_1^* c_{12} & \cdots & y_1^* c_{1n} \\ y_2^* c_{21} & C_{22}^* & \cdots & y_2^* c_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ y_n^* c_{n1} & y_n^* c_{n2} & \cdots & C_{nn}^* \end{pmatrix},$$

and

$$C_{ii}^* = b_i + 2c_{ii}y_i^* + \sum_{j \neq i} c_{ij}y_j^*.$$

Hence, for example, for the trivial equilibrium $Y^* = 0$, we have that

$$J(Y^*) = \text{diag}(b_i),$$

and then, the origin is unstable when some b_i is positive and it is locally stable if $b_i < 0$ for all $i = 1, \dots, n$.

On the other hand, for a strictly positive equilibrium Y^* , using (13), we get that

$$J(Y^*) = \text{diag}(y_i^*)C.$$

The existence of Y^* and its local stability have been recently studied in [5]. In the following section we study the global stability of the equilibria, which, in particular, provides information on local stability of all equilibria.

3.2. Global stability

We are interested in the global stability of non-trivial equilibrium. We present a result that assures the existence of a globally stable non-trivial equilibrium. From that, first we need some notation.

Definition 7. Suppose C is an $n \times n$ real matrix. We say that $C \in S_w$ if there exists a positive diagonal matrix W such that $WC + C^TW$ is negative definite, i.e., $y^T(WC + C^TW)y < 0$ for all $y \in \mathbb{R}^n \setminus \{0\}$.

The following result follows from [17], see also [18].

Theorem 8. Assume that $C \in S_w$. Then, (11) possesses a nonnegative and globally stable equilibrium point Y^* for each $b \in \mathbb{R}^n$.

It is not hard to show that if $C \in S_w$ then every principal submatrix also belongs to S_w . Hence, we can conclude

Corollary 9. If $C \in S_w$, then every reduced system of (11) has a nonnegative and globally stable equilibrium point for each $b \in \mathbb{R}^n$.

Remark 10. In fact, the equilibrium point Y^* satisfies (see [18])

$$b_i + \sum_{j=1}^n c_{ij}y_j^* \leq 0 \quad \text{for } i = 1, \dots, n. \quad (14)$$

In general, it is a hard task to prove if a matrix C belongs to S_w . In the following result we prove that, under the condition (7), our system (3) has a nonnegative and globally stable equilibrium point, showing that the matrix of the system (3) belongs to S_w .

Theorem 11. Suppose $\beta < 1$ and that (7) holds, i.e.,

$$\gamma_1\gamma_2 < \frac{1 + \beta(P-1)}{P} \frac{1 + \beta(A-1)}{A}.$$

Then, (3) possesses a nonnegative and globally stable equilibrium $W^* \in E$ point in \overline{C}^+ , i.e. for every $w_0 \in C^+$ it holds that

$$\lim_{t \rightarrow \infty} \|w(t; w_0) - W^*\| = 0.$$

This result is giving a nonnegative stationary solution, which, in general, can possess zero components. Observe that if we consider (3) with, for instance, the i -component of the initial data equal to zero, then associated solution satisfies (3) removing equation i , with $i \in \{1, \dots, n\}$. Moreover, as the matrix for any subset of equations of (3) is also in S_w , we can apply Theorem 11 iteratively. This is the key argument allowing us to describe the connections between equilibria in the global attractor which we describe in Section 5.

Proof of Theorem 11. Remember that $C \in S_w$ if there exists a positive diagonal matrix W such that

$$\mathcal{C} := WC + C^T W$$

is negative definite. Observe that \mathcal{C} is a symmetric matrix, so it suffices to show that its eigenvalues are negative.

Observe that

$$C^T = \begin{bmatrix} B_1^T & \Gamma_2^T \\ \Gamma_1^T & B_2^T \end{bmatrix}_{(P+A) \times (P+A)}$$

and that $B_1^T = B_1$, $B_2^T = B_2$, $\Gamma_1^T = \gamma_1 \mathcal{I}_{A \times P}$ and $\Gamma_2^T = \gamma_2 \mathcal{I}_{P \times A}$, see the notation in the Appendix.

Taking into account the structure of C , we choose W as follows:

$$W = \begin{bmatrix} W_1 & \emptyset \\ \emptyset & W_2 \end{bmatrix}_{(P+A) \times (P+A)}$$

where $W_1 = \text{diag}(w_1)$ and $W_2 = \text{diag}(w_2)$ are diagonal matrices of order P and A , respectively, and $w_1, w_2 > 0$.

It is clear that

$$\mathcal{C} = WC + C^T W = \begin{bmatrix} D_1 & C_1 \\ C_2 & D_2 \end{bmatrix}_{(P+A) \times (P+A)},$$

where (see again the Appendix)

$$\begin{aligned} D_1 &= D(-2w_1, -2w_1\beta; P), & D_2 &= D(-2w_2, -2w_2\beta; A), \\ C_1 &= (w_1\gamma_1 + w_2\gamma_2)\mathcal{I}_{P \times A}, & C_2 &= (w_1\gamma_1 + w_2\gamma_2)\mathcal{I}_{A \times P}. \end{aligned}$$

We want to choose $w_1, w_2 > 0$ such that the eigenvalues of $\mathcal{C} = WC + C^T W$ are negative. For that, we evaluate the characteristic polynomial

$$p(\lambda) = |\mathcal{C}(\lambda)| = |\mathcal{C} - \lambda I| = |WC + C^T W - \lambda I|.$$

Observe that

$$\mathcal{C}(\lambda) = \begin{bmatrix} F_1 & C_1 \\ C_2 & F_2 \end{bmatrix}_{(P+A) \times (P+A)},$$

where

$$F_1 = D(-2w_1 - \lambda, -2w_1\beta; P), \quad F_2 = D(-2w_2 - \lambda, -2w_2\beta; A).$$

Then, applying Proposition 27 (see Appendix), we get

$$p(\lambda) = (-2w_1 - \lambda + 2w_1\beta)^{P-1}(-2w_2 - \lambda + 2w_2\beta)^{A-1} \cdot q(\lambda)$$

where

$$\begin{aligned} q(\lambda) &= ((-2w_1 - \lambda - 2w_1\beta(P-1))(-2w_2 - \lambda - 2w_2\beta(A-1)) - PA(w_1\gamma_1 + w_2\gamma_2)^2) \\ &= 4 \left[\left(w_1 + \frac{\lambda}{2} + w_1\beta(P-1) \right) \left(w_2 + \frac{\lambda}{2} + w_2\beta(A-1) \right) - \frac{PA}{4}(w_1\gamma_1 + w_2\gamma_2)^2 \right]. \end{aligned}$$

Hence, the eigenvalues of \mathcal{C} are

$$\begin{cases} \lambda = 2w_1(\beta - 1) & \text{with multiplicity } P - 1, \\ \lambda = 2w_2(\beta - 1) & \text{with multiplicity } A - 1, \\ \text{the roots of } q(\lambda). \end{cases}$$

The roots of $q(\lambda)$ are the roots of the following polynomial of degree 2,

$$m(\lambda) = \frac{\lambda^2}{4} + R_1(w_1, w_2)\frac{\lambda}{2} + R_2(w_1, w_2)$$

where

$$\begin{aligned} R_1(w_1, w_2) &= w_1(1 + \beta(P-1)) + w_2(1 + \beta(A-1)), \\ R_2(w_1, w_2) &= w_1w_2(1 + \beta(P-1))(1 + \beta(A-1)) - \frac{PA}{4}(w_1\gamma_1 + w_2\gamma_2)^2. \end{aligned}$$

Taking into account that $R_1 > 0$, in order to have negative roots of $m(\lambda)$, we need that

$$R_2(w_1, w_2) > 0.$$

This is equivalent to

$$w_1w_2(1 + \beta(P-1))(1 + \beta(A-1)) > \frac{PA}{4}(w_1^2\gamma_1^2 + w_2^2\gamma_2^2 + 2w_1w_2\gamma_1\gamma_2),$$

that is,

$$0 > \left(\frac{w_2}{w_1} \right)^2 \gamma_2^2 + 2 \left(\frac{w_2}{w_1} \right) \left(\gamma_1\gamma_2 - \frac{2}{PA}(1 + \beta(P-1))(1 + \beta(A-1)) \right) + \gamma_1^2.$$

Using (7), there exist $w_1, w_2 > 0$ verifying the above inequality provided of

$$- \frac{(\gamma_1\gamma_2 - \frac{2}{PA}(1 + \beta(P-1))(1 + \beta(A-1)))^2}{\gamma_2^2} + \gamma_1^2 < 0$$

for which, it suffices that

$$\gamma_1\gamma_2 < \frac{2}{PA}(1 + \beta(P-1))(1 + \beta(A-1)) - \gamma_1\gamma_2$$

which is true by (7). \square

4. Characterization of global attractors: attracting networks

In this section we will describe the geometrical structure of the global attractor for gradient semigroups, which will allow a full description of the attractor for system (3).

4.1. Structure and dynamics of attractors for gradient systems

Definition 12. Let $\{T(t) : t \geq 0\}$ be a semigroup on X . We say that an invariant set $E \subset X$ for the semigroup $\{T(t) : t \geq 0\}$ is an *isolated invariant set* if there is an $\epsilon > 0$ such that E is the maximal invariant subset in the neighborhood $\mathcal{O}_\epsilon(E)$.

A disjoint family of isolated invariant sets is a family $\{E_1, \dots, E_m\}$ of isolated invariant sets with the property that,

$$\mathcal{O}_\epsilon(E_i) \cap \mathcal{O}_\epsilon(E_j) = \emptyset, \quad 1 \leq i < j \leq m,$$

for some $\epsilon > 0$.

Definition 13. The unstable manifold of an isolated invariant set E_i is the set

$$W^u(E_i) = \{z \in X : \text{there is a backwards solution } \zeta(\cdot) \text{ through } z \text{ such that } \lim_{t \rightarrow -\infty} \text{dist}(\zeta(t), E_i) = 0\}.$$

4.1.1. Lyapunov functions

Definition 14. We say that a semigroup $\{T(t) : t \geq 0\}$ with a global attractor \mathcal{A} and a disjoint family of isolated invariant sets $\mathbf{E} = \{E_1, \dots, E_m\}$ is a *gradient semigroup* with respect to \mathbf{E} if there exists a continuous function $V : X \rightarrow \mathbb{R}$ such that

- (i) $[0, \infty) \ni t \mapsto V(T(t)x) \in \mathbb{R}$ is non-increasing for each $x \in X$;
- (ii) V is constant in E_i , for each $1 \leq i \leq m$; and
- (iii) $V(T(t)x) = V(x)$ for all $t \geq 0$ if and only if $x \in \bigcup_{i=1}^m E_i$.

In this case we call V a Lyapunov functional related to \mathbf{E} .

Any Morse decomposition $\mathbf{E} = \{E_1, \dots, E_m\}$ of a compact invariant set \mathcal{A} leads to a partial order among the isolated invariant sets E_i , given by a decreasing order or energy levels of the sets given by the Lyapunov function, that is, we can define an order between two isolated invariant sets E_i and E_j if it holds that $V|_{E_i} < V|_{E_j}$ (see [19]).

For gradient semigroups, the structure of the global attractor can be described as follows:

Theorem 15. Let $\{T(t) : t \geq 0\}$ a gradient semigroup with respect to the finite set $\mathbf{E} := \{E_1, E_2, \dots, E_m\}$. If $\{T(t) : t \geq 0\}$ has a global attractor \mathcal{A} , then \mathcal{A} can be written as the union of the unstable manifolds related to each set in \mathbf{E} , i.e.,

$$\mathcal{A} = \bigcup_{j=1}^m W^u(E_j). \quad (15)$$

Remark 16. When E_j are equilibria Y_j^* , the attractor is described as the union of the unstable manifolds associated to them

$$\mathcal{A} = \bigcup_{j=1}^m W^u(Y_j^*).$$

This description shows a geometrical picture of the global attractor, in which all the stationary points are ordered by connections related to its level of attraction or stability.

4.1.2. Morse decomposition of a global attractor

Next we introduce the notion of a Morse decomposition for the attractor \mathcal{A} of a semigroup $\{T(t) : t \geq 0\}$ (see [20,21] or [22]). We start with the notion of an attractor–repeller pair.

Definition 17. Let $\{T(t) : t \geq 0\}$ be a semigroup with a global attractor \mathcal{A} . We say that a non-empty subset A of \mathcal{A} is a *local attractor* if there is an $\epsilon > 0$ such that $\omega(\mathcal{O}_\epsilon(A)) = A$, where $\omega(B)$ is the ω -limit set of B , defined as

$$\omega(B) = \{x \in X : T(t_n)x_n \rightarrow x, \text{ for some } x_n \in B, t_n \rightarrow \infty\}.$$

The *repeller* A^* associated to a local attractor A is the set defined by

$$A^* := \{x \in \mathcal{A} : \omega(x) \cap A = \emptyset\}.$$

The pair (A, A^*) is called an *attractor–repeller pair* for $\{T(t) : t \geq 0\}$.

Note that if A is a local attractor, then A^* is closed and invariant.

Definition 18. Given an increasing family $\emptyset = A_0 \subset A_1 \subset \dots \subset A_m = \mathcal{A}$, of $m + 1$ local attractors, for $j = 1, \dots, m$, define $E_j := A_j \cap A_{j-1}^*$. The ordered n -tuple $\mathbf{E} := \{E_1, E_2, \dots, E_m\}$ is called a *Morse decomposition* for \mathcal{A} .

An equivalent definition of a Morse decomposition (see [23]) for the attractor \mathcal{A} of a semigroup $\{T(t) : t \geq 0\}$ is the following.

Definition 19. Let $\{T(t) : t \geq 0\}$ be a semigroup with a global attractor \mathcal{A} . A *Morse decomposition* of \mathcal{A} is a collection $\mathbf{E} = \{E_1, E_2, \dots, E_m\}$ of disjoint, compact and invariant subsets of \mathcal{A} such that for a given global solution $\xi : \mathbb{R} \rightarrow \mathcal{A}$ of $\{T(t) : t \geq 0\}$

- (i) either $\xi(t) \in E_i$, for all $t \in \mathbb{R}$ and some $i = 1, \dots, m$;
- (ii) or there exist $1 \leq i < j \leq m$ such that $E_j \xrightarrow{t \rightarrow -\infty} \xi(t) \xrightarrow{t \rightarrow \infty} E_i$.

A semigroup satisfying (i) and (ii) is called *dynamically gradient* (see [23,24,15]).

4.2. Topological structural stability

It has been proved in [23] that a semigroup $\{T(t) : t \geq 0\}$ is gradient with respect to \mathbf{E} if and only if it is dynamically gradient with respect to \mathbf{E} :

Theorem 20. Given a disjoint family of isolated invariant sets $\mathbf{E} = \{E_1, \dots, E_m\}$ for a semigroup $T(t)$, the following three properties are equivalent:

- (i) $T(\cdot)$ is dynamically gradient;
- (ii) there exists an associated ordered family of local attractor–repellers; and
- (iii) there exists a Lyapunov functional related to \mathbf{E} .

The results in [25] show dynamically gradient nonlinear semigroups are stable under perturbation, so that we conclude that gradient semigroups are stable under perturbation as well; that is, the existence of a continuous Lyapunov function is robust under perturbation of parameters.

5. Morse decomposition of attractors for mutualistic systems

In this section we will describe the geometrical structure of the global attractor for system (3). In particular, we show a Morse Decomposition of the attractor given by the set E of equilibria of (3), drawing

a complex networks of nodes and connections. Each node given by a partially feasible equilibrium point in the attractor represents an attracting complex network. Thus, the attractor can be understood as a new complex dynamical net of networks containing all the possible feasible long time behavior. In particular, the global attractor contains all the abstract information related to future scenarios of biodiversity.

The main result of this section proves the existence of a Morse Decomposition on the global attractor \mathcal{A} of (11), assuming that the matrix $C \in S_w$, which implies the existence of a globally asymptotically stable stationary solution of (11).

Theorem 21. Assume that $C \in S_w$ and let $E := \{Y_1^*, \dots, Y_m^*\}$ the set of stationary points for (11). Then, E defines a Morse decomposition for the global attractor \mathcal{A} of (11). As a consequence, (11) is a gradient system. In particular, given $z \in \mathcal{A} \setminus E$ there exist $i < j \in \{1, \dots, m\}$ such that

$$\lim_{t \rightarrow -\infty} \|y(t; z) - Y_j^*\| = 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} \|y(t; z) - Y_i^*\| = 0.$$

Proof. We will construct an increasing sequence of local attractors

$$A_1 \subset A_2 \subset \dots \subset A_m = \mathcal{A}.$$

Note that a Morse decomposition will be given by

$$E_i = A_i \cap A_{i-1}^*.$$

The way we will construct A_i , $i = 1, \dots, M$ implies that $E_i \in E$, the set of equilibria for (11).

Step 1:

Let call Y_1^* the stationary point given by Theorem 8, i.e., the one globally asymptotically stable in C^+ , and we denote $Y_1^* = \{Y_1^*(1), \dots, Y_1^*(n)\}$. Recall $D = \{1, \dots, n\}$. Let

$$I_1 = \{i \in D / Y_1^*(i) = 0\}, \\ J_1 = D \setminus I_1 = \{j \in D / Y_1^*(j) > 0\}.$$

We suppose $J_1 \neq \emptyset$, as in other case the result is trivial. We order the $m_1 \leq n$ elements of set J_1

$$j_1 < j_2 < \dots < j_{m_1}.$$

Define the open hyperplanes E_{j_k} con $k \in \{1, \dots, m_1\}$, as

$$E_{j_k} = \{u \in \bar{C}^+ / u(j_k) = 0 \text{ and all the other components } u(i) > 0\}.$$

We define $A_1 = \{Y_1^*\}$. Then A_1 is a local attractor, which attracts every solution starting in

$$\bar{C}^+ \setminus \bigcup_{k=1}^{m_1} E_{j_k}.$$

Then, its associated repeller in \bar{C}^+ is given by

$$A_1^* = \bigcup_{k=1}^{m_1} E_{j_k}.$$

Step 2:

As each E_{j_k} is a positively invariant set, and Theorem 8 can be once more applied, let $Y_{j_k}^*$ the globally stationary points in E_{j_k} , $k \in \{1, \dots, m_1\}$. Thus, in particular, $Y_{j_1}^*$ is a local attractor in E_{j_1} .

Let

$$A_2 = A_1 \cup W^u(Y_{j_1}^*),$$

i.e., A_2 contains A_1 , the hyperplane E_{j_1} and all connections from $Y_{j_1}^*$ to Y_1^* . Now we construct the associated repeller to A_2 .

For $Y_{j_1}^*$, let

$$\begin{aligned} I_{j_1} &= \{i \in D/Y_{j_1}^*(i) = 0\}; \quad \text{in particular } j_1 \in I_{j_1}, \\ J_{j_1} &= D \setminus I_{j_1} = \{j \in D/Y_{j_1}^*(j) > 0\}. \end{aligned}$$

We order J_{j_1} as

$$j_{1,j_1} < j_{2,j_1} < \cdots < j_{m_2,j_1}$$

and consider

$$E_{j_1,j_1} = \{u \in E_{j_1}/u(j_{1,j_1}) = 0 \text{ and all the other components } u(i) > 0\}.$$

Then $Y_{j_1}^*$ is a local attractor in E_{j_1} , which attracts every solution starting in

$$\overline{E_{j_1}} \setminus \bigcup_{k=1}^{\overline{m_2}} E_{j_k,j_1}.$$

Then

$$A_2^* = \left(\bigcup_{k=1}^{\overline{m_2}} E_{j_k,j_1} \right) \cup \left(\bigcup_{k=2}^{\overline{m_1}} E_{j_k} \right).$$

We now repeat this same argument in Step 2 for each E_{j_k} , for $k \in \{2, \dots, m_1\}$.

Step 3:

Now, again we repeat the arguments in Step 2 for the hyperplane E_{j_1,j_1} , so that, again by [Theorem 8](#), we find an asymptotically stable stationary point Y_{j_1,j_1}^* in E_{j_1,j_1} , which is a local attractor in E_{j_1,j_1} , and from which we can define

$$A_3 = A_2 \cup W^u(Y_{j_1,j_1}^*),$$

which possesses an associated repeller A_3^* .

Once more, we repeat the arguments in Step 2 for the hyperplane E_{j_k,j_1} , for $k \in \{2, \dots, m_2\}$.

Step m:

In general, we build, for some stationary solution,

$$A_{m+1} = A_m \cup W^u(Y_{j_1,\dots,j_1}^*)$$

and associated repellers $A_{m_0+1}^*$.

Observe that A_m^* are

- (i) Invariant closed sets
- (ii) They do not intersect with $\bigcup_{k=1}^m A_k$
- (iii) They contain the rest of stationary points not in $\bigcup_{k=1}^m A_k$. \square

As an immediate consequence we get,

Corollary 22. Assume (7) and let $E := \{W_1^*, \dots, W_M^*\}$ the set of stationary points for (3). Then, E defines a Morse decomposition for the global attractor \mathcal{A} of (3). As a consequence, (3) is a gradient system. In particular, given $z \in \mathcal{A} \setminus E$ there exist $i < j \in \{1, \dots, m\}$ such that

$$\lim_{t \rightarrow -\infty} \|w(t; z) - W_j^*\| = 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} \|w(t; z) - W_i^*\| = 0.$$

6. Application: a 3D-model

In a recent paper [26] we study a three dimensional model consisting in three differential equations, two nodes in the first group (u_1 and u_2) and just another node in the second group (u_3) with cooperative relations with the first ones. Observe that, in this case, the initial real network is just composed of three nodes. We have

$$\begin{cases} u_1' = u_1(\alpha_1 - u_1 - \beta u_2 + \gamma_1 u_3) \\ u_2' = u_2(\alpha_2 - u_2 - \beta u_1 + \gamma_1 u_3) \\ u_3' = u_3(\alpha_3 - u_3 + \gamma_2 u_1 + \gamma_2 u_2), \\ (u_1(0), u_2(0), u_3(0)) = (u_1^0, u_2^0, u_3^0), \end{cases} \quad (16)$$

where $\alpha_1, \alpha_2, \alpha_3 \in \mathbb{R}$, $0 < \beta < 1$, $\gamma_1, \gamma_2 > 0$ and we suppose positive initial data.

Assume that

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

Then, there exists a unique solution for (16), and we can define a semigroup which possesses a global attractor $\mathcal{A} \subset \mathbb{R}^3$.

For (16), it is easy to show that the eight stationary points

$$\mathbf{E} := \{E_{ijk}\}, \quad i, j, k = 0, 1,$$

are given by

$$\begin{aligned} E_{000} &= (0, 0, 0), & E_{100} &= (\alpha_1, 0, 0), & E_{010} &= (0, \alpha_2, 0), & E_{001} &= (0, 0, \alpha_3), \\ E_{011} &= \left(0, \frac{\alpha_2 + \gamma_1 \alpha_3}{1 - \gamma_1 \gamma_2}, \frac{\alpha_3 + \gamma_2 \alpha_2}{1 - \gamma_1 \gamma_2}\right), \\ E_{101} &= \left(\frac{\alpha_1 + \gamma_1 \alpha_3}{1 - \gamma_1 \gamma_2}, 0, \frac{\alpha_3 + \gamma_2 \alpha_1}{1 - \gamma_1 \gamma_2}\right), \\ E_{110} &= \left(\frac{\alpha_1 - \beta \alpha_2}{1 - \beta^2}, \frac{\alpha_2 - \beta \alpha_1}{1 - \beta^2}, 0\right), \\ E_{111} &= \begin{pmatrix} \frac{\alpha_1(1 - \gamma_1 \gamma_2) + \alpha_2(\gamma_1 \gamma_2 - \beta) + \alpha_3 \gamma_1(1 - \beta)}{(1 - \beta)(1 + \beta - 2\gamma_1 \gamma_2)} \\ \frac{\alpha_1(\gamma_1 \gamma_2 - \beta) + \alpha_2(1 - \gamma_1 \gamma_2) + \alpha_3 \gamma_1(1 - \beta)}{(1 - \beta)(1 + \beta - 2\gamma_1 \gamma_2)} \\ \frac{(\alpha_1 + \alpha_2)\gamma_2 + \alpha_3(1 + \beta)}{1 + \beta - 2\gamma_1 \gamma_2} \end{pmatrix}^T. \end{aligned}$$

To analyze the stability of these points, we calculate the eigenvalues of the Jacobian matrix at a stationary point (u_1, u_2, u_3) given by

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

We have the following result (see [26]):

- Theorem 23.** (a) When the components of E_{111} are strictly positive, then E_{111} is locally stable and the semi-trivial stationary points E_{011} , E_{101} and E_{110} are unstable.
- (b) Assume that E_{111} exists. Then, it is globally asymptotically stable in the interior of \mathbb{R}_+^3 . As a consequence, system (16) is permanent, i.e., asymptotically there exists coexistence of the three nodes.
- (c) The global attractor $\mathcal{A} \subset \mathbb{R}^3$ is given by

$$\mathcal{A} = \bigcup_{i,j,k=0}^1 W^u(E_{ijk}).$$

Theorem 23(c) shows that the global attractor is gradient-like. In fact, we can follow in detail the steps described in Theorem 21, as the associated semigroup for (16) is dynamically gradient, and the stationary points in the global attractor are the Morse sets, given by $A_i \cap A_{i-1}^*$, which describes the hierarchy on how the long-time dynamics develops with respect to positive solutions. Indeed, in the case all the positive stationary points E_{ijk} exist, the argument in Theorem 21 would develop as follows:

$A_1 = E_{111}$ is the first local attractor. The associated repeller A_1^* is given by the union of closed planes XY, XZ, YZ respectively.

Consider E_{110} , which is the local attractor in open plane XY . Then,

$$A_2 = A_1 \cup W^u(E_{110})$$

and then A_2^* the union of closed planes XZ, YZ .

Now consider E_{101} , i.e., the local attractor in open plane XZ . Then,

$$A_3 = A_2 \cup W^u(E_{101})$$

and A_3^* the closed plane YZ .

In the next step take E_{011} , the local attractor in open plane YZ . Then,

$$A_4 = A_3 \cup W^u(E_{011})$$

and then A_4^* the union of closed semi axes OX, OY and OZ .

Then take E_{100} , local attractor in open semi axis OX .

$$A_5 = A_4 \cup W^u(E_{100})$$

and A_5^* the union of closed semi axes OY and OZ .

For E_{010} , local attractor in open semi axis OY , define

$$A_6 = A_5 \cup W^u(E_{010})$$

and A_6^* the closed semi axes OZ ,

and or E_{001} , local attractor in open semi axis Oz , define

$$A_7 = A_6 \cup W^u(E_{001})$$

and $A_7^* = E_{000}$.

Finally, $A_8 = \mathcal{A}$.

This simplified model allows us to describe in detail the dependence of the associated attracting networks on parameters, showing that, in particular, to a fix phenomenological network of three species, corresponds a bigger and more complex set of possible future configurations given by different architectures of the global attractor, described from the equilibria and their oriented connections. For example, the case described above corresponds to the drawing bottom right in Fig. 2, associated to E_{111} to be globally asymptotically

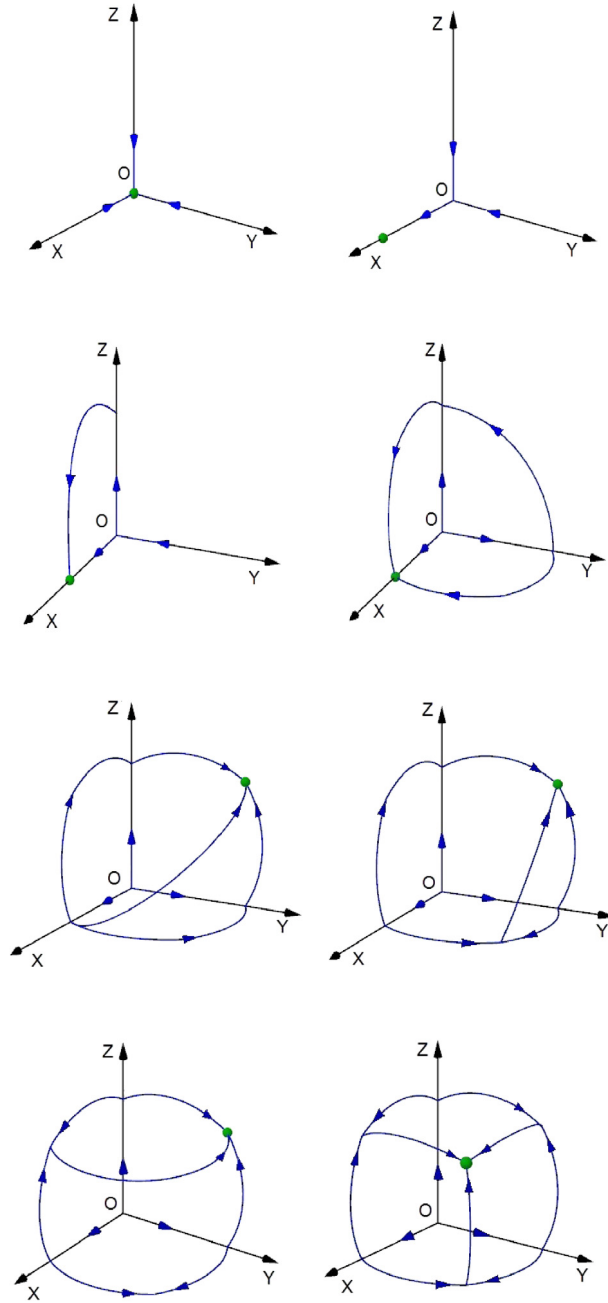


Fig. 2. Eight possible attracting complex networks in the 3D case. Each network shows the case of a different asymptotically globally stable equilibria, the one with the lower energy level given by Lyapunov function. Networks depend on the values of the parameters in (16) as described by Theorem 24. Observe that all this set of possible attracting networks correspond to the same phenomenological characterization given by the three nodes u_1, u_2 and u_3 .

stable. In the following result (see [27]) we characterize the values of the parameters α_i that assure the global stability of each of the eight equilibrium points, thus corresponding to eight attracting networks in Fig. 2:

- Theorem 24.** 1. Assume that α_1, α_2 and $\alpha_3 < 0$. Then, E_{000} is globally asymptotically stable.
 2. Assume that $\alpha_1 > 0$, $\alpha_2 < \beta\alpha_1$ and $\alpha_3 < -\gamma_2\alpha_1$. Then, E_{100} is globally asymptotically stable.
 3. Assume that $\alpha_2 > 0$, $\alpha_1 < \beta\alpha_2$ and $\alpha_3 < -\gamma_2\alpha_2$. Then, E_{010} is globally asymptotically stable.

4. Assume that $\alpha_3 > 0$, $\alpha_1 < -\gamma_1\alpha_3$ and $\alpha_2 < -\gamma_1\alpha_3$. Then, E_{001} is globally asymptotically stable.

5. Assume that

$$\alpha_1 > \beta\alpha_2, \quad \alpha_2 > \beta\alpha_1, \quad (\alpha_1 + \alpha_2)\gamma_2 + \alpha_3(1 + \beta) < 0. \quad (17)$$

Then, E_{110} is globally asymptotically stable.

6. Assume that

$$\begin{cases} \alpha_1 + \gamma_1\alpha_3 > 0, \\ \alpha_3 + \gamma_2\alpha_1 > 0, \\ \alpha_1(\gamma_2\gamma_1 - \beta) + \alpha_2(1 - \gamma_1\gamma_2) + \alpha_3\gamma_1(1 - \beta) < 0. \end{cases} \quad (18)$$

Then, E_{101} is globally asymptotically stable.

7. Assume that

$$\begin{cases} \alpha_2 + \gamma_1\alpha_3 > 0, \\ \alpha_3 + \gamma_2\alpha_2 > 0, \\ \alpha_1(1 - \gamma_1\gamma_2) + \alpha_2(\gamma_1\gamma_2 - \beta) + \alpha_3\gamma_1(1 - \beta) < 0. \end{cases} \quad (19)$$

Then, E_{011} is globally asymptotically stable.

8. Assume that E_{111} exists. Then, E_{111} is globally asymptotically stable.

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Appendix

In this Appendix we prove the auxiliary results included in the proof of [Theorem 11](#).

Definition 25. Given $M, N \in \mathbb{N}$, and $a, b \in \mathbb{R}$, we denote by

$$D(a, b; M) = \begin{bmatrix} a & b & b & \cdots & b \\ b & a & b & \cdots & b \\ b & b & a & \cdots & b \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ b & b & b & \cdots & a \end{bmatrix}_{M \times M}$$

and

$$\mathcal{I}_{M \times N} = (a_{ij}), \quad a_{ij} = 1, \quad i = 1, \dots, M; \quad j = 1, \dots, N.$$

With this notation, the matrix C of (3) is a matrix with order $P + A$ defined by

$$C = \begin{bmatrix} B_1 & \Gamma_1 \\ \Gamma_2 & B_2 \end{bmatrix}_{(P+A) \times (P+A)}, \quad (20)$$

where

$$B_1 = D(-1, \beta; P), \quad B_2 = D(-1, \beta; A), \quad \Gamma_1 = \gamma_1 \mathcal{I}_{P \times A}, \quad \Gamma_2 = \gamma_2 \mathcal{I}_{A \times P},$$

that is:

$$B_1 = \begin{bmatrix} -1 & -\beta & \cdots & -\beta \\ -\beta & -1 & \cdots & -\beta \\ \vdots & \vdots & \ddots & \vdots \\ -\beta & -\beta & \cdots & -1 \end{bmatrix}_{P \times P}, \quad B_2 = \begin{bmatrix} -1 & -\beta & \cdots & -\beta \\ -\beta & -1 & \cdots & -\beta \\ \vdots & \vdots & \ddots & \vdots \\ -\beta & -\beta & \cdots & -1 \end{bmatrix}_{A \times A},$$

$$\Gamma_1 = \begin{bmatrix} \gamma_1 & \gamma_1 & \cdots & \gamma_1 \\ \gamma_1 & \gamma_1 & \cdots & \gamma_1 \\ \vdots & \vdots & \ddots & \vdots \\ \gamma_1 & \gamma_1 & \cdots & \gamma_1 \end{bmatrix}_{P \times A}, \quad \Gamma_2 = \begin{bmatrix} \gamma_2 & \gamma_2 & \cdots & \gamma_2 \\ \gamma_2 & \gamma_2 & \cdots & \gamma_2 \\ \vdots & \vdots & \ddots & \vdots \\ \gamma_2 & \gamma_2 & \cdots & \gamma_2 \end{bmatrix}_{A \times P},$$

where $0 < \beta < 1$, $\gamma_1, \gamma_2 > 0$.

In the following result we study the matrix $D(a, b; M)$.

Lemma 26. Consider $a, b \in \mathbb{R}$ and $M \in \mathbb{N}$.

1. We have that:

$$|D(a, b; M)| = (a + (M - 1)b)(a - b)^{M-1}. \quad (21)$$

2. It holds that

$$D(a, b; M)^{-1} = \frac{1}{(a - b)(a + (M - 1)b)} D(d, -b; M)$$

where

$$d = a + (M - 2)b.$$

Proof. (a) Subtracting the first row to the other, we get

$$|D(a, b; M)| = \begin{vmatrix} a & b & b & b & \cdots & b \\ b - a & a - b & 0 & 0 & \cdots & 0 \\ b - a & 0 & a - b & 0 & \cdots & 0 \\ b - a & 0 & 0 & a - b & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ b - a & 0 & 0 & 0 & \cdots & a - b \end{vmatrix}_{M \times M}.$$

Now, adding all the columns to the first, we finally obtain

$$|D(a, b; M)| = \begin{vmatrix} a + (M-1)b & b & b & b & \cdots & b \\ 0 & a-b & 0 & 0 & \cdots & 0 \\ 0 & 0 & a-b & 0 & \cdots & 0 \\ 0 & 0 & 0 & a-b & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & a-b \end{vmatrix}_{M \times M} \\ = (a + (M-1)b)(a-b)^{M-1}.$$

(b) It is an easy task to show that $D(a, b; M) \cdot D(a, b; M)^{-1} = I$. \square

In the following result we calculate the eigenvalues of similar matrices to C . Consider the more general matrix

$$C = \begin{bmatrix} D_P & C_1 \\ C_2 & D_A \end{bmatrix}_{(P+A) \times (P+A)},$$

where

$$D_P = D(a_1, d_1; P), \quad D_A = D(a_2, d_2; A), \quad C_1 = c_1 \mathcal{I}_{P \times A}, \quad C_2 = c_2 \mathcal{I}_{A \times P},$$

and $a_1, d_1, a_2, d_2, c_1, c_2 \in \mathbb{R}$. We have:

Proposition 27. *It holds that,*

$$|C| = (a_1 - d_1)^{P-1} (a_2 - d_2)^{A-1} ((a_1 + (P-1)d_1)(a_2 + (A-1)d_2) - c_1 c_2 AP).$$

Proof. *Case 1:* Assume that D_P^{-1} exists, that is $a_1 \neq d_1$ and $a_1 \neq d_1(1-P)$. In this case, we get that

$$|C| = |D_P| |D_A - C_2 D_P^{-1} C_1|. \quad (22)$$

First, we calculate $C_2 D_P^{-1} C_1$. It is not hard to show that

$$C_2 D_P^{-1} C_1 = c_2 c_1 \mathcal{I}_{A \times P} D_P^{-1} \mathcal{I}_{P \times A}.$$

Using now [Lemma 26](#) to the expression of D_P^{-1} , we get

$$D_P^{-1} \mathcal{I}_{P \times A} = \frac{1}{(a_1 + (P-1)d_1)} \mathcal{I}_{P \times A},$$

and then,

$$\begin{aligned} \mathcal{I}_{A \times P} D_P^{-1} \mathcal{I}_{P \times A} &= \frac{1}{(a_1 + (P-1)d_1)} \mathcal{I}_{A \times P} \mathcal{I}_{P \times A} \\ &= \frac{P}{(a_1 + (P-1)d_1)} \mathcal{I}_{A \times A}. \end{aligned}$$

From here, we can deduce that

$$C_2 D_P^{-1} C_1 = \frac{c_1 c_2 P}{(a_1 + (P-1)d_1)} \mathcal{I}_{A \times A}.$$

We denote by

$$\mathcal{D} = D_A - C_2 D_P^{-1} C_1,$$

and we obtain that

$$\mathcal{D} = D \left(a_2 - \frac{c_1 c_2 P}{(a_1 + (P-1)d_1)}, d_2 - \frac{c_1 c_2 P}{(a_1 + (P-1)d_1)}; A \right).$$

Using again Lemma 26, it yields

$$|\mathcal{D}| = (a_2 - d_2)^{A-1} \left(a_2 - \frac{c_1 c_2 P}{(a_1 + (P-1)d_1)} + (A-1) \left(d_2 - \frac{c_1 c_2 P}{(a_1 + (P-1)d_1)} \right) \right).$$

Hence, using (22) we have that

$$\begin{aligned} |\mathcal{C}| &= (a_1 - d_1)^{P-1} (a_1 + (P-1)d_1) (a_2 - d_2)^{A-1} \\ &\quad \cdot \left(a_2 - \frac{c_1 c_2 P}{(a_1 + (P-1)d_1)} + (A-1) \left(d_2 - \frac{c_1 c_2 P}{(a_1 + (P-1)d_1)} \right) \right) \\ &= (a_1 - d_1)^{P-1} (a_2 - d_2)^{A-1} ((a_1 + (P-1)d_1)(a_2 + (A-1)d_2) - c_1 c_2 AP). \end{aligned}$$

This completes the proof in this case.

Case 2: $a_1 = d_1$. In this case, the P -first rows are similar, and so $|\mathcal{C}| = 0$.

Case 3: $a_1 = d_1(1 - P)$. We subtract the P -th row to the first $P - 1$ ones,

$$|\mathcal{C}| = \begin{vmatrix} Pd_1 & 0 & \cdots & 0 & -Pd_1 & 0 & 0 & \cdots & 0 \\ 0 & Pd_1 & \cdots & 0 & -Pd_1 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & \cdots & Pd_1 & -Pd_1 & 0 & 0 & \cdots & 0 \\ d_1 & d_1 & \cdots & d_1 & d_1(1-P) & c_1 & c_1 & \cdots & c_1 \\ c_2 & c_2 & \cdots & c_2 & c_2 & a_2 & d_2 & \cdots & d_2 \\ c_2 & c_2 & \cdots & c_2 & c_2 & d_2 & a_2 & \cdots & d_2 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ c_2 & c_2 & \cdots & c_2 & c_2 & d_2 & d_2 & \cdots & a_2 \end{vmatrix}_{(P+A) \times (P+A)}$$

we subtract the $P + 1$ -st column, to the last $A - 1$ ones, and we get that:

$$|\mathcal{C}| = \begin{vmatrix} Pd_1 & 0 & \cdots & 0 & -Pd_1 & 0 & 0 & \cdots & 0 \\ 0 & Pd_1 & \cdots & 0 & -Pd_1 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & \cdots & Pd_1 & -Pd_1 & 0 & 0 & \cdots & 0 \\ d_1 & d_1 & \cdots & d_1 & d_1(1-P) & c_1 & 0 & \cdots & 0 \\ c_2 & c_2 & \cdots & c_2 & c_2 & a_2 & d_2 - a_2 & \cdots & d_2 - a_2 \\ c_2 & c_2 & \cdots & c_2 & c_2 & d_2 & a_2 - d_2 & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ c_2 & c_2 & \cdots & c_2 & c_2 & d_2 & 0 & \cdots & a_2 - d_2 \end{vmatrix}_{(P+A) \times (P+A)}$$

and then,

$$|\mathcal{C}| = \begin{vmatrix} Pd_1 & 0 & \cdots & 0 & -Pd_1 & 0 & 0 & \cdots & 0 \\ 0 & Pd_1 & \cdots & 0 & -Pd_1 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & \cdots & Pd_1 & -Pd_1 & 0 & 0 & \cdots & 0 \\ d_1 & d_1 & \cdots & d_1 & d_1(1-P) & c_1 & 0 & \cdots & 0 \\ 2c_2 & 2c_2 & \cdots & 2c_2 & 2c_2 & a_2 + d_2 & d_2 - a_2 & \cdots & 0 \\ c_2 & c_2 & \cdots & c_2 & c_2 & d_2 & a_2 - d_2 & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ c_2 & c_2 & \cdots & c_2 & c_2 & d_2 & 0 & \cdots & a_2 - d_2 \end{vmatrix}_{(P+A) \times (P+A)}.$$

Developing by the last column, we get

$$|\mathcal{C}| = (a_2 - d_2) \begin{vmatrix} Pd_1 & 0 & \cdots & 0 & -Pd_1 & 0 & 0 & \cdots & 0 \\ 0 & Pd_1 & \cdots & 0 & -Pd_1 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & \cdots & Pd_1 & -Pd_1 & 0 & 0 & \cdots & 0 \\ d_1 & d_1 & \cdots & d_1 & d_1(1-P) & c_1 & 0 & \cdots & 0 \\ 2c_2 & 2c_2 & \cdots & 2c_2 & 2c_2 & a_2 + d_2 & d_2 - a_2 & \cdots & 0 \\ c_2 & c_2 & \cdots & c_2 & c_2 & d_2 & a_2 - d_2 & \cdots & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots \\ c_2 & c_2 & \cdots & c_2 & c_2 & d_2 & 0 & \cdots & a_2 - d_2 \end{vmatrix}_{(P+A-1) \times (P+A-1)}.$$

Repeating this process $A - 1$ times, we obtain

$$|\mathcal{C}| = (a_2 - d_2)^{A-1} \begin{vmatrix} Pd_1 & 0 & \cdots & 0 & -Pd_1 & 0 \\ 0 & Pd_1 & \cdots & 0 & -Pd_1 & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & Pd_1 & -Pd_1 & 0 \\ d_1 & d_1 & \cdots & d_1 & d_1(1-P) & c_1 \\ Ac_2 & Ac_2 & \cdots & Ac_2 & Ac_2 & a_2 + (A-1)d_2 \end{vmatrix}_{(P+1) \times (P+1)}.$$

Now, we continue developing the determinant by the last column, and we take into account that

$$\begin{vmatrix} Pd_1 & 0 & \cdots & 0 & -Pd_1 \\ 0 & Pd_1 & \cdots & 0 & -Pd_1 \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & \cdots & Pd_1 & -Pd_1 \\ d_1 & d_1 & \cdots & d_1 & d_1(1-P) \end{vmatrix}_{(P+1) \times P} = 0,$$

we have that

$$|\mathcal{C}| = -c_1(a_2 - d_2)^{A-1} \begin{vmatrix} Pd_1 & 0 & \cdots & 0 & -Pd_1 \\ 0 & Pd_1 & \cdots & 0 & -Pd_1 \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & \cdots & Pd_1 & -Pd_1 \\ Ac_2 & Ac_2 & \cdots & Ac_2 & Ac_2 \end{vmatrix}_{P \times P}.$$

Now, we subtract the last column to the other ones,

$$|C| = -c_1(a_2 - d_2)^{A-1} \begin{vmatrix} -2Pd_1 & -Pd_1 & \cdots & -Pd_1 & -Pd_1 \\ -Pd_1 & -2Pd_1 & \cdots & -Pd_1 & -Pd_1 \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ -Pd_1 & -Pd_1 & \cdots & -2Pd_1 & -Pd_1 \\ 0 & 0 & \cdots & 0 & Ac_2 \end{vmatrix}_{P \times P},$$

and then developing by the last row,

$$|C| = -c_1 c_2 A (a_2 - d_2)^{A-1} \begin{vmatrix} -2Pd_1 & -Pd_1 & \cdots & -Pd_1 & -Pd_1 \\ -Pd_1 & -2Pd_1 & \cdots & -Pd_1 & -Pd_1 \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ -Pd_1 & -Pd_1 & \cdots & -Pd_1 & -2Pd_1 \end{vmatrix}_{(P-1) \times (P-1)},$$

and so,

$$|C| = -c_1 c_2 A (-Pd_1)^{P-1} (a_2 - d_2)^{A-1} \begin{vmatrix} 2 & 1 & \cdots & 1 & 1 \\ 1 & 2 & \cdots & 1 & 1 \\ \vdots & \vdots & \cdots & \vdots & \vdots \\ 1 & 1 & \cdots & 1 & 2 \end{vmatrix}_{(P-1) \times (P-1)}.$$

Finally, using [Lemma 26](#), we obtain

$$|C| = (-1)^P c_1 c_2 A (Pd_1)^{P-1} (a_2 - d_2)^{A-1} P = (-1)^P A d_1^{P-1} (a_2 - d_2)^{A-1} P^P c_1 c_2.$$

This concludes the proof. \square

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