STRUCTURAL STABILITY OF INVASION GRAPHS FOR GENERALIZED LOTKA-VOLterra SYSTEMS

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ABSTRACT. In this paper we study in detail the structure of the global attractor for a generalized Lotka-Volterra system with Volterra-Lyapunov stable structural matrix. We provide the full characterization of this structure and we show that it coincides with the invasion graph as recently introduced in \cite{15}. We also study the stability of the structure with respect to the perturbation of the problem parameters. This allows us to introduce a definition of structural stability in Ecology in coherence with the classical mathematical concept where there exists a detailed geometrical structure, governing the transient and asymptotic dynamics, which is robust under perturbation.

1. Introduction. Invasion graphs and ecological assembly

The relations between populations of interacting species in ecosystems can be described by structured networks, where nodes represent species, and the edges represent the fact that the presence of one species affects another one \cite{1}. In order to understand the behavior of the ecosystem, however, it is necessary to study the dynamics of the interactions between species, i.e. how their quantities vary in time in relation to each other. The classical study of ecological dynamical models has been focused in their asymptotic behavior \cite{21}, but what is actually observed during the evolution in time of real systems is the presence of transient states \cite{13}. These transient states are known to last for hundreds of generations in many natural systems in which stochasticity is an integral part of their dynamics \cite{14}, so a major goal in current theoretical ecology is to evaluate the impact of transient dynamics on the persistence of communities in a constantly changing environment \cite{13}. The interplay between transient and asymptotic dynamics is particularly important when we want to analyze the way in which the communities assemble or the phenomena of invasion of one or more species to a given state of the ecosystem. The description of the sequence of potential assemblies or invasions (bottom-up), or disassemblies (top-down) is usually described by a network structure whose nodes are subcommunities and edges represent the possibility of evolution from one subcommunity to another \cite{12}. Full knowledge of such structure allows us to draw a complete landscape of all possible states in all possible times for the associated ecosystem. As it encompasses the essential information on the ecosystem, following our earlier terminology, we call it the informational structure (IS), cf. \cite{8, 25}. The IS is the key object to investigate...
for a deeper understanding of system dynamics as it represents both the transient states and
the asymptotic dynamics. The complete characterization of the IS gives the full information
on the mechanics of ecological assembly. Indeed, given the close connection between the IS
and the concept of assembly or community transition graph traditionally used in ecology
[12, 24, 28], the IS gives a complete picture of the pattern of all possible developments of the
ecological community containing the species present in the ecosystem.

If a model is a dissipative system of autonomous Ordinary Differential Equations which
has a finite number of equilibria and a Lyapunov function, then the underlying IS represents
the structure of its global attractor. The nodes of IS correspond to the equilibria of the
system and the edges to the heteroclinic connections between them. In this paper we focus
on the generalized Lotka–Volterra system of ODEs. While we choose this relatively simple
model, there may exist many other factors affecting the evolution of an ecosystem, so that
modelling can include the variety of forms, from very basic ones to highly nonlinear vector
fields including stochastic delay, or higher order terms. The system under consideration has
the form
\[ u'_i = u_i \left( b_i + \sum_{j=1}^{n} a_{ij} u_j \right) \] for \( i \in \{1, \ldots, n\} \).

We assume that the matrix \( A = (a_{ij})_{i,j=1}^{n} \) is Volterra–Lyapunov stable (see Definition 1).

For such a system, based on recent discoveries by Hofbauer and Schreiber [15], we present
an algorithm to construct the full structure of the global attractor, the IS, and we show that
it is equivalent to the Invasion Graph (IG) as proposed in [15]. Thus we complement the
results of [15] which states, in a more general framework, that the structure of the global
attractor is a subset of the IG, but the possibility that IG is essentially bigger is generally
not excluded. We show that for a particular case of Lotka–Volterra problem with Volterra–
Lyapunov stable matrix the two structures coincide. In this way, we give a joint framework
for the study of ecological assembly [28], Invasion Graphs [15] and Information Structures
[8, 25].

We stress that our argument works only in the Volterra–Lyapunov stable case where the IG
(and equivalently IS) is the directed acyclic graph and the results of [29] allow to construct the
unique minimal element, the globally asymptotically stable stationary point (GASS). While
this assumption may be restrictive, the advantage is that we explicitly describe, for the first
time in the literature, the full attractor structure, which is always a non-trivial fact for a
given dynamical system. As in the general case the Lotka–Volterra systems may encompass
many rich dynamic phenomena such as limit cycles or winnerless competition [22, 11], the
analytical algorithm to construct the whole dynamics for a general \( n \)-dimensional system is
still unknown.
The problem of structural stability is of a fundamental importance in biology: it concerns the question of whether the state of a system and its stability will survive upon the small perturbation of the problem parameters. Recently, Rohr et al. \cite{27} represented the structural stability of ecological networks as a problem of community persistence. Essentially, the aim is to provide a measure of the range of admissible perturbations to a system under which no interacting species become extinct, i.e. the community is feasible. Feasibility refers here to the existence of a saturated equilibrium vector, that is, given a particular combination of species interaction parameters and intrinsic growth rates ($a_{ij}$ and $b_i$ in \cite{1}, respectively) all of the abundances are strictly positive at the equilibrium. Thus, there is a connection between structural stability, as it is currently used in ecology, and the Modern Coexistence Theory (MCT) \cite{3}, which aims at determining the number of species that can coexist in an ecosystem \cite{3}. Invasion Graphs, as introduced by \cite{15}, extends the concept of assembly graphs to the invasibility criteria of the MCT: the condition that a set of persisting interacting species should have positive per capita growths rates when rare \cite{6,3}. A novel contribution of our paper is to provide a link between Information Structures and Invasion Graphs through a measure of structural stability of global attractors that integrate both the transient and asymptotic dynamics. This achievement can be of paramount importance for a more detailed understanding of community coexistence and functioning in variable environments.

Inspired by these considerations, and by the study on the stability of the global attractor structure \cite{5}, we obtain the result, that not only the stable equilibrium but also the whole assembly remains unchanged upon the small perturbation of model parameters. This result is interesting from a mathematical point of view as we get the result on structural stability for a problem which is not necessarily Morse–Smale, contrary to many classical structural stability results (see \cite{5} and references therein). On the other hand its interest from the point of view of ecology is that it links the concept of structural stability from \cite{27} with ecological assembly \cite{28}. Indeed, the notion of stability of all the assembly can be viewed as the refinement of the notion of the stability of the persistent equilibrium (see \cite{27}) as it induces the decomposition of the stability cones for the latter case into the smaller cones of the stability of assemblies.

The structure of the paper is as follows: in Section \ref{sec:2} we formulate the problem, and summarize its basic properties, in particular we recall the result of \cite{29} on the existence and characterization of globally asymptotically stable steady state. The next section \ref{sec:3} is devoted to local properties of the system: we explicitly linearize it around the equilibria and study the properties of this linearization. The first main result of the paper, which states that the IS coincides with the IG is contained in Section \ref{sec:4}. The following Section \ref{sec:5} contains the second main result, on the problem structural stability, and on the stability
cones for the assembly. Finally, in the appendices, we show that the considered problem is not necessarily Morse–Smale, we formulate the open questions for the cases which are not Volterra–Lyapunov stable and we remind the necessary facts about some classes of stable matrices.

2. LOTKA–VOLTERRA SYSTEMS, THEIR GLOBAL ATTRACTORS AND THEIR STRUCTURE.

In this section we introduce the Lotka–Volterra systems and, for Volterra–Lyapunov stable matrices in the governing equation, we formulate the results on the underlying dynamics. The key concept for this aim is the global attractor. In particular, we recall the result which states that the attractor can be described in its finest geometrical structure, composed by minimal invariants (in our case, the equilibria) and complete trajectories joining them in a hierarchical way. In our case, each admissible equilibrium or stationary point describes a subcommunity of the system. If this admissible equilibrium has strictly positive components, it is also feasible. Equilibria are joined by complete trajectories, i.e., global solutions of the system defined for all \( t \in \mathbb{R} \). This structure encodes all possible states of the system and the underlying backwards and forwards behavior of the dynamics. It is a directed and acyclic graph, which has been defined as information structure in \([8, 17, 25]\) and it induces a full landscape of the phase space defined as informational field \([17]\).

**Definition 1.** A real matrix \( A \in M^{n \times n} \) is Volterra-Lyapunov stable (VL-stable) if there exists a matrix \( H = \text{diag}\{h_1, \ldots, h_n\} \) with \( h_i > 0 \) such that \( HA + A^T H \) is negative definite (i.e. stable). In that case we write \( M \in S_w \).

Consider the following Lotka–Volterra system with Volterra–Lyapunov stable matrix \( A = (a_{ij})_{i,j=1}^n \) and a vector \( b \in \mathbb{R}^n \).

\[
  u'_i = F_i(u) = u_i \left( b_i + \sum_{j=1}^{n} a_{ij} u_j \right) \quad \text{for } i \in \{1, \ldots, n\}. 
\]  

(1)

Let \( n \in \mathbb{N} \). We denote

\[
  \overline{C}_+ = \{ x = (x_1, \ldots, x_n) \in \mathbb{R}^n : x_i \geq 0 \text{ for } i \in \{1, \ldots, n\} \},
\]

and

\[
  C_+ = \text{int} \overline{C}_+ = \{ x = (x_1, \ldots, x_n) \in \mathbb{R}^n : x_i > 0 \text{ for } i \in \{1, \ldots, n\} \}.
\]

Now let \( x = (x_1, \ldots, x_n) \in \overline{C}_+ \). If \( J \subset \{1, \ldots, n\} \) is a set of indexes then we will use a notation

\[
  C_+^J = \{ x \in \overline{C}_+ : x_i > 0 \text{ for } i \in J \}.
\]
If \( x \in \overline{C}_+ \), then we denote \( J(x) = \{ i \in \{1, \ldots, n \} : x_i > 0 \} \). Having such \( x \in \overline{C}_+ \), we have
\[
C^J_+(x) = \{ y \in \overline{C}_+ : y_i > 0 \text{ for } i \in J(x) \}.
\]

We remind a result on the system (1) from [29]. We will be first interested in its equilibria in \( \overline{C}_+ \). Clearly \( 0 = (0, \ldots, 0) \in \mathbb{R}^n \) is one of them. If we choose the nonempty subset of indexes \( J \subset \{1, \ldots, n\} \), say \( J = \{ i_1, \ldots, i_m \} \), then we will say that this set defines a admissible equilibrium if there exists a point \( x \in C^J_+ \) with \( x_i = 0 \) for \( i \not\in J \) which is an equilibrium of (1). The statement will be made more precise with some auxiliary notation introduced with the next definition.

**Definition 2.** Let \( A = (a_{ij})_{i,j=1}^n \in \mathbb{R}^{n \times n} \) be a matrix. If \( m < n \), then \( m \times m \) principal submatrix of \( A \) is obtained by removing any \( n - m \) columns and \( n - m \) rows with the same indexes from \( A \), i.e. if \( 1 \leq i_1 < i_2 < \ldots < i_m \leq n \) then the principal submatrix of \( A \) associated with the set \( J = \{ i_1, \ldots, i_m \} \) has a form \( A(J) = (a(J)_{jk})_{j,k=1}^m = (a_{i_ji_k})_{j,k=1}^m \).

Also for a vector \( b \in \mathbb{R}^n \) we can associate with a set of indexes \( J = \{ i_1, \ldots, i_m \} \) its subvector \( b(J) = (b_{i_j})_{j=1}^m \). So, the set \( J \) defines a feasible equilibrium of the subsystem consisting only of the equations indexed by elements of \( J \) and taking the variables outside \( J \) as zero, if the solution of the system \( A(J)v = -b(J) \) has all coordinates strictly positive. The associated admissible equilibrium of the original \( n \)-dimensional system is given by \( u_i = 0 \) for \( i \not\in J \), and \( u_i = v_j \) for \( j \in \{1, \ldots, m\} \), i.e., \( i_j \in J \).

Since every subset of \( \{1, \ldots, n\} \) can potentially define an admissible equilibrium, there may be maximally \( 2^n \) of them (including zero), each of them determined uniquely by splitting \( \{1, \ldots, n\} \) into the sum of two disjoint subsets: the set \( J \) on which the coordinates are strictly positive (this set defines the equilibrium) and the remainder on which they must be zero.

It is not difficult to prove that for every subset of indexes \( J \subset \{1, \ldots, n\} \) the set
\[
\{ x \in \overline{C}_+ : x_i = 0 \text{ for } x \in J \} = \overline{C}_+ \setminus C^J_+
\]
is positively and negatively invariant with respect to the flow defined by (1).

We cite the asymptotic stability result from [29].

**Theorem 3** ([29], Theorem 3.2.1). If \( A \) is Volterra–Lyapunov stable then for every \( b \in \mathbb{R}^n \) there exists a unique equilibrium \( u^* \in \overline{C}_+ \) of (1) which is globally asymptotically stable in the sense that for every \( u_0 \in C^J_+(u^*) \) the solution \( u(t) \) of (1) with the initial data \( u_0 \) converges to \( u^* \) as time tends to infinity. This \( u^* \) is the unique solution of the linear complementarity problem \( LCP(-A, -b) \). In particular, if the solution \( \overline{u} \) of the system \( Au = -b \) is positive, then \( u^* = \overline{u} \).

We will denote this \( u^* \) as GASS (globally asymptotically stable stationary point). The following result is a straightforward consequence of the previous theorem.
Corollary 4. If \( u^* \) is a GASS for the problem governed by (1), then for every set \( J = \{j_1, \ldots, j_k\} \subset \{1, \ldots, n\} \), such that \( J(u^*) \subset J \) the point \( y \in \mathbb{R}^k \) defined by \( y_i = u^*_{j_i} \) for \( i \in \{1, \ldots, k\} \) is a GASS for the \( k \) dimensional problem with \( A(J) \) and \( b(J) \).

We remind a definition of a global attractor ([11]):

**Definition 5.** Let \( X \) be a metric space and let \( S(t) : X \to X \) be a semigroup of mappings parameterized by \( t \geq 0 \). The set \( A \subset X \) is called a global attractor for \( \{S(t)\}_{t \geq 0} \) if it is nonempty, compact, invariant (i.e. \( S(t)A = A \) for every \( t \geq 0 \)), and it attracts all bounded sets of \( X \) (i.e. if \( B \subset X \) is nonempty and bounded then \( \lim_{t \to \infty} \text{dist}(S(t)B, A) = 0 \), where \( \text{dist}(C, D) = \sup_{x \in C} \inf_{y \in D} d(x, y) \) is the Hausdorff semidistance between sets \( C, D \subset X \)).

If the mappings \( S(t) : X \to X \) are continuous, for the global attractor existence we need two properties to hold: the dissipativity and asymptotic compactness [26]. As a consequence of Theorem 3 we have the following result.

**Theorem 6.** For every \( u_0 \in \overline{U}_+ \) the problem governed by (1) has a unique solution which is a continuous function of time, and the initial data. Moreover assuming the Volterra–Lyapunov stability of \( A \), the problem has a global attractor.

**Proof.** The result follows the argument of [10]. We only need to prove the dissipativity, i.e. the existence of the bounded absorbing set, once we have it, the asymptotic compactness is trivial. To this end it is sufficient to prove that if \( \sum_{i=1}^n u_i w_i \geq R \) for \( R \) large enough with some fixed weights \( w_i > 0 \), then

\[
\frac{d}{dt} \sum_{i=1}^n u_i w_i \leq -D(R).
\]

Indeed defining \( |u| \) as \( \sum_{i=1}^n u_i w_i \),

\[
\frac{d}{dt} |u| = \frac{d}{dt} \sum_{i=1}^n u_i w_i = \sum_{i=1}^n u_i b_i w_i + \sum_{i,j=1}^n u_i a_{ij} w_i u_j = \sum_{i=1}^n u_i b_i w_i + \frac{1}{2} \sum_{i,j=1}^n u_i (a_{ij} w_i + a_{ji} w_j) u_j \leq c |u| - d |u|^2.
\]

where \( c > 0 \) and \( d > 0 \) are some constants. Then if \( |u| \geq \frac{2c}{d} \), then the right-hand side of the last expression is decreasing as a function of \( |u| \), and

\[
\frac{d}{dt} |u| \leq \frac{2c^2}{d} - d \frac{4c^2}{d^2} = -\frac{2c^2}{d},
\]

which is enough for the global attractor existence. \( \square \)

**Definition 7.** The semigroup \( \{S(t)\}_{t \geq 0} \) of mappings \( S(t) : X \to X \) is gradient if there exists a continuous function \( L : X \to \mathbb{R} \) such that
(i) $L(S(t)x) \leq L(x)$ for every $x \in X$ and $t \geq 0$.
(ii) if $L(S(t)x) = L(x)$ for every $t \geq 0$, then $S(t)x = x$ for every $t \geq 0$, i.e. $x$ is an equilibrium.

The above definition is valid on any metric space $X$, in our case it will be $\mathbb{C}_+$. We cite the result of [10].

**Theorem 8** ([10], Theorem 21). The semigroup of mappings $S(t) : \mathbb{C}_+ \to \mathbb{C}_+$ defined by the solutions of (1) is gradient. In consequence, the equilibria can be put in order $E = \{u_0, u_1, \ldots, u_K\}$ such that for every nonconstant trajectory $\gamma$ in the global attractor there exist numbers $i < j$ such that $\lim_{t \to -\infty} \|\gamma(t) - u_i\| = 0$ and $\lim_{t \to \infty} \|\gamma(t) - u_j\| = 0$.

# 3. Equilibria and the local dynamics

While it is straightforward to find all the equilibria of (1) (it suffices to solve $2^n$ linear systems and determine the ones whose solutions are strictly positive, see also [19] for the efficient algorithm), finding the connections between them appears a harder task. Our aim is to give an algorithm that can be used to determine the gradient dynamics given in Theorem 8, i.e. to find exactly which equilibria are connected with each other and which are not. Before we pass to the study of the dynamics, we focus in this chapter of the local behavior in the neighbourhood of the equilibria. To this end we remind the theorems on the local properties of the system for hyperbolic and non-hyperbolic case, and we study the spectrum of the matrix of the linearization.

## 3.1. Local stable and unstable manifold theorems

We begin by reminding the local unstable manifold theorem in the setting which is not necessarily hyperbolic, cf. [18] Theorem 1, [9] Theorem 3.2.1.

**Theorem 9** (Unstable manifold theorem). Let $f : \mathbb{R}^n \to \mathbb{R}^n$ be a function of class $C^k$ ($k \geq 3$) such that $f(0) = 0$ and let $M = Df(0)$. Divide the spectrum of $M$ into three parts $\sigma_s, \sigma_c, \sigma_u$ such that

$$\text{Re} \lambda \begin{cases} > 0 & \text{for } \lambda \in \sigma_u, \\ = 0 & \text{for } \lambda \in \sigma_c, \\ < 0 & \text{for } \lambda \in \sigma_s. \end{cases}$$

Denote by $E_u, E_s, E_c$ the generalized eigenspaces associated with $\sigma_u, \sigma_s, \sigma_c$. There exists a neighbourhood $U$ of 0 in $E_u$ and a function $\Phi : U \to E_s + E_c$ of class $C^k$ with $\Phi(0) = 0$ and $D\Phi(0) = 0$ such that

$$\text{graph}(\Phi) = \{x + \Phi(x) : x \in U\} = W^{u}_{loc}(0),$$
i.e. the graph of $\Phi$ is a local unstable manifold of 0, that is, for the flow $\{S(t)\}_{t \in \mathbb{R}}$ given by the solutions of $u' = f(u)$ the set $\text{graph}(\Phi)$ is negatively invariant and $\lim_{t \to -\infty} S(t)u = 0$ for every $u \in \text{graph}(\Phi)$.

In the hyperbolic case we have the following result

**Theorem 10** (Hadamard–Perron theorem). Let $f : \mathbb{R}^n \to \mathbb{R}^n$ be a function of class $C^k$ ($k \geq 3$) such that $f(0) = 0$ and let $M = Df(0)$. Assume that $\sigma(M) \cap \{\text{Re } z = 0\} = \emptyset$, that is, $M$ is hyperbolic. Divide the spectrum of $M$ into two parts $\sigma_s, \sigma_u$ such that $\text{Re } \lambda \begin{cases} > 0 & \text{for } \lambda \in \sigma_u, \\ < 0 & \text{for } \lambda \in \sigma_s. \end{cases}$

Denote by $E_u, E_s$ the generalized eigenspaces associated with $\sigma_u, \sigma_s$. There exist neighbourhoods $U, V$ of 0 in $E_u, E_s$ and functions $\Phi : U \to E_s$ and $\Psi : V \to E_u$ of class $C^k$ with $\Phi(0) = 0$, $\Psi(0) = 0$, $D\Phi(0) = 0$ and $D\Psi(0) = 0$ such that

$$\text{graph}(\Phi) = \{x + \Phi(x) : x \in U\} = W^u_{\text{loc}}(0),$$

and

$$\text{graph}(\Psi) = \{y + \Psi(y) : y \in V\} = W^s_{\text{loc}}(0).$$

i.e. the graph of $\Phi$ is a local unstable manifold of 0, i.e., it is is negatively invariant and the solutions on it converge to zero as $t \to -\infty$ and the graph of $\Psi$ is the local stable manifold of 0, i.e., it is positively invariant and the solutions on it converge to 0 as $t \to \infty$.

Note that while in the nonhyperbolic case $W^u_{\text{loc}}(0)$ does not have to contain all points from the neighborhood of 0 which backward converge to this equilibrium, in the hyperbolic case $W^u_{\text{loc}}(0)$ and $W^s_{\text{loc}}(0)$ necessarily contain all points from the neighborhood of the equilibrium which, respectively, converge to it in the backward and forward sense.

### 3.2. Linearization and its properties.

We construct the linearized system in the neighborhood of the equilibrium $u^*$ of (I). Let $u^*$ be an equilibrium and denote $v = u - u^*$. Then (I) is equivalent to the system

$$v'_i = (v_i + u^*_i) \left( b_i + \sum_{j=1}^{n} a_{ij}(v_j + u^*_j) \right)$$

$$= v_i \left( b_i + 2a_{ii}u^*_i + \sum_{j=1,j\neq i}^{n} a_{ij}u^*_j \right) + \sum_{j=1,j\neq i}^{n} v_j a_{ij}u^*_i + v_i \sum_{j=1}^{n} a_{ij}v_j$$

$$= \sum_{j=1}^{n} \frac{\partial F_i(u^*)}{\partial x_j} v_j + G_i(v),$$

where $F_i(u^*) = \sum_{j=1,j\neq i}^{n} a_{ij}u^*_j + v_i \sum_{j=1}^{n} a_{ij}v_j$, and $G_i(v)$ represents the nonlinearity.
where $G_i(v) = \sum_{j=1}^{n} a_{ij} v_j v_i$ is the quadratic remainder term. In shorthand we may write

$$v' = DF(u^*)v + G(v).$$

Assume that $u^*$ is an equilibrium in which the variables are sorted in such a way that $u_i^* \neq 0$ for $i = 1, \ldots, k$ and $u_i^* = 0$ for $i = k + 1, \ldots, n$. Then for $i = 1, \ldots, k$ we have

$$v_i' = v_i \left( b_i + 2a_{ii}u_i^* + \sum_{j=1, j \neq i}^{k} a_{ij}u_j^* \right) + \sum_{j=1, j \neq i}^{k} v_j a_{ij}u_i^* + \sum_{j=k+1}^{n} v_j a_{ij}u_i^* + G_i(v).$$

Since $b_i + \sum_{j=1}^{k} a_{ij}u_j^* = 0$ this can be rewritten in a simpler form

$$v_i' = \sum_{j=1}^{k} v_j a_{ij}u_i^* + \sum_{j=k+1}^{n} v_j a_{ij}u_i^* + G_i(v).$$

For $i = k + 1, \ldots, n$ the equation takes the form

$$u_i' = v_i \left( b_i + \sum_{j=1}^{k} a_{ij}u_j^* \right) + G_i(v),$$

Thus, the linearized system has the following form for $i = 1, \ldots, k$

$$w_i' = \sum_{j=1}^{k} w_j a_{ij}u_i^* + \sum_{j=k+1}^{n} w_j a_{ij}u_i^*,$$

and for $i = k + 1, \ldots, n$

$$w_i' = w_i \left( b_i + \sum_{j=1}^{k} a_{ij}u_j^* \right).$$

We can rewrite this as

$$w' = Bw = \begin{pmatrix} B_{11}^{11} & B_{11}^{12} \\ 0 & B_{22}^{22} \end{pmatrix} w,$$

where the matrix $B_{22}^{22}$ is diagonal and $B_{ii}^{22} = b_i + \sum_{j=1}^{k} a_{ij}u_j^*$, while $B_{ij}^{11} = a_{ij}u_i^*$.

We will call the subsets $J \subset \{1, \ldots, n\}$ corresponding to the admissible equilibria, by admissible communities, according to the next definition.

**Definition 11.** The set (community) $J \subset \{1, \ldots, n\}$ is admissible if there exists the nonnegative equilibrium $u^* = (u_1^*, \ldots, u_n^*)$ of (1) with $u_i^* > 0$ if and only if $i \in I$. The family of all admissible communities will be denoted by $E \subset 2^{\{1, \ldots, n\}}$. The corresponding set of equilibria is denoted by $E = \{u_0, \ldots, u_K\}$.

The following lemmas summarize the properties of the tangent matrix at the equilibria of the system. Note that similar observations were made in different context in [19].
Lemma 12. Assume that the matrix $A$ of the system (1) is Volterra-Lyapunov stable. Consider the admissible community $I$ and the corresponding equilibrium $u^*$. The system linearized around $u^*$ has the form (2), where $B_{11}^{ij} = a_{ij}u^*_i$. The spectrum of the matrix $B_{11}^{11}$ is contained in the open half-plane with the negative real part, i.e. $\sigma(B_{11}^{11}) \subset \{ z \in \mathbb{C} : \text{Re} \, z < 0 \}$.

Proof. The matrix $\{a_{ij}\}_{i,j \in I}$ as a principal submatrix of $A$ is Volterra-Lyapunov stable, cf. Lemma 46. Hence it is also $D$-stable by Fact 41. This means that the product $\text{diag}((u_i)_{i \in I})(a_{ij})_{i,j \in I}$ is stable. This product is exactly $B_{11}^{11}$. \qed

We are in position to formulate a result of the properties of the linearized system (2).

Lemma 13. Spectrum of the matrix $B$, denoted by $\sigma(B)$ is given by $\sigma(B) = \sigma(B_{11}^{11}) \cup \{ \lambda_{i}^{22} \}_{i = k+1}^{n}$, where $\sigma(B_{11}^{11}) \subset \{ \text{Re} \, \lambda < 0 \}$. So if for some $\lambda \in \sigma(B)$ we have $\text{Re} \, \lambda \geq 0$ then $\lambda$ is real and $\lambda = \lambda_{i}^{22}$ for some $i \in k + 1, \ldots, n$. The associated eigenvector is given by $x = (x_1, \ldots, x_k, 0, \ldots, 0, 1, 0, \ldots, 0)$, where $1$ is on the position $i$ and $(x_j)_{j=1}^{k}$ is some vector.

Proof. The assertion that $\sigma(B_{11}^{11}) \subset \{ \text{Re} \, \lambda < 0 \}$ follows from Lemma 12.

Now we prove that $x = (x_1, \ldots, x_k, 0, \ldots, 0, 1, 0, \ldots, 0)$ is the eigenvector associated with eigenvalue $\lambda_{i}^{22}$. We need to have

$$
B_{11}^{11} \begin{pmatrix} x_1 \\ \vdots \\ x_k \end{pmatrix} + B_{12}^{12} \begin{pmatrix} 0 \\ \vdots \\ 0 \end{pmatrix} = B_{ii}^{22} \begin{pmatrix} x_1 \\ \vdots \\ x_k \end{pmatrix}.
$$

Such $(x_1, \ldots, x_k)$ can be found because the matrix $B_{11}^{11} - B_{ii}^{22}I$ is invertible as $B_{ii}^{22} \geq 0$ and it cannot be the eigenvalue of the matrix $B_{11}^{11}$ as all its eigenvalues have negative real part. Moreover

$$
0 \begin{pmatrix} x_1 \\ \vdots \\ x_k \end{pmatrix} + B^{22} \begin{pmatrix} 0 \\ \vdots \\ 0 \end{pmatrix} = B_{ii}^{22} \begin{pmatrix} 0 \\ \vdots \\ 0 \end{pmatrix},
$$

holds trivially. \qed

4. Invasion graphs are information structures

The main aim of this section is to propose the algorithm to determine the network of connections between equilibria, i.e. the partial order in $E = \{u_0, u_1, \ldots, u_K\}$ such that $u_i <$
If and only if there exists a trajectory $\gamma(t)$ which connects $u_i$ with $u_j$, i.e. $\lim_{t \to -\infty} \|\gamma(t) - u_i\| = 0$ and $\lim_{t \to \infty} \|\gamma(t) - u_j\| = 0$. Such trajectories are called the heteroclinic connections. The graph such that the equilibria of the system correspond to its nodes, and the edges correspond to the heteroclinic connections, describes the dynamics of the system, i.e. the structure of the global attractor. We show in this section that, in the Volterra–Lyapunov stable case, if we assume that all equilibria of the system are hyperbolic, then this graph is exactly the same as the Invasion Graph (IG) as defined by Hofbauer and Schreiber in [15].

4.1. Invasion rates and invasion graphs. Let $I \in \mathcal{E}$, i.e. $I$ is a admissible community of (1). For every species $i \in \{1, \ldots, n\}$, following Chesson [6] we define the invasion rates $r_i(I)$ (see [3] for the recent overview of Chesson coexistence theory in which the key role is played by the invasion rates).

**Definition 14.** Let $I \in \mathcal{E}$ and let $u^*$ be the related equilibrium such that $u^*_i > 0$ for $i \in I$ and $u^*_i = 0$ for $i \notin I$. Then the invasion rate of the species $i$ of the community $I$ is defined as

$$r_i(I) = b_i + \sum_{j \in I} a_{ij} u^*_j.$$

We first observe that the invasion rates are always zero for $i \in I$, this is a counterpart of Lemma 1 from [15].

**Remark 15.** If $i \in I$ then $r_i(I) = 0$. This follows from the fact that $u^*$ is an equilibrium, whence $A(I)u^* = -b(I)$.

The remaining invasion rates are the eigenvalues of the system linearization at the equilibrium $u^*$.

**Remark 16.** If $i \notin I$ then the entries $B^2_{ii}$ of the linearization matrix $B$ given in Lemma [15] by $B^2_{ii} = b_i + \sum_{j \in I} a_{ij} u^*_j$, are the invasion rates $r_i(I)$.

Following [15] we present the construction of the Invasion Graph (IG) together with the result that all heteroclinic connections between the equilibria correspond to some edges in this graph. The construction and results in [15] are very general, they do not need the minimal isolated invariant sets to be equilibria only, the case of more general structures is covered too (such as periodic solutions which can exist in the class of Lotka–Volterra systems [22], in such situation the invasion rate is defined for the minimal isolated invariant set, not necessarily the equilibrium). We restrict the presentation in this section to the simpler situation where the minimal isolated invariant sets (and thus the supports of the ergodic invariant measures) are only the equilibria of the system, and the global attractor
is gradient. While this is guaranteed to be true in the case of Lyapunov–Volterra stable matrix, cf. Theorem 8, this assumption is hard to verify in the case of general $A$.

We remind the algorithm of the construction of the IG, presented in [15].

**Algorithm 17.** Invasion graph is constructed in two steps, the first step defines its vertexes, and the second one its edges.

**(Step 1)** The set of vertexes of the graph is $E$, i.e. the vertexes are given by all admissible communities.

**(Step 2)** The graph contains the edge from $I$ to $J$ (we denote it by $I \rightarrow J$) if $I \neq J$, $r_i(I) > 0$ for every $i \in J \setminus I$, and $r_i(J) < 0$ for every $i \in I \setminus J$.

The key property of IG obtained in [15] is contained in the next result, cf. [15, Lemma 2].

**Lemma 18.** Let $A, b$ be such that the system (1) is gradient-like and let $r_i(I) \neq 0$ for every $I \in \mathcal{E}$ and for every $i \notin I$. Assume that $\gamma(t)$ is the trajectory of (1) with $\lim_{t \to -\infty} \|\gamma(t) - u_i^*\| = 0$ and $\lim_{t \to \infty} \|\gamma(t) - u_2^*\| = 0$. Then in the invasion graph there exists the edge from $J(u_1^*)$ to $J(u_2^*)$.

Finally, following [15] we define the Invasion Scheme as the table of the signs of the invasion rates, i.e.

$$\mathbb{I}(i, I) = \text{sgn} r_i(I) \quad \text{for} \quad I \subset \mathcal{E}, i \in \{1, \ldots, n\}.$$ 

If $i \in I$ then always $\mathbb{I}(i, I) = 0$. If for some $i \notin I$ we have $\mathbb{I}(i, I) = 0$ then the equilibrium associated with $I$ is nonhyperbolic. Otherwise always $\mathbb{I}(i, I) = 1$ or $\mathbb{I}(i, I) = -1$. Knowledge of this matrix is sufficient to construct the IG.

### 4.2. Finding the connections between equilibria.

Lemma 18 guarantees that existence of the edge in IG is the necessary condition for the existence of the connection between the equilibria. This section is devoted to the proof that it is also sufficient for the Volterra–Lyapunov stable matrix $A$.

**Theorem 19.** Let $A$ be a Volterra–Lyapunov stable matrix. Let $u^*$ be a admissible equilibrium which corresponds to the community $I \in \mathcal{E}$. If the set $K \supset I$ is such that for every $j \in K \setminus I$ we have $r_j(I) > 0$ then there exists a trajectory $\gamma$ of (1) such that $\lim_{t \to -\infty} \gamma(t) = u^*$ and $\lim_{t \to \infty} \gamma(t)$ is a GASS for the community $K$.

**Proof.** It is enough to show that the unstable manifold of the point $u^*$ in the nonnegative cone intersects the interior of the cone associated with $K$, denoted by $C^+_K$. Then the result follows by Theorem 3. For the equilibrium $u^*$, by Lemma 13 the local unstable space $E^u$ contains the vector $(x_1, \ldots, x_k, 1_{i \in K \setminus I})$, where the characteristic vector $1_{i \in K \setminus I}$ has coordinates.
equal to 1 if \( i \in K \setminus I \) and 0 otherwise. Now by Theorem 9, the local unstable manifold of \( u^* \) contains points
\[
\bar{u}^\varepsilon = u^* + \varepsilon(y_1, \ldots, y_k, 1_{i \in K \setminus I}) + \Phi(\varepsilon(y_1, \ldots, y_k, 1_{i \in K \setminus I}))
\]
where \((y_1, \ldots, y_k)\) are given vectors independent of \( \varepsilon \). By the Taylor theorem for \( j \in K \setminus I \)
\[
u_j^\varepsilon = \varepsilon + C\varepsilon^2,
\]
where \( C \) is a constant depending on \((y_1, \ldots, y_k)\) and the maximum norm of the hessian of \( \Phi \)
on the set \( U \). Hence for sufficiently small \( \varepsilon > 0 \) the local unstable manifold of \( u^* \) contains points with all entries in \( K \setminus I \) positive. As \( u^* \) is positive on coordinates associated with \( I \), the proof is complete. \( \square \)

The above result justifies the following algorithm (see Appendix C for the definition of Linear Complementary Problem), in which we call the constructed graph the Information Structure (IS).

**Algorithm 20** (Construction of IS). In Step 1 for each subcommunity \( J \) of \( \{1, \ldots, n\} \) (including the empty set and the full subcommunity) we construct its GASS. Any trajectory with the initial data having positive entries on the coordinates in \( J \) and zeros on coordinates outside \( J \) will converge to this GASS.

(Step 1) For all \( 2^n \) subcommunities in \( \{1, \ldots, n\} \) find their GASSes according to the following algorithm which for each community \( J \) returns its GASS \( u^* \) together with the set of its nonzero coordinates.

\( \text{FindGASS}(J) \):

1. Assume that \( J = \{i_1, \ldots, i_N\} \). If the procedure \( \text{FindGASS}(J) \) has been run before, then return the previously found GASS \( u^* \) and set of nonzero coordinates assigned to the set \( J \).
2. If \( \#J = 0 \) return \( u^* = 0 \) and the empty set of nonzero coordinates. Otherwise solve the linear complementarity problem \( LCP(-A(J), -b(J)) \) in order to find the GASS for the community \( J \). \( LCP \) returns \( u^* \) and the set of nonzero coordinates. For every \( i \in J \) run \( \text{FindGASS}(J \setminus \{i\}) \).

The algorithm is started by \( \text{FindGASS}(\{1, \ldots, n\}) \).

Note that in Step 1 we not only constructed GASSes for all communities in \( \{1, \ldots, n\} \), but also we have found the set \( \mathcal{E} \) of all admissible communities.

(Step 2) For every \( I \in \mathcal{E} \) denote \( u^* \) the associated equilibrium. Draw outgoing edges from \( I \) according to the algorithm below.
(1) For every \( i \in \{1, \ldots, n\} \setminus I \) calculate the invasion rate

\[
r_i(I) = b_i + \sum_{j \in I} a_{ij} u^*_j.
\]

Take \( J \) as the set of those \( i \in \{1, \ldots, n\} \setminus I \) for which \( r_i(u^*) > 0 \), i.e. those species which can successfully invade the equilibrium community \( I \).

(2) For every set \( K \) such that \( I \subset K \subset I \cup J \) draw an edge from \( I \) to \( \text{GASS}(K) \).

By Theorem 19 we have the following Corollary

**Corollary 21.** Let \( A \) be Volterra–Lyapunov stable. If the above algorithm produces the edge from the equilibrium \( u^*_1 \) to the equilibrium \( u^*_2 \) then there exists the trajectory \( \gamma \) of (1) such that \( \lim_{t \to -\infty} \gamma(t) = u^*_1 \) and \( \lim_{t \to \infty} \gamma(t) = u^*_2 \).

By above corollary we can be sure that if the above algorithm produces the edge then this edge represents the actual connection between the equilibria of the system. It is hence kind of “inner approximation”. On the other hand Lemma 18 implies that IG of [15] is the “outer approximation” because every existing connection is represented in IG. So if we are able to prove that every connection present in IG is also constructed by the above algorithm we have the following chain of graphs, where each preceding graph is the subgraph of the next one,

(IS of Algorithm \( 20 \)) \( \subset \) (Global Attractor) \( \subset \) (Invasion Graph) \( \subset \) (IS of Algorithm \( 20 \)).

and all three structures must coincide. The inclusion (1) follows from Corollary 21 and needs \( A \) to be Volterra–Lyapunov stable. The inclusion (2) follows from Lemma 18 and does not necessarily need the Volterra–Lyapunov stability. We continue by proving (3).

**Theorem 22.** Assume the \( A \) is Volterra–Lyapunov stable and that \( u^*_1, u^*_2 \) are the two admissible equilibria with the sets of corresponding nonzero coordinates given by \( I_1 \) and \( I_2 \). Assume that the connection \( u^*_1 \to u^*_2 \) exists in IG, that is for every \( j \in I_2 \setminus I_1 \) we have \( r_j(I_1) > 0 \) and for every \( j \in I_1 \setminus I_2 \) we have \( r_j(I_2) < 0 \). Then the graph constructed by Algorithm 20 contains the edge \( u^*_1 \to u^*_2 \).

**Proof.** Consider the system restricted to the variables in \( I_1 \cup I_2 \), i.e. set \( u_i = 0 \) for \( i \notin I_1 \cup I_2 \). Clearly Algorithm 20 produces the edge from \( u^*_1 \) to the node \( u^* \) which is the GASS for the community \( I_1 \cup I_2 \). We need to prove that this GASS is \( u^*_2 \). Suppose that \( u^*_2 \) is not the GASS, i.e. \( u^* \neq u^*_2 \). Then in the arbitrary neighbourhood of \( u^*_2 \) there exist points (in the interior of the cone \( C^+_{I_1 \cup I_2} \), strictly positive in the restricted variables) which are attracted to \( u^* \). Since the matrix \( B^{11} \) at the point \( u^*_2 \) is stable by Lemma 12 and remaining eigenvalues (that of
are given by \( r_j(I_2) < 0 \) for \( j \in I_1 \setminus I_2 \) it follows that the spectrum of the Jacobian at \( u_2^* \) satisfies
\[
\sigma(B) \subset \{ \lambda \in \mathbb{C} : \text{Re}\lambda < 0 \}.
\]
In particular \( B \) is hyperbolic and local stable manifold of \( u_2^* \) is the whole neighborhood of this point. But, since there exists a point in any neighborhood of \( u_2^* \) attracted to \( u^* \neq u_2^* \), the contradiction follows.

**Corollary 23.** Assume that \( A \) is Volterra–Lyapunov stable then the IG is a subgraph of the global attractor. If additionally all invasion rates \( r_i(J) \) are nonzero for \( i \notin J \) for all admissible communities \( J \in \mathcal{E} \) then both graphs coincide. Since Algorithm 17 does not need to find GASSes and solve LCP, the construction of IG is the way to find the global attractor structure with the lower computational effort.

**Remark 24.** We can summarize the obtained results as follows

\[ A \text{ is Volterra–Lyapunov stable } \Rightarrow \]

\[ (\text{IS of Algorithm 20})^{(1)}(\text{Global Attractor}). \]

\[ r_i(J) \neq 0 \text{ for } i \notin J \text{ and the system is gradient-like } \Rightarrow \]

\[ (\text{Global Attractor})^{(2)}(\text{Invasion Graph}). \]

\[ A \text{ is Volterra–Lyapunov stable } \Rightarrow \]

\[ (\text{Invasion Graph})^{(3)}(\text{IS of Algorithm 20}). \]

**Remark 25.** In the proof of Theorem 22 we have also shown that if \( A \) is Volterra–Lyapunov stable then the fact that \( \sigma(DF(u^*)) \) is hyperbolic (its spectrum does not intersect the imaginary axis) is equivalent to the statement that \( r_i(J) \neq 0 \) for every \( i \notin J \). This fact follows from Lemma 12. Note that Theorem 19 remains valid even for nonhyperbolic case due to the use of the nonhyperbolic version of the unstable manifold theorem, cf. Theorem 9 and we do not have to assume the extra hyperbolicity in Theorem 22. Hence in the nonhyperbolic case the inclusions (1) and (3) remain valid, but not necessarily the inclusion (2). So without the hyperbolicity assumption, the IG is included in the global attractor, but not necessarily the otherwise.

## 5. Structural stability of invasion graphs

### 5.1. Local structural stability
If the system is Morse–Smale, then it is also structurally stable, i.e. \( C^1 \) small perturbation of its vector field produces a system whose global attractor
has the same structure (see \cite{5, Theorem 2}). In this section we show that, although the system governed by (1) is not necessarily Morse–Smale, cf. Example \cite{33}, if all equilibria are hyperbolic, the small perturbation of $A$ and $b$ produces the system with the same global attractor structure. In the next result $B(A, \varepsilon)$ denotes the euclidean ball in $\mathbb{R}^{n^2}$ and $B(b, \varepsilon)$ in the euclidean ball in $\mathbb{R}^n$. Moreover denote by $\mathcal{E}(A, b)$ the set of admissible communities for the problem with matrix $A$ and vector $b$. For $I \in \mathcal{E}(A, b)$ and $i \not\in I$ we will use the notation $r_i^{A,b}(I)$ to denote the invasion rate corresponding to $A, b$.

**Theorem 26.** Let $\overline{A}$ be a Volterra–Lyapunov stable matrix and let $\overline{b} \in \mathbb{R}^n$ be such that for all admissible communities $I \in \mathcal{E}(\overline{A}, \overline{b})$ the corresponding equilibria are hyperbolic. Then there exists $\varepsilon > 0$ such that for all matrices $A \in B(\overline{A}, \varepsilon)$ and all vectors $b \in B(\overline{b}, \varepsilon)$ we have $\mathcal{E}(A, b) = \mathcal{E}(\overline{A}, \overline{b})$. Moreover for every $I \in \mathcal{E}(\overline{A}, \overline{b})$ and every $i \not\in I$ we have

\[ r_i^{\overline{A}, \overline{b}}(I) > 0 \Rightarrow r_i^{A,b}(I) > 0, \]
\[ r_i^{\overline{A}, \overline{b}}(I) < 0 \Rightarrow r_i^{A,b}(I) < 0. \]

Hence the edges in both Invasion Graphs for $\overline{A}, \overline{b}$ and $A, b$ are the same. This implies that the structures of the global attractors for the problems with $\overline{A}, \overline{b}$ and $A, b$ coincide and the problem for $\overline{A}, \overline{b}$ is structurally stable.

**Proof.** The fact that all equilibria are hyperbolic means that $r_i(I) \neq 0$ for every $i \not\in I$ and every $I \in \mathcal{E}(\overline{A}, \overline{b})$. Note that since the eigenvalues depend continuously on the matrix, the set of Volterra–Lyapunov stable matrices is open and hence we can choose $\varepsilon$ such that every $A \in B(\overline{A}, \varepsilon)$ is Volterra–Lyapunov stable. Now the fact that $I \in \mathcal{E}(\overline{A}, \overline{b})$ means that $\overline{A}(I)u^* = -\overline{b}(I)$ has a positive solution $u^*$. From that fact that the mapping $(A, b) \mapsto u^*$ which assigns to a nonsingular $k \times k$ matrix $A$ and vector $b \in \mathbb{R}^k$ the solution $u^*$ of the system $Au^* = -b$ is continuous we deduce that we can find $\varepsilon > 0$ such that all admissible communities remain admissible.

We prove that a nonadmissible community cannot produce an admissible one upon sufficiently small perturbation. Assume that $I \subset \{1, \ldots, n\}$ is not admissible. If at least one of the coordinates of the solution of the system $\overline{A}(I)u^* = -\overline{b}(I)$ is negative, then this negativity is preserved upon small perturbation of $(\overline{A}, \overline{b})$. If all are nonnegative, but at least one is zero, say $u_j^* = 0$, then

\[ \sum_{i \in I, i \neq j} a_{ki}u_i^* + b_k = 0 \quad \text{for every} \quad k \in I. \]

In particular

\[ \sum_{i \in I \setminus \{j\}} a_{ji}u_i^* + b_j = 0. \]
Denote by $I_0 \subset I$ the (possibly empty) set of coordinates for which entries of $u^*$ are positive. Then $I_0$ corresponds to the admissible community. The last equality means that $r^i_{j,I}(I_0) = 0$ which contradicts the assumption of hyperbolicity. We have proved that $\mathcal{E}(A, b) = \mathcal{E}(\overline{A}, \overline{b})$.

The invasion rates $r_i(I)$ are the continuous functions of the vector $b$, matrix $A$ and the equilibrium $u^*$ related to the admissible community $I$. This means that if $r_i(I)$ is nonzero for the system governed by $\overline{A}, \overline{b}$, it remains nonzero, and does not change sign, in a small neighbourhood of $\overline{A}, \overline{b}$, which completes the proof.

\square

5.2. The regions of structural stability. In this section we fix the matrix $A$ and we study the properties of the sets of vectors $b \in \mathbb{R}^n$ for which the Invasion Graphs remain unchanged.

**Theorem 27.** Let $A$ be a Volterra–Lyapunov stable matrix and let $\overline{b} \in \mathbb{R}^n$ be such that for all admissible communities $I \in \mathcal{E}(A, \overline{b})$ the corresponding equilibria are hyperbolic. Then there exists the unique maximal open neighbourhood $\mathcal{N}$ of $\overline{b}$ in $\mathbb{R}^n$ such that for every $b \in \mathcal{N}$ we have $\mathcal{E}(A, b) = \mathcal{E}(A, \overline{b})$, all admissible equilibria corresponding to $A, b$ are hyperbolic, and the Invasion Graphs coincide.

**Proof.** From Theorem 26 we know that there exists an open neighborhood of $\overline{b}$ such that the properties required by the theorem are satisfied. Let us denote by $\mathfrak{N}(\overline{b})$ the family of all such neighbourhoods. It is nonempty. We introduce a partial order on $\mathfrak{N}(\overline{b})$ by inclusion and consider a chain in $\mathfrak{N}(\overline{b})$. The sum of all elements of the chain belongs to $\mathfrak{N}(\overline{b})$. Hence, by the Kuratowski–Zorn lemma there exists a maximal neighbourhood in $\mathfrak{N}(\overline{b})$. It is unique, because otherwise the sum of two distinct maximal elements of $\mathfrak{N}(\overline{b})$ would also belong to $\mathfrak{N}(\overline{b})$ which contradicts the maximality.

\square

We continue by proving the lemma on convexity

**Lemma 28.** Let $A$ be Volterra–Lyapunov stable. Suppose that $b_1, b_2 \in \mathbb{R}^n$ are such that

- $\mathcal{E}(A, b_1) = \mathcal{E}(A, b_2) = \mathcal{E}$,
- for every $I \in \mathcal{E}$ and for every $i \notin I$ we have $r^i_{1,b_1}(I) \neq 0$, $r^i_{1,b_2}(I) \neq 0$, and $r^i_{1,b_1}(I) > 0 \iff r^i_{1,b_2}(I) > 0$.

Then for every $\lambda \in [0, 1]$, denoting $b_\lambda = \lambda b_1 + (1 - \lambda) b_2$, we have

- $\mathcal{E}(A, b_\lambda) = \mathcal{E}$,
- for every $I \in \mathcal{E}$ and for every $i \notin I$ we have $r^i_{1,b_\lambda}(I) \neq 0$, and $r^i_{1,b_\lambda}(I) > 0 \iff r^i_{1,b_\lambda}(I) > 0$.

**Proof.** Assume that $I \in \mathcal{E}$. Then $A(I)u_1^* = -b_1(I)$ and $A(I)u_2^* = -b_2(I)$. This means that $A(I)(\lambda u_1^* + (1 - \lambda) u_2^*) = -b_\lambda(I)$ and $I$ is admissible for $b_\lambda$. On the other hand assume that $I$ is admissible for $b_\lambda$, i.e. $I \in \mathcal{E}(A, b_\lambda)$ but $I \notin \mathcal{E}$. Restrict the system to those unknowns which correspond to the indexes of $I$. The fact that $I$ is admissible for the problem with $b_\lambda$ means
that this system has the strictly positive equilibrium, i.e. the solution \( v \) of \( A(I)v = -b_\lambda(I) \) has all coordinates strictly positive, and by Theorem \( \text{[3]} \), it has to be the GASS of the system with \( A(I), b_\lambda(I) \), and the solution of \( LCP(-A(I), -b_\lambda(I)) \). On the other hand, as \( I \not\in \mathcal{E} \), the solutions \( u^*_1 \) and \( u^*_2 \) of the problems \( LCP(-A(I), -b_1(I)) \) and \( LCP(-A(I), -b_2(I)) \), cannot have all coordinates strictly positive, and, because the invasion schemes \( IS \) for \( b_1(I) \) and \( b_2(I) \) coincide, the indexes of zero and nonzero coordinates in both of must be the same. Then \( \lambda u^*_1 + (1 - \lambda)u^*_2 \) must solve \( LCP(-A(I), -b_\lambda(I)) \) and hence it must be a GASS for the problem with \( b_\lambda(I) \), a contradiction with the fact that this GASS has all coordinates strictly positive.

A straightforward calculation shows that for for \( I \in \mathcal{E} \)
\[
r_i^{A,b_\lambda}(I) = \lambda r_i^{A,b_1}(I) + (1 - \lambda)r_i^{A,b_2}(I),
\]
which is sufficient to complete the proof of the Lemma.

\( \square \)

**Remark 29.** Note that, by Lemma \( \text{[13]} \) the assumption that all invasion rates \( r_i(I) \) are nonzero for \( i \not\in I \) is equivalent to saying that the admissible equilibrium corresponding to \( I \) is hyperbolic.

The next theorem states that the maximal neighbourhoods of Theorem \( \text{[27]} \) are convex cones and they group all points with a given invasion scheme \( IS \), i.e. the given configuration of equilibria and signs of invasion rates.

**Theorem 30.** The maximal neighbourhood \( \mathcal{N} \) of \( \overline{b} \) given in Theorem \( \text{[27]} \) is an open and convex cone. Moreover, if for some point \( b \in \mathbb{R}^n \) with all admissible equilibria being hyperbolic the invasion schemes for \( A, b \) and \( A, \overline{b} \) are the same, then \( b \in \mathcal{N} \).

**Proof.** We first prove the second assertion. Take \( b \in \mathbb{R}^n \) satisfying the assumptions of the theorem. By Lemma \( \text{[28]} \) the same assumptions are satisfied by every \( b_\lambda \in \{ \lambda \overline{b} + (1 - \lambda)b : \lambda \in [0, 1] \} \). By Theorem \( \text{[26]} \) for each \( \lambda \in [0, 1] \) there exists an open neighborhood of \( b_\lambda \) on which the same assumptions also hold. The sum of these neighborhoods is an open neighborhood of \( \overline{b} \) which must be contained in \( \mathcal{N} \) and contains \( b \).

Now, convexity of \( \mathcal{N} \) follows from Lemma \( \text{[28]} \). To prove that \( \mathcal{N} \) is a cone it is sufficient to see that \( A(I)(u^*) = -b(I) \Rightarrow A(I)(\alpha u^*) = -\alpha b(I) \) and \( r_i^{A,\alpha b}(I) = \alpha r_i^{A,b}(I) \). \( \square \)

As a consequence of the above results we can represent the space \( \mathbb{R}^n \) as a sum of finite number of disjoint open convex cones \( \mathcal{N}_k \), with each cone corresponding to a given structure of the Invasion Graph, or equivalently, to a given \( IS \). This \( IS \) is the same for every \( b \) in the cone. The points of nonhyperbolicity (such vectors \( b \) where at least one of the admissible
equilibria is nonhyperbolic) constitute the residual set $\mathcal{C}$.

$$\mathbb{R}^n = \sum_{k=1}^{K} \mathcal{N}_k \cup \mathcal{C}.$$ 

By Remark 25 we can make the following statement:

$$b \in \mathcal{C} \iff \text{there exists } I \subset \{1, \ldots, n\} \text{ and } i \notin I,$$

such that $r_i(I) = 0$ and $u^*(I) > 0$, where $A(I)u^*(I) = -b(I)$.

In other words, denoting by $(A(I)^{-1})_{ij} = a_{ij}(I)^{-1}$ the entries of the inverse matrix to $A(I)$.

$$b \in \mathcal{C} \iff \text{there exists } I \subset \{1, \ldots, n\} \text{ and } i \notin I,$$

such that

$$A(I)^{-1}b(I) < 0 \text{ and } b_i + \sum_{k \in I} \sum_{j \in I} a_{ij}a_{jk}(I)^{-1}b_k = 0.$$ 

This means that

$$\mathcal{C} \subset \bigcup_{I \subset \{1, \ldots, n\}} \bigcup_{i \in \{1, \ldots, n\} \setminus I} \left\{ b \in \mathbb{R}^n : b_i + \sum_{k \in I} \sum_{j \in I} a_{ij}a_{jk}(I)^{-1}b_k = 0 \right\},$$

i.e. the set of points of nonhyperbolicity is a subset of the union of a finite number of $n-1$ dimensional hyperspaces in $\mathbb{R}^n$. In particular, $\mathcal{C}$ is "small" compared to the sets $\mathcal{N}_k$.

6. Appendix A. The dynamical system generated by (1) is not Morse–Smale.

The purpose of this short section is to show that the Lotka–Volterra system (1) is not necessarily Morse–Smale. Hence, while the structural stability results are know to hold for Morse-Smale systems, cf., for example, [5], our Theorem 26 is a structural stability result beyond this class. We begin from a definition of a Morse–Smale system. We do not recall all needed concepts: we refer to, for example, [5, Section 2.1] for details on all notions presented in this chapter. Note that related definition in [5] is more general: it allows for existence of periodic orbits. We present its simplified version only for gradient-like systems.

**Definition 31.** Let $X$ be a Banach space and let $S(t): X \to X$ for $t \geq 0$ be a $C^1$ reversible semigroup with a global attractor $\mathcal{A} \subset X$. We denote the set of equilibria of $\{S(t)\}_{t \geq 0}$ as $\mathcal{E}$, i.e. $\mathcal{E} = \{u \in X : S(t)u = u\}$ for every $t \geq 0$. The semigroup is Morse–Smale if

- The global attractor consists of the equilibria $\mathcal{E}$, and nonconstant trajectories $\gamma: \mathbb{R} \to X$ such that $\lim_{t \to -\infty} \gamma(t) = u^*_1$ and $\lim_{t \to \infty} \gamma(t) = u^*_2$ where $u^*_1, u^*_2 \in \mathcal{E}$.
- The set $\mathcal{E}$ is finite and all equilibria in $\mathcal{E}$ are hyperbolic.
- If $z \in \mathcal{A}$ is a nonequilibrium point such that $\lim_{t \to -\infty} S(t)z = u^*_1$ and $\lim_{t \to \infty} S(t)z = u^*_2$, then the unstable manifold of $u^*_1$ and stable manifold of $u^*_2$ intersect transversally.
at every point \( z \) of intersection, that is the sum of their tangent spaces at \( z \) span the whole space \( X \): 
\[ T_z(W^u(u_1^*)) + T_z(W^s(u_2^*)) = X. \]

We show that the Lotka–Volterra system with Volterra–Lyapunov stable matrix, and nonzero invasion rates \( r_i(I) \) for \( I \in E \) and \( i \not\in I \) although satisfies first two items of the above definition, does not have to satisfy the third item and hence can be non-Morse–Smale.

**Remark 32.** The semiflow defined by the solutions of \([1]\) is not defined on a Banach space, only in the nonnegative cone \( \mathbb{C}_+ \) of \( \mathbb{R}^n \). It can be, however, extended to whole \( \mathbb{R}^n \) and the next example, demonstrating that the system does not have to be Morse–Smale remains valid.

**Example 33.** Consider the system

\[
\begin{align*}
u_1' &= u_1(-u_1 + 0.08u_2 - 0.47u_3 + 0.43), \\
u_2' &= u_2(0.66u_1 - u_2 + 0.12u_3 - 0.05), \\
u_3' &= u_3(0.56u_1 - 0.28u_2 - u_3 + 0.28). \end{align*}
\]

Two of its admissible communities are \( \{3\} \) and \( \{1, 3\} \) with the corresponding equilibria \( u_1^* = (0, 0, 0.28) \) and \( u_2^* = (0.2362255, 0, 0.4122863) \). The matrix \( A \), as it is diagonally dominant, is Volterra–Lyapunov stable, and hence the Invasion Graph represents the global attractor. This graph is presented in Fig. 1 and it contains the connection \( \{3\} \to \{1, 3\} \). But both unstable manifold of \( \{3\} \) and stable manifold of \( \{1, 3\} \) are contained in the \( \{1, 3\} \) plane. In fact \( W^u(\{3\}) \subset W^s(\{1, 3\}) \) and hence the sum of their tangent spaces cannot span the whole space.

The lack of transversality can be also seen from analysis of the dimensions of \( W^u(\{3\}) \subset W^s(\{1, 3\}) \). Indeed the jacobians of the vector field at the equilibria \( u_1^* \) and \( u_2^* \) are given by

\[
DF(u_1^*) = \begin{pmatrix} 0.2984 & 0 & 0 \\ 0 & -0.0164 & 0 \\ 0.1568 & -0.0784 & -0.28 \end{pmatrix}, \quad DF(u_2^*) = \begin{pmatrix} -0.2362255 & 0.018898 & -0.11103 \\ 0 & 0.155383 & 0 \\ 0.132826 & -0.11544 & -0.4122863 \end{pmatrix}.
\]

Matrix \( DF(u_1^*) \) has one positive eigenvalue (equal to \( r_1(\{3\}) \)) and hence \( \dim W^u(\{3\}) = 1 \), invasion by the species \( \{2\} \) is not possible. On the other hand, matrix \( DF(u_2^*) \) has two negative eigenvalues and hence \( \dim W^s(\{1, 3\}) = 2 \). This means that \( \dim W^u(\{3\}) + \dim W^s(\{1, 3\}) = 3 \) and hence the intersection of these two manifolds cannot be transversal because if it was transversal then the sum of the dimensions would have to be equal at least 4, as the sum of the tangent spaces must be three-dimensional and at least one direction, tangent to the flow must be in both tangent spaces \( T_z(W^u(u_1^*)) \) and \( T_z(W^s(u_2^*)) \).
Figure 1. Invasion Graph for the example given by (3) for an ecological community with three species. The graph admits a maximum of 2^n equilibriums of the community as circles in the vertex of a cube. Hence, out a maximum of eight admissible equilibriums, this particular parameter configuration yields only six. The open circle is the empty community, u^* = (0, 0, 0), and the circle surrounded by a red ring is the GASS. The three different colours of the solutions denote the identity of each species, and the pie chart represent the relative abundance of each species in that particular stationary solution. In this case, the GASS represents a feasible community (all species are present), u^* = (0.2633778, 0.1695335, 0.377100).

Also note, that if we set u_2 = 0 and restrict the system to u_1, u_3 variables only, for the resulting two dimensional system

\begin{align*}
  u_1' &= u_1(-u_1 - 0.47u_3 + 0.43), \\
  u_3' &= u_3(0.56u_1 - u_3 + 0.28),
\end{align*}

(4)

the same intersection, which was non-transversal in 3D problem, becomes transversal, and the system is Morse–Smale.
7. Appendix B. Questions and open problems

7.1. Wider classes of stable matrices. The first question that we pose is related with the fact that in [27] the authors conjecture about stability of admissible equilibria for more general class of matrices $A$ - D-stable ones and stable ones. As our result on the structure of attractors relies on Theorem 3 which uses the logarithmic Lyapunov function valid only in the class of Volterra–Lyapunov stable matrices $A$, it remains open to see if it holds in those wider classes.

**Question 34.** Does the Invasion Graph (IG) correspond to the structure of the global attractor if the matrix $A$ is D-stable or merely stable in place of being Volterra–Lyapunov stable?

7.2. Symmetric case. If the matrix $A$ is symmetric then the following function, as proposed by MacArthur [20] is Lyapunov

$$V(u) = -\sum_{i=1}^{n} b_i u_i - \frac{1}{2} \sum_{i,j=1}^{n} a_{ij} u_i u_j.$$ 

Indeed, after calculations we get,

$$\frac{d(V(u(t)))}{dt} = V'(u)u'(t) = -\sum_{i=1}^{n} \left( b_i + \sum_{j=1}^{n} a_{ij} u_j \right) u_i, $$ \hspace{1cm} (5)

If we assume that $A$ together with all its principal minors is nonsingular, then the problem (1) has the finite number of admissible equilibria which can all be explicitly calculated and one can construct the IG with the vertexes being exactly the equilibria. Again, the open question appears.

**Question 35.** Does the IG correspond to the structure of a global attractor for a not necessarily Volterra–Lyapunov stable but symmetric matrix $A$ which, together with its all principal minors, is nonsingular?

While we do not know how to answer this question we show that for symmetric case the Lyapunov function $V$ drops along every edge in the IG. While this fact does not guarantee the existence of the connection between the equilibria, this shows that the criterium associated with the Lyapunov function $V$ cannot exclude the edges in IG.

**Lemma 36.** Let $A$ be symmetric such that together with all its principal minors it is nonsingular and let $u_1$ and $u_2$ be admissible equilibria of (1) which correspond to the communities $I_1, I_2$. If there exists an edge $I_1 \rightarrow I_2$ in IG then $V(u_1) > V(u_2)$. 
Proof. We may assume without loss of generality that $I_1 \cup I_2 = \mathbb{R}^n$. Otherwise we remove from the system the equations which correspond to the variables outside $I_1 \cup I_2$. We represent $\mathbb{R}^n = \mathbb{R}^{I_1 \setminus I_2} \cup \mathbb{R}^{I_1 \cap I_2} \cup \mathbb{R}^{I_2 \setminus I_1}$, and we denote the projections on three subspaces as $\Pi_1, \Pi_2, \Pi_3$. Then, the matrix $A$ of the system can be written as

$$A = \begin{pmatrix}
B & C & D \\
C^\top & E & F \\
D^\top & F^\top & G
\end{pmatrix}.$$

Now as $u_1$ is equilibrium related with $I_1$, hence $\Pi_3 u_1 = 0$, $B\Pi_1 u_1 + C\Pi_2 u_1 = -\Pi_1 b$, and $C^\top \Pi_1 u_1 + E\Pi_2 u_1 = -\Pi_2 b$. Moreover, as the invasion rates at $u_1$ must be positive, it follows that $D^\top \Pi_1 u_1 + F^\top \Pi_2 u_1 > -\Pi_3 b$. Similar analysis at $u_2$ yields $\Pi_1 u_2 = 0$, $E\Pi_2 u_2 + F\Pi_3 u_2 = -\Pi_2 b$, and $F^\top \Pi_2 u_2 + G\Pi_3 u_2 = -\Pi_3 b$. Finally as invasion rates at $u_2$ are negative we have $C\Pi_2 u_2 + D\Pi_3 u_2 < -\Pi_1 b$. It follows that

$$(\Pi_3 u_2)^\top D^\top \Pi_1 u_1 + (\Pi_3 u_2)^\top F^\top \Pi_2 u_1 > -(\Pi_3 u_2)^\top \Pi_3 b,$$

$$(\Pi_1 u_1)^\top C\Pi_2 u_2 + (\Pi_1 u_1)^\top D\Pi_3 u_2 < -(\Pi_1 u_1)^\top \Pi_1 b.$$

Combining the two above inequalities we deduce

$$(\Pi_1 u_1)^\top C\Pi_2 u_2 + (\Pi_1 u_1)^\top \Pi_1 b < (\Pi_3 u_2)^\top F^\top \Pi_2 u_1 + (\Pi_3 u_2)^\top \Pi_3 b.$$

But

$$(\Pi_2 u_2)^\top C^\top \Pi_1 u_1 + (\Pi_2 u_2)^\top E\Pi_2 u_1 = -(\Pi_2 u_2)^\top \Pi_2 b,$$

$$(\Pi_2 u_1)^\top E\Pi_2 u_2 + (\Pi_2 u_1)^\top F\Pi_3 u_2 = -(\Pi_2 u_1)^\top \Pi_3 b.$$

Hence

$$-(\Pi_2 u_2)^\top \Pi_2 b - (\Pi_2 u_2)^\top E\Pi_2 u_1 + (\Pi_1 u_1)^\top \Pi_1 b < -(\Pi_2 u_1)^\top \Pi_2 b - (\Pi_2 u_1)^\top E\Pi_2 u_2 + (\Pi_3 u_2)^\top \Pi_3 b.$$

As $E$ is symmetric this means that

$$-u_2^\top b < -u_1^\top b,$$

which exactly implies the assertion as at equilibrium $V(u) = -\frac{1}{2} u^\top b$. \hfill \Box

8. Appendix C. Classes of stable matrices and Linear Complementarity Problem

We remind the definitions and some known properties and examples of certain classes of stable matrices, which are used in the text.

**Definition 37.** A real matrix $A \in M^{n \times n}$ is stable if $\sigma(A) \subset \{ \lambda \in \mathbb{C} : \text{Re}\lambda < 0 \}$, where $\sigma(A)$ is the spectrum of $A$. 
Definition 38. A real matrix $A \in M^{n \times n}$ is D-stable if for every matrix $D = \text{diag}\{d_1, \ldots, d_n\}$ with $d_i > 0$ for every $i$ the matrix $DA$ is stable.

Fact 39. It is clear that every D-stable matrix is stable because it is enough to take $D = I$. To see that the opposite does not hold let us take the matrix

$$A = \begin{pmatrix} -2 & -3 \\ 1 & 1 \end{pmatrix}.$$  

It is stable as $\sigma(A) = \{-1/2 - i\sqrt{3}/2, -1/2 + i\sqrt{3}/2\}$. Take

$$D = \begin{pmatrix} 1 & 0 \\ 0 & 3 \end{pmatrix}$$

Then

$$DA = \begin{pmatrix} -2 & -3 \\ 3 & 3 \end{pmatrix}$$

and $\sigma(DA) = \{1/2 - i\sqrt{11}/2, 1/2 + i\sqrt{11}/2\}$. The example comes from [2].

Definition 40. A real matrix $A \in M^{n \times n}$ is Volterra-Lyapunov stable (VL-stable) if there exists a matrix $H = \text{diag}\{h_1, \ldots, h_n\}$ with $h_i > 0$ such that $HA + A^T H$ is negative definite (i.e. stable). In that case we write $M \in S_w$.

Fact 41. Following [29, Lemma 3.2.1] we prove that every VL-stable matrix is D-stable. Take diagonal $D > 0$. We will prove that $DA$ is VL-stable. Indeed, defining $M = HD^{-1}$ we have $HA + A^T H = HD^{-1} DA + A^T DD^{-1} H = (HD^{-1})(DA) + (DA)^T(HD^{-1}) = M(DA) + (DA)^T M$ which is negative definite and the proof of VL-stability of $DA$ is complete. Stability of $DA$ follows from Lyapunov theorem but we provide short proof. Assume that $(DA)x = \lambda x$. Then $\overline{\lambda} x^T = \overline{x}^T(\overline{DA})^T$. Hence $\overline{x}^T(MDA + (DA)^T M)x = \overline{x}^T M\lambda x + \overline{x}^T Mx = 2\text{Re}\lambda \overline{x}^T Mx = 2\text{Re}\lambda \sum_{i=1}^n m_i |x_i|^2 < 0$, which means that $\text{Re}\lambda < 0$, and the proof is complete. Using the criteria for 3*3 matrices coming from [7] it is possible to verify that the matrix

$$\begin{pmatrix} -1 & 0 & 50 \\ -1 & -1 & 0 \\ -1 & -1 & -1 \end{pmatrix}$$

is D-stable but not LV-stable. The example comes from [16].

Hence

$$\text{LV-stable } \subset \text{D-stable } \subset \text{stable}$$

But,
Fact 42. [4, Theorem 2] If $a_{ij} \geq 0$ for $i \neq j$ (for cooperative problems) then the three above classes coincide.

Definition 43. The matrix $A = (a_{ij})_{i,j=1}^{n} \in \mathbb{R}^{n \times n}$ is called row negative diagonal quasidominant if there exist positive numbers $(\pi_i)_{i=1}^{n}$ such that for every $i \in \{1, \ldots, n\}$ there holds

$$-\pi_i a_{ii} - \sum_{j=1, j\neq i}^{n} \pi_j |a_{ij}| > 0$$

Lemma 44 ([23], Theorem 3). If a matrix is row negative diagonal quasidominant then it is Volterra–Lyapunov stable.

The following result is clear

Lemma 45. If a matrix is row negative diagonal quasidominant then every of its principal submatrix is row negative diagonal quasidominant.

From the fact that any principal submatrix of a negative definite matrix must be negative definite it follows that

Lemma 46 ([7], Theorem 1 c). If a matrix is Volterra–Lyapunov stable than every its principal submatrix is Volterra–Lyapunov stable.

It is also clear that since the Volterra–Lyapunov stable matrix is stable it must be non-singular.

In the end we remind the definition of a linear complementarity problem. Given a matrix $B \in \mathbb{R}^{n^2}$ and a vector $c \in \mathbb{R}^{n}$ the linear complementarity problem $LCP(B, c)$ consists in finding a vector $x \in \mathbb{R}^{n}$ such that

$$Bx + c \geq 0,$$
$$x \geq 0,$$
$$x^\top (Bx + c) = 0.$$

If the matrix $A$ is Volterra-Lyapunov stable then the problem $LCP(-A, -b)$ has a unique solution for every $b \in \mathbb{R}^{n}$, cf. [29] Lemma 3.2.1 and Lemma 3.2.2. This solution is a GASS of (1), cf Theorem 3. Then the first inequality in the definition of $LCP$ corresponds to the fact that invasion rates for a GASS cannot be positive. The second one corresponds to the fact that the equilibrium is admissible, and the last one to the fact that GASS is an equilibrium.

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