Symbiosis, Stability, and Persistence

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Abstract

We investigate the stability of generalized Lotka-Volterra equations in several network topologies, such as trees and complete graphs. In particular, we have proved results on the stability of solutions where all species are nonzero, namely all species persist. Our main results on tree networks are independent of the specific symbiotic interaction type, such as amensalism, commensalism, mutualism, competition, and parasitism and also independent of the strength of the interaction. We also present findings on the types of networks and interactions that are characterized by the largest real and imaginary parts of the eigenvalues of their corresponding Jacobian matrices. Specifically, we show that antagonistic interactions on complete graphs yield eigenvalues with the largest imaginary part, while amensalistic and commensalistic yield eigenvalues with the largest real part.

Keywords: Lotka-Volterra, symbiosis, stability, persistent, tree network, complete graph

1 Introduction

1.1 Motivation

Species in nature are part of complex networks comprised of several trophic levels [22] and other types of interactions, such as parasitism [11, 19] and mutualism [3]. The stability of these complex ecological communities has been attracting the interest of theoretical ecologists for many decades [1, 8, 14, 21]. Robert May in 1972 was among the first to investigate the role of the number of species, the average connectance of their interaction network and the interaction strength in the stability of their community [14]. In his context, and ours as well, stability refers to local asymptotic stability of the equilibrium where all populations are positive. More recently, May’s results have been revisited under more specific assumptions. Specifically, in [21] network architecture and dynamics were investigated for communities where both mutualistic and antagonistic interactions were allowed. It was determined that while high connectance promotes stability in mutualistic networks, the opposite is true in antagonistic networks. Similarly, in [1] rather than assuming random interactions, the authors focused on prey-predator, mutualistic and competitive interactions and separated the influence of network structure and interaction strength to stability. This separation once again offered several novel insights: predator-prey interactions tend to stabilize the community, while mutualistic and competitive interactions are destabilizing.

In the past few years, analogous investigations have become the focus of attention in microbial ecology [2, 6, 13]. This is a rapidly-developing area due to the prevalence and importance of microorganisms. For instance, it has long been known that soil microbial communities affect element cycling in ecosystems [7]. Microbiota have been found to also affect the development and reproduction of mosquitoes [15], so they may be used in biocontrol of vector-borne diseases. Last but not least, the gut microbiome has emerged as a determinant of human health, since the stability of the gut microbial community has been shown to enhance its host’s good health [6]. However, due to the sheer size of microbial communities and the large number of parameters, which are not possible to be calibrated from data, the description of the interactions
is required to occur at a high level. Lotka-Volterra equations is one of the best-known and well-studied systems of equations for multi-species interactions and has been already been used in recent microbial community studies [6, 13].

Overall, Lotka-Volterra systems have been extensively studied in terms of local stability of equilibrium points [1, 6], transient dynamics of food webs [5], global stability of equilibrium points [4], and permanence [6, 10]. In permanent communities no species becomes extinct regardless of how large the perturbation from the equilibrium point is. Hence, this is a more general concept than local stability and can be thought of as a repelling property of the boundary of the state state. However, due to computational cost, we do not perform permanence analysis in this work.

Our goal is to state local stability results that depend only on network structure, and not so much on the individual interaction weights. We achieve that by presenting analytic results for tree networks for several types of symbiotic interactions. We also present findings on complete graphs that are characterized by the largest real and imaginary parts of the eigenvalues of their corresponding Jacobian matrices, and present numerical.

The rest of the article is structured as follows. In the remainder of this section we provide the details of the model and state the problem (section 1.2), describe the interactions under consideration (section 1.3) and define the notion of stability that we will consider (section 1.4). In section 2 we present our general stability findings, while in section 3 we show results on some extremal cases in terms of network architecture. We conclude in section 4 with a discussion and future study directions.

1.2 Model and Problem Statement

We study the generalized Lotka–Volterra (GLV) model

\[ x_i' = x_i \left( r_i + \sum_j c_{ij} x_j \right), \quad x_i(0) > 0, \quad i = 1, \ldots, n, \] (1)

where \( x_i \) is the biomass of species \( i \), \( r_i \) is its intrinsic rate of change and \( c_{ij} \) denotes the interaction strength between species \( i \) and \( j \).

The main topic of consideration in this paper is whether or not there is asymptotically stable persistence, i.e. (1) supports an attracting fixed point \( x^* \) with \( x^*_i > 0 \) for all \( i \). In particular, we are interested in understanding this question with the minimal necessary information about the coupling strengths.

More concretely, we could pose the following question: if we only know an underlying “signed network topology”, i.e. a pattern of which entries of \( C = \{c_{ij}\} \) are positive, negative, or zero, what can we say about asymptotically stable persistence even if we have no idea about the magnitudes of the coupling terms? One of the main results of this paper is that for a large class of network topologies, the weight magnitudes are irrelevant. We are also interested in the converse question of determining the maximal spread of eigenvalues for a class of networks with the same signed topology.

1.3 Types of interactions and sign conventions

We consider five types of interactions between species: amensalism, commensalism, mutualism, antagonism, and competition. Each of these cases corresponds to a certain sign (or zero) pattern in the coupling between the two species. More specifically, we have the following:

Definition 1.1. We consider five types of interactions in this paper. Each type of interaction will correspond to a label as described below:

- **Amensalism**, labeled by \( A \). We say that species \( i \) and \( j \) have an amensalistic relationship if \( c_{ij} c_{ji} = 0 \) and \( \min(c_{ij}, c_{ji}) < 0 \). In other words, one of the two coupling coefficients is zero and the other is negative.

- **Commensalism**, labeled by \( C \). We say that species \( i \) and \( j \) have a commensalistic relationship if \( c_{ij} c_{ji} = 0 \) and \( \max(c_{ij}, c_{ji}) > 0 \). In other words, one of the two coupling coefficients is zero and the other is positive.
Fig 1: Example ecological network and a consistent community matrix.

- **Mutualism**, labeled by \( M \). We say that species \( i \) and \( j \) have a mutualistic relationship if \( c_{ij} > 0 \) and \( c_{ji} > 0 \).

- **Antagonism**, labeled by \( P \) (the \( P \) coming from parasitism or prey-predator). We say that species \( i \) and \( j \) have an antagonistic relationship if \( c_{ij}c_{ji} < 0 \), i.e. one is negative and the other is positive.

- **Competition**, labeled by \( R \) (the \( R \) coming from “rivalry”). We say that species \( i \) and \( j \) have a competitive relationship if \( c_{ij} < 0 \) and \( c_{ji} < 0 \).

We give biological examples of each of these types of interactions in Example 1.4 below.

**Definition 1.2.** An **ecological network** is the triple \( N = (V, E, L) \) where \( V \) is a set of vertices, \( E \subseteq V \times V \) is a set of edges, and \( L : E \to \{A, C, M, P, R\} \) is a function that associates one of the five labels to each edge. The **unlabeled version** of a network is the undirected graph \( G = (V, E) \).

We consider the correspondence between a weighted graph with \( n \) nodes and an \( n \times n \) matrix \( C \) as follows: the weight on the (directed) edge \( i \to j \) is the entry \( c_{ij} \).

**Definition 1.3.** Given an ecological network with \( n \) vertices, an \( n \times n \) matrix \( C \) is a **community matrix consistent** with the ecological network if two things are true:

- The diagonal entries of \( C \) are negative.
- Any non-diagonal entry is consistent with the definitions given in Definition 1.1 above. For example, if the edge \((i, j) \in E\) is labeled \( A \), then one of \( \{c_{ij}, c_{ji}\} \) is negative and the other is zero, etc.

We now make a notational convention that allows us to see the sign choices in the community matrix more clearly. As mentioned above, we always assume that \( c_{ii} < 0 \), so we always right this as \( -d_i \), where \( d_i = |c_{ii}| \). Whenever \( c_{ij} \neq 0 \), we use the following convention: we write \( a_{ij} = |c_{ij}| \), and thus the entries of \( C \) can be written \( \pm a_{ij} \) depending on sign. When we’ve made such a choice, we will typically denote this representative matrix by \( A \) instead of \( C \). We give an example in Figure 1.

As we see in Figure 1, one can recreate the ecological network from the sign pattern in the matrix \( A \), even when the weights are unspecified: for example, we see that the \((1, 4)\) weights are \( a_{41}, -a_{14} \), which gives an antagonistic (\( P \)) relationship, etc.

**Example 1.4.** The interaction of the bread mold Penicillium with bacteria is a well-known example of amensalism [16]. Penicillium produces penicillin that destroys many forms of bacteria, though Penicillium does not benefit from the death of these bacteria.

Cattle egrets and cattle are examples of commensalism [20]. Cattle egrets follow herds of livestock, and benefit from eating the insects flushed by grazing cattle, without affecting the cattle in the process.

Predation and parasitism are both examples of antagonism.
The interaction between plants and pollinators is a well known mutualistic interaction. Another striking mutualism is between Cecropia trees, which provide housing to aggressive ants, and in return the ants protect the plant from herbivores [20].

Finally, many species compete for the same resources in an ecosystem, like cheetahs and lions which both feed on similar prey.

1.4 Asymptotically stable persistence

Definition 1.5. We say that the system (1) with growth rates \( r \) and interaction matrix \( C \) exhibits **asymptotically stable persistence** if it has an attractive fixed point \( x^* \) with \( x^*_i > 0 \) for all \( i \).

In theory, we might expect that we would need to know \( x^* \) and \( C \) to determine

Definition 1.6. We say that an ecological network is **unconditionally stable** if any choice of edge weights consistent with the labeling give a stable community matrix.

We say that an ecological network is **conditionally stable** if there exist choices of edge weights consistent with the labeling that give an unstable community matrix.

We will focus most on the case where there is **asymptotically stable persistence**, i.e. (1) supports an attracting fixed point \( x^* \) with \( x^*_i > 0 \) for all \( i \). First note that if we choose \( r = -Ax^* \), we have \( x^* \) a fixed point of the dynamics. In particular, for any fixed \( A \), we can choose \( r \) in such a way that \( x^* \) is a fixed point, so that we can prescribe any persistent solution that we would like. However, as we show in the following lemma, the question of asymptotic stability is in a sense independent of \( x^* \), and so we need to consider only \( A \):

Lemma 1.7. Let \( A \) be an \( n \times n \) matrix and \( x^* \in \mathbb{R}^n_+ \) be fixed, and set \( r = -Ax^* \). Then \( x^* \) is an asymptotically stable fixed point of (1) if and only if \( A \) is strictly positive definite.

Proof. We first note that if \( r = -Ax^* \), then the right-hand side of (1) is zero for all \( i \). If we linearize (1) around the point \( x^* \), we see that the Jacobian at \( x^* \) takes the form

\[
J_{x^*} = -\begin{pmatrix}
    a_{11}x^*_1 & a_{12}x^*_1 & \cdots & a_{1n}x^*_1 \\
    a_{21}x^*_2 & a_{22}x^*_2 & \cdots & a_{2n}x^*_2 \\
    \vdots & \vdots & \ddots & \vdots \\
    a_{n1}x^*_n & a_{n2}x^*_n & \cdots & a_{nn}x^*_n
\end{pmatrix}.
\]

This can be more compactly written as

\[
J = -A \circ (x \otimes 1^T),
\]

where \( \circ \) is the Hadamard product of two matrices, and \( \otimes \) represents the Kronecker product. The Schur product theorem says that the product of a positive definite matrix and a positive semidefinite matrix is positive definite. Moreover, we can see that the eigenvalues of \( x \otimes 1^T \) are \( \sum_i x^*_i > 0 \) and \( n-1 \) copies of zero, so it is positive semidefinite. Therefore, if \( A \) is positive definite so is \( -J \).

For the converse, note that

\[
A = -J \circ (x^{-1} \otimes 1^T),
\]

and the same argument applies. \( \square \)

From this, we can assume without loss of generality that \( x^*_i = 1 \) for all \( i \), and look for positive definiteness of \( A \).
2 General results on stability

2.1 Results for trees

In this section, we assume that the ecological network has an underlying tree topology.

Theorem 2.1. Let \( N = (V, E, L) \) be an ecological network with a tree topology and let \(-d_i\) be the self-limiting rate for species \(i\). Then:

1. If all of the edges are in the set \( \{A, C, M, R\} \), then the network is conditionally stable. In this case, the eigenvalues are always real, and, moreover, we can make the community matrix unstable by choosing any one of the coupling coefficients large enough;

2. If all of the edges are in the set \( \{A, C, P\} \), then the network is unconditionally stable. Moreover, let us define

\[
d_{\text{min}} = \min_i (-d_i), \quad d_{\text{max}} = \max_i (-d_i).
\]

Then if the edges are all in the set \( \{A, C, P\} \), the real parts of the eigenvalues of the network lie in the interval \( I = (d_{\text{min}}, d_{\text{max}}) \). (Note that \( d_{\text{min}} \leq d_{\text{max}} < 0 \).) Moreover, if the edges are in the set \( \{A, C\} \), then the eigenvalues of the network are exactly the numbers \( \{-d_i\}\).

Note that this means we have characterized all tree networks except those where there is at least one edge labeled \(P\) and one edge in \(\{M, R\}\). The next question to ask is what we can say when we have edges of all five types. As this is a quite general setting, it is not possible to say much about the whole family, but we can get estimates for stability:

Theorem 2.2. Let \( N = (V, E, L) \) be an ecological network with a tree topology, and let \( N' \) be the \(\{M, R\}\)-subnetwork of \(N\). Note that the eigenvalues of \(N'\) are real. If the eigenvalues of \(N'\) are contained in the interval \(I\), then the eigenvalues of \(N\) are also contained in \(I\). However, the converse is false.

The main idea of the proof is as follows. Our community matrix is of the form \(A = D + U\), where \(D\) is a diagonal matrix (with negative entries) and \(U\) is the off-diagonal part of the matrix. We first show that in the case of a tree topology, the community matrix is isospectral with a simpler matrix with the same diagonal part, i.e. of the form \(B = D + V\). Moreover, in the first case of Theorem 2.1, we can choose \(B\) to be antisymmetric, and in the second case, we can choose \(B\) to be symmetric. We can then apply standard tools from linear algebra to analyze these simpler cases. Since the simpler matrices are isospectral, the result follows.

Lemma 2.3. Let \( A \) be the community matrix for an ecological network with the tree topology. Let us choose \( B \) to be any matrix such that

\[
b_{ii} = a_{ii} \text{ for all } i, \quad a_{ij}a_{ji} = b_{ij}b_{ji} \text{ for all } i \neq j.
\]

Then \(A\) and \(B\) are isospectral.

Proof. To prove this, we will show that \(A\) and \(B\) have the same characteristic polynomial, and the result follows. And in fact, this will follow from the fact that every time \(a_{ij}\) or \(a_{ji}\) appears in the characteristic polynomial for \(A\), it appears as a product \(a_{ij}a_{ji}\). If we use the product form of the determinant, we have

\[
det Q = \sum_{\pi \in S_n} (-1)^\pi \prod_{i=1}^n q_i^{\pi(i)}.
\]

Now we claim that the only permutations \(\pi\) that can appear are those in which the orbit of any number under applications of \(\pi\) has period at most two. For example, assume that there is a permutation \(\pi\) such that the orbit of \(i_0\) under applications of \(\pi\) has period \(p > 2\). Then we have \(i_0, i_1, i_2, \ldots, i_{p-1}\), all distinct, such that \(\pi(i_k) = i_{k+1}\) and \(\pi(i_{p-1}) = i_0\). If all of the terms \(a_{i_k,i_{k+1}}\) and \(a_{i_{p-1},i_0}\) are nonzero, then this corresponds to a loop of length \(p\) in the graph, which contradicts that it is a tree.
Now consider the characteristic polynomial \( p_A(t) = \det(A - tI) \). By the previous argument, if \( i \neq j \), then every time \( a_{ij} \) appears in this determinant, it must also have a corresponding \( a_{ji} \). This is because if \( \pi(i) = j \) with \( j \neq i \), then by the previous we have that the length of the orbit of \( i \) is exactly 2, and thus \( \pi(j) = i \).

\[\Box\]

**Example 2.4.** Let us consider the \( 4 \times 4 \) community matrices

\[
A = \begin{pmatrix}
-34 & -35 & 0 & 0 \\
20 & -8 & -26 & 0 \\
0 & 23 & -41 & -19 \\
0 & 0 & 25 & -47
\end{pmatrix}, \quad B = \begin{pmatrix}
-34 & -10\sqrt{7} & 0 & 0 \\
10\sqrt{7} & -8 & -\sqrt{598} & 0 \\
0 & \sqrt{598} & -41 & -5\sqrt{19} \\
0 & 0 & 5\sqrt{19} & -47
\end{pmatrix}.
\]

To construct \( B \) from \( A \), we set \( b_{ii} = a_{ii} \), and for \( i < j \) choose \( b_{ij} = -\sqrt{a_{ij}a_{ji}} \), \( b_{ji} = \sqrt{a_{ij}a_{ji}} \). Note here that the off-diagonal part of \( B \) is antisymmetric, but \( A \) and \( B \) have the same characteristic polynomial

\[p_A(t) = p_B(t) = x^4 + 130x^3 + 7668x^2 + 234858x + 3290348.\]

As such, they have the same eigenvalues (but, of course, not the same eigenvectors).

**Algorithm 2.5.** Now, given a community matrix \( A \), we will perform the following algorithm to obtain \( B \). First, choose the diagonal entries of \( B \) to be the same as those of \( A \). For the edge \((i,j)\) is labeled \( \Lambda, \mathbb{C} \), we set \( b_{ij} = b_{ji} = 0 \). If the edge \((i,j)\) is labeled \( \mathbb{P} \), for \( i < j \) we set \( b_{ij} = -\sqrt{a_{ij}a_{ji}} \), \( b_{ji} = \sqrt{a_{ij}a_{ji}} \). Finally, if the edge \((i,j)\) is labeled \( \mathbb{M} \) or \( \mathbb{R} \), we set \( b_{ij} = b_{ji} = \sqrt{a_{ij}a_{ji}} \).

**Lemma 2.6.** Consider a community matrix \( A = D + U \) with \( D \) the diagonal part of \( A \) and \( U \) the off-diagonal part. Applying the algorithm 2.5 to \( A \) gives \( B = D + V \) isospectral with \( A \). This algorithm has the property that if the labels lie in the set \( \{ \Lambda, \mathbb{C}, \mathbb{P} \} \), then \( V \) is antisymmetric, if the labels lie in the set \( \{ \Lambda, \mathbb{C}, \mathbb{M}, \mathbb{R} \} \), then \( V \) is symmetric with nonnegative off-diagonal entries, and if the labels lie in \( \{ \Lambda, \mathbb{C} \} \), then \( V \) is zero.

**Proof.** From Lemma 2.3, \( A \) and \( B \) are isospectral, since \( a_{ij}a_{ji} = b_{ij}b_{ji} \) by construction.

It is clear from the descriptions that if the edges lie in \( \{ \Lambda, \mathbb{C} \} \), then all of the off-diagonal terms are zero. If, moreover, some of the edges are in \( \mathbb{P} \), then \( V \) is clearly antisymmetric. Alternatively, if some edges lie in \( \mathbb{M}, \mathbb{R} \), then \( V \) is symmetric.

\[\Box\]

We now use the Courant–Fischer theorem to understand the spectrum of \( B \); we do this in the following two lemmas.

**Lemma 2.7.** If \( B = D + V \) with \( D \) diagonal, where \( -d_i \) are the diagonal entries of \( D \), and \( V \) is antisymmetric, then all of the eigenvalues of \( B \) have real parts in the range \([d_{\min}, d_{\max}]\). Note also that \( B^* = D - V \), so replacing the off-diagonal term with its negative does not change the real parts of the eigenvalues at all.

**Proof.** Note that \( B^* = D - V \), so \( B + B^* = D \). Now, let \( Bx = \lambda x \) for \( x \neq 0 \) and a (complex) scalar \( \lambda \). Then we have

\[\langle Bx, x \rangle = \langle \lambda x, x \rangle = \lambda \langle x, x \rangle,
\]

while

\[\langle B^* x, x \rangle = \langle x, Bx \rangle = \langle x, \lambda x \rangle = \overline{\lambda} \langle x, x \rangle
\]

so we have

\[\langle Dx, x \rangle = \left( \frac{B + B^*}{2} \right) \langle x, x \rangle = \text{Re}(\lambda) \langle x, x \rangle
\]

and therefore

\[\text{Re}(\lambda) = \frac{\langle Dx, x \rangle}{\langle x, x \rangle}.
\]
From the Courant-Fischer Theorem, the maximal value of the quotient in (2) is the maximal eigenvalue of $D$, which is $d_{\text{max}}$, and the minimal value of the quotient is $d_{\text{min}}$, so this gives

$$d_{\text{min}} \leq \text{Re}(\lambda) \leq d_{\text{max}}.$$  

\[ \square \]

**Lemma 2.8.** Let $B = D + V$ with $D$ diagonal and entries $-d_i$, and let $V$ be symmetric with nonnegative entries. Then we can make $B$ become unstable (i.e. have an eigenvalue with positive real part) by increasing any of the nonzero entries of $V$ and preserving symmetry.

Note that $B$ is itself symmetric, and thus has real eigenvalues.

**Proof.** Fix $i \neq j$. Then if we choose $x$ to be the vector with a one in the $i$th and $j$th slots, and zero otherwise, we have

$$\langle Bx, x \rangle = b_{ii} + b_{jj} + b_{ij} + b_{ji} = -d_i - d_j + 2b_{ij}.$$  

Clearly, if $2b_{ij} > d_i + d_j$, then there exists a vector $x$ with $\langle Bx, x \rangle > 0$, and again by Courant-Fischer this means that the largest eigenvalue of $B$ is positive.  

\[ \square \]

**Proof of Theorem 2.1.** The proof follows from all of the lemmas. If the edges of the network are all labeled $\mathbb{A}$ or $\mathbb{C}$, then by Lemmas 2.3 and 2.6, we have that $A$ is isospectral with $D$, and its eigenvalues are given directly by the $-d_i$.

If the edges of the network are in the set $\{\mathbb{A}, \mathbb{C}, \mathbb{P}\}$, then we can replace $A$ with $B = D + V$ where $V$ is antisymmetric by Lemmas 2.3 and 2.6, and by Lemma 2.7 this implies that the real parts of the eigenvalues of $A$ all lie in the range $[d_{\text{min}}, d_{\text{max}}]$.

Finally, if the edges of the network are in the set $\{\mathbb{A}, \mathbb{C}, \mathbb{M}, \mathbb{R}\}$, then we can replace $A$ with $B = D + V$ where $V$ is symmetric by Lemmas 2.3 and 2.6, and by Lemma 2.8 imply that we can make the (real) eigenvalues of $A$ as large as we like by increasing any one off-diagonal term.  

\[ \square \]

**Proof of Theorem 2.2.** This is similar to the proof of the previous theorem. Let $A$ be the community matrix associated with $N$ and $A'$ with $N'$ (note that $A, A'$ will have the same diagonal parts). If we then write $A = D + U$ and $A' = D + U'$, we can similarly transform using the algorithm described above to obtain $B = D + V$ and $B' = D + V'$. By Lemma 2.6, $V'$ is symmetric and thus $B'$ (and thus $A'$) has real eigenvalues.

We now show that $V - V'$ is antisymmetric. If the edge $(i, j)$ is of type $\mathbb{A}, \mathbb{C}, \mathbb{M}, \mathbb{R}$, then we have $V_{ij} = V'_{ij}$ and $V_{ji} = V'_{ji}$ (every edge of type $\mathbb{A}$ or $\mathbb{C}$ corresponds to a pair of zero entries for each of these, and every edge of type $\mathbb{M}$ or $\mathbb{R}$ corresponds to the same symmetric pair). The only entries where $V, V'$ differ are for those of type $\mathbb{P}$, and by Algorithm 2.5 we have $V_{ij} = -V_{ji}$ and $V'_{ij} = V'_{ji} = 0$. Thus $V - V'$ is antisymmetric.

By a proof very similar to that of Lemma 2.7, this implies that if the eigenvalues of $D + V'$ lie in the interval $I$, then the eigenvalues of $D + V = D + V' + (V - V')$ also lie inside the interval $I$.

Finally, we give an example to show the converse is false. Consider a two-node graph with a single edge of type $\mathbb{P}$. Let the diagonal entries be $-\alpha < -\beta$ and let the weight on the single edge be $t$. Then the community matrix is

$$A = \begin{pmatrix} -\alpha & -t \\ t & -\beta \end{pmatrix}$$

and we can compute directly that the eigenvalues are

$$\lambda_{\pm} = \frac{1}{2} \left( -\alpha + \beta \pm \sqrt{(\alpha - \beta)^2 - 4t^2} \right).$$

When $t = 0$ we get exactly $-\alpha, -\beta$, but note that for $t \neq 0$, the real part of the radical is strictly decreasing in $t$, so that the real parts of the $\lambda_{\pm}$ strictly approach each other until they meet at the mean of $-\alpha, -\beta$. In
Figure 2: Plot of the real parts (left subfigure) and imaginary parts (right subfigure) of the eigenvalues of
the one parameter family of matrices $A_t = D + tU$, and $U$ is the interaction matrix that comes from a tree
with all edges in $\mathbb{P}$. In the left subfigure, the red curves correspond to real eigenvalues and the blue curves
to the real parts of complex pairs of eigenvalues — thus blue curves emerge from the collision of two red
curves, as $t$ moves away from zero.

In particular, the real parts of $\lambda_\pm$ are strictly inside $(-\alpha, -\beta)$ for all $t > 0$. By symmetry, this extends to all
$t \neq 0$.

Remark 2.9. Although the counterexample given in the proof of Theorem 2.2 is specific, this general phenomenon
seems ubiquitous: in a tree topology, increasing the strength of edges of type $\mathbb{P}$ seems to always strictly “tighten” the
spectrum. See Figure 2.

In figure 2 we show a case where we took a tree with $n = 10$ nodes and with all edges in $\mathbb{P}$. The weights
on the edges are chosen randomly in $[0, 1]$, and the diagonal entries $d_i$ are also chosen randomly in $[0, 1]
(meaning that the diagonal entries of $A$ are uniformly distributed in $[-1, 0]$). This gives a community matrix
of the form $A = D + U$, and we considered the one-parameter family of matrices given by $A_t = D + tU$.

If $U$ is antisymmetric, then the picture should be invariant with respect to the involution $t \mapsto -t$, but of
course from the arguments above $U$ can be effectively considered antisymmetric. We see at $t = 0$ we get
10 distinct negative real eigenvalues in $[-1, 0]$, and these correspond exactly to the $-d_i$. As we increase $t$ in
either direction, the eigenvalues get “tighter” — specifically, the spread in the real parts of the eigenvalues
is decreasing in $|t|$. Moreover, we see that for $|t|$ sufficiently large, the imaginary parts of the eigenvalues
grow linearly in $|t|$.

While the tightening of the real parts is observed here in just one example chosen at random, this ob-
servation seems general and we conjecture that it is always true. Note that this conjecture however, it is
stronger than the theorem: the theorem only implies that the real parts of the eigenvalues must be contained
inside the range of the diagonal elements — the tightening is not implied by the theorem. For example, it
would be consistent with the theorem above if the curves in the left subfigure of Figure 2 oscillated, as long
as they stayed inside the bounds given at $t = 0$, but in fact they seem to always strictly decrease.

3 Extremal results

In the previous section, we worked hard to find bounds for the eigenvalues, and in particular to guarantee
stability over all choices of parameters. In this section, we consider something like a converse to that
question, stated as: which networks give the largest spread of eigenvalues in either the real or the imaginary
directions or give the extremal eigenvalues in the real direction?
For the purposes of this section, we want to concentrate on the topologies of the networks and as such we consider only those cases where the interaction strengths are all the same. Without loss of generality, we assume that for \( i \neq j \), \(|c_{ij}| = 1\) or 0 (basically, for every edge that exists, we get the sign(s) from the type of edge and we assume that the weights are ±1). We also assume that \( d_i = d \). As such, our matrix can always be written \( A = D + U \) where \( D = -dI_n \) and \( U \) has entries of 0, ±1. As such, we can study just the spectrum of \( U \), since adding back \( D \) just shifts all eigenvalues by the fixed amount \(-d\).

For the remainder of this section, we first present some examples that are extremal, or nearly, extremal, and then present some numerical results on random networks to show how far away from extremal the typical random network is.

### 3.1 Analysis of extremal examples

As mentioned above, we are only considering those community matrices where the inter-species interaction terms are 0, ±1. If we let \( D_{n-1} = \{ z \in \mathbb{C} : |z| \leq n - 1 \} \) then by Gershgorin’s Theorem [9, Lemma 6.2.2.] the eigenvalues of \( U \) are contained inside \( D_{n-1} \). From this we know that if we have examples of \( U \) with eigenvalues on the boundary of this circle, then these examples are extremal; if we have examples of \( U \) with eigenvalues asymptotically close to this boundary, they are asymptotically extremal.

We first consider the example of extreme real parts of the eigenvalues. Now let us consider the network which is a complete graph with all edges in \( M \), or, equivalently, let \( U \) be the matrix with all off-diagonal entries equal to unity and diagonal entries equal to zero. We see that \( U1 = (n - 1)1 \), so that \( U \) has an eigenvalue \((n - 1)\). With a bit more work, we can see that \( U \) is actually a rank one matrix, and therefore all of the other eigenvalues are zero. This is the largest positive eigenvalue possible for an \( n \)-species example by the Gershgorin consideration above. In particular, to make this community matrix stable we need \( d > n - 1 \), which means that the strength of self-limiting terms for any one species needs to be comparable to the total number of species. Similarly, if we consider \(-U\) this corresponds to a complete graph of \( R \), and gives an eigenvalue of \(-(n - 1)\), which is again maximal by Gershgorin.

On reflection, it is not so surprising that mutualism gives rise to the largest amount of instability (or competition, stability). The next natural question to ask is what is the maximal amount of instability we can generate from a purely \( \{A, C, P\} \) network. As we have seen above, edges of type \( P \) add stability, so this inspires the following series of examples. Let \( n \) be odd, and consider the matrix defined by the following rule: choose \( i < j \). If \( i \bmod 2 = j \bmod 2 \), then let \( c_{ij} = -1, c_{ji} = 0 \). If \( i \bmod 2 \neq j \bmod 2 \), then let \( c_{ij} = 0, c_{ji} = 1 \). Graphically, this corresponds to

\[
U = \begin{pmatrix}
0 & -1 & 0 & -1 & \cdots & -1 & 0 \\
0 & 0 & -1 & 0 & \cdots & 0 & -1 \\
1 & 0 & 0 & -1 & \cdots & -1 & 0 \\
\vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 1 & 0 & 1 & \cdots & 0 & -1 \\
1 & 0 & 1 & 0 & \cdots & 0 & 0
\end{pmatrix} = V_n^{A,C}.
\]

(3)

Note that every edge is of type \( A \) or \( C \), and graphically this means that all edges where \( d(i, j) \bmod n \) is odd are of type \( A \) and all where the distance is even are of type \( C \). We first claim that this matrix has a real eigenvalue of \( \lambda_n := (n - 1)/2 \), and this is the largest real part of any of the eigenvalues. To see this, consider the characteristic polynomial \( p_{V_n^{A,C}}(t) := \det(tI - V_n^{A,C}) \), evaluated at \( t = \lambda_n \), which is

\[
p_n(\lambda_n) = \det(V_n^{A,C} - \lambda_n I_n) = \det \begin{pmatrix}
-\frac{n-1}{2} & -1 & 0 & -1 & \cdots & -1 & 0 \\
0 & -\frac{n-1}{2} & -1 & 0 & \cdots & 0 & -1 \\
1 & 0 & -\frac{n-1}{2} & -1 & \cdots & -1 & 0 \\
\vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 1 & 0 & 1 & \cdots & -\frac{n-1}{2} & -1 \\
1 & 0 & 1 & 0 & \cdots & 0 & -\frac{n-1}{2}
\end{pmatrix}.
\]
Adding all odd columns to the last one and all even columns to the one before the last produces a matrix with two identical columns. From this it follows that $\lambda_n = (n - 1)/2$ is an eigenvalue of $V_n^{A C}$. Moreover, counting the off-diagonal terms and using Gershgorin’s Theorem again, we see that this eigenvalue must be the largest real part. It is possible that there is a matrix with a larger positive eigenvalue in the $\{A, C, P\}$ network class, but at least this is an example with an eigenvalue of $O(n)$.

We can also consider the question of how large a spread in imaginary parts the eigenvalues can have (this corresponds, dynamically, to high frequency rotation around the fixed point). We show now that the case with a complete graph of $P$ edges is nearly extremal. Consider the case with

$$V_n^P = \begin{pmatrix} 0 & -1 & \ldots & -1 & -1 \\ 1 & 0 & \ldots & -1 & -1 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 1 & 1 & \ldots & 1 & 0 \end{pmatrix}. $$

Note first that $V_n^P$ is anti-symmetric, and thus has purely imaginary eigenvalues. In particular, it follows from this that $p_{V_n^P}(t)$, the characteristic polynomial of $V_n^P$, is even (resp. odd) when $n$ is even (resp. odd), and the eigenvalues are invariant under the involution $t \mapsto -t$.

Let us concentrate on the case where $n$ is even. We have

$$p_{V_n^P}(t) = \sum_{k=0}^{n} \binom{n}{k} t^{n-k}, \quad (4)$$

since if one observes that the coefficient of the power $\mu^{n-j}$ is equal to the number of distinct paths on $j$ nodes, and in a complete graph this number is $\binom{n}{j}$.

Next, we consider the auxiliary polynomial $P(t) := (1 + t)^n = \sum_{k=0}^{n} \binom{n}{k} t^{n-k}$. When $n$ is even, it follows from (4) that $P(t) + P(-t) = 2p_{V_n^P}(t)$, or

$$p_{V_n^P}(t) = \frac{(1 + t)^n + (1 - t)^n}{2}. \quad (5)$$

If we let $\zeta = e^{i2\pi/n}$ be a primitive $n$-th root of unity, we see that roots of (5) correspond to $(1 + t)^n = (1 - t)^n$, or

$$(1 + t) = \zeta^k (1 - t) \quad (6)$$

for any $k \in \mathbb{Z}$ such that $\zeta^k \neq -1$. Solving for $t$ gives

$$t = \frac{\zeta^k - 1}{\zeta^k + 1} = \frac{\zeta^{k/2} - \bar{\zeta}^{k/2}}{\zeta^{k/2} + \bar{\zeta}^{k/2}} = \frac{2i \sin(\pi k/2n)}{2 \cos(\pi k/2n)} = i \tan(\pi k/2n),$$

where the restriction is that we do not have $k = n/2 \mod n$. As $k$ runs through the integers, this gives a range of values, but it is not too hard to see that this is maximized when we choose $k = n - 1$, and expanding this around $n \to \infty$ gives

$$\tan \left( \frac{\pi}{2n} (n - 1) \right) = \frac{2n}{\pi} - \frac{\pi}{6n} + O(n^{-3}),$$

From this, we have that $V_n^P$ has an imaginary eigenvalue of size $\approx 0.63662n$.

### 3.2 Numerical examples

In the analysis above, we see that the extremal examples are ones where the interaction network is dense; in particular, the underlying topology was always the complete graph. We now consider communities with interactions that can be described by a complete graph and study the spectrum of the community matrix, and we restrict our edge types to the set $\{A, C, P\}$ (cf. [17, 18, 16]).
For \( n = 3, 4, 5 \), we plot every matrix of this type (there are \( 3^{n(n-1)/2} \) such distinct matrices, so 27, 727, and 59049 for \( n = 3, 4, 5 \)) and for \( n \geq 6 \) we generate a random sample of size 500,000 for each \( n \). (By “random” here we mean that for each (unordered) pair \((i, j)\), we choose it to be of type A, C, or P, each with probability \(1/3\).)

In figure 4 we focus on the range of the maximum of the real and imaginary parts of the eigenvalues of each matrix. For each \( n \) we show the entire range of these maximum values for all 500,000 matrices. Here, we consider \( 2 \leq n \leq 20 \). These ranges are the light blue and magenta shaded regions for the real and imaginary parts, respectively. We also plot in the corresponding panels the theoretical results for the maximum real part of the eigenvalues \( \frac{n-1}{2} \) (black stars) for odd values of \( n \) and the maximum imaginary part \( \frac{2n}{\pi} \) (red stars). It can be seen that the simulations capture the theoretical predictions up to approximately \( n = 8 \), but fail for higher values of \( n \) due to the large number of possible matrices that are required to be simulated.

### 4 Conclusion and Discussion

In this article we have presented a variety of findings for ecological dynamics on communities characterized by symbiotic interactions, namely amensalism \((-/-)\), commensalism \((+/0)\), mutualism \((+/+)\), competition \((-/-)\) and antagonism \((+/-)\). We presented analytic results for tree graphs, as well as extremal and numerical results for complete graphs. Specifically, we have proved that tree networks with amensalistic, commensalistic and antagonistic interactions are unconditionally stable and tree networks with amensalistic, commensalistic, mutualistic and competitive interactions are conditionally stable. For the latter, we have shown the reality of the spectrum and demonstrated that the community matrix can become unstable.
Figure 4: 500,000 interaction networks that are complete graphs were generated for each $n$. For each corresponding Jacobian matrix, the maximum real and imaginary part of the eigenvalues was recorded and then the maximum and minimum over all 500,000 matrices was saved for each $n$. In the top panel, the blue shaded area corresponds to the range of simulated real parts of $\mu$, while the stars correspond to the analytical maximum $\frac{n-1}{2}$. In the bottom panel, the magenta shaded area corresponds to the range of simulated imaginary parts of $\mu$, while the stars correspond to the analytical maximum $\frac{2n}{\pi}$.
by choosing any of the coupling coefficients large enough. We also investigated the networks that yield the largest spread of eigenvalues in the real and imaginary directions. We found that complete graphs with an alternating pattern of amensalistic and commensalistic interactions are characterized by a real positive eigenvalue that grows linearly with the number of species. Also, we showed that complete networks with only antagonistic interactions have purely imaginary eigenvalues, the largest of which grows linearly with the number of species.

Recent studies [6, 16] have reemphasized the role of asymmetric interactions such as amensalism and commensalism, namely interactions where one species has an affect on another but is not affected by them in return. Such interactions were usually overlooked in the literature, but see [4, 5]. However, amensalistic and commensalistic interactions are important, since they have been found to yield more unstable communities [16]. Similarly, in [4] it was shown through numerical simulations in random networks that as the proportion of antagonistic interactions decreases, so does the probability that the community is stable. Through our extremal results we demonstrate analytically, that among amensalistic, commensalistic and antagonistic interactions, the former ones indeed yield unstable communities, while the latter one stable ones.

An important direction that is left for future work and has not been addressed here, involves the question of unstable coexistence. That is, the coexistence of all species on limit cycles or chaotic orbits [10, 12]. Permanence and global stability analysis will shed light into whether extreme deviations from a steady state where all species persist will lead to species extinction or more complex dynamics. Moreover, while network connectance is varied in most works [4, 6, 16], in this work we consider two extreme cases, namely trees and complete graphs. It would be interesting to obtain analytical predictions along the lines of what has been presented here for other types of networks. In summary, the mechanisms that promote species coexistence in large communities are not fully understood and many questions still remain open.

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Conflict of interest

All authors declare no conflicts of interest in this paper.

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