

The equations of nature and the nature of equations

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Abstract

Systems of N equations in N unknowns are ubiquitous in mathematical modeling. These systems, often nonlinear, are used to identify equilibria of dynamical systems in ecology, genomics, control, and many other areas. Structured systems, where the variables that are allowed to appear in each equation are pre-specified, are especially common. For modeling purposes, there is a great interest in determining circumstances under which physical solutions exist, even if the coefficients in the model equations are only approximately known.

The structure of a system of equations can be described by a directed graph G that reflects the dependence of one variable on another, and we can consider the family $\mathcal{F}(G)$ of systems that respect G . We define a solution X of $F(X) = 0$ to be robust if for each continuous F^* sufficiently close to F , a solution X^* exists. Robust solutions are those that are expected to be found in real systems. There is a useful concept in graph theory called “cycle-coverable”. We show that if G is cycle-coverable, then for “almost every” $F \in \mathcal{F}(G)$ in the sense of prevalence, every solution is robust. Conversely, when G fails to be cycle-coverable, each system $F \in \mathcal{F}(G)$ has no robust solutions.

Failure to be cycle-coverable happens precisely when there is a configuration of nodes that we call a “bottleneck,” a criterion that can be verified from the graph. A “bottleneck” is a direct extension of what ecologists call the Competitive Exclusion Principle, but we apply it to all structured systems.

Keywords: structured systems; nonlinear systems; robust solutions; missing links; link prediction; complex networks; generic rank; prevalence; dilation

Significance

There is a comprehensive literature available on linear networks. However, most interactions within a network are nonlinear. In this work, we extend the linear theory to nonlinear networks. We borrow a geometrical tool “Cycle Cover” from graph theory and the idea of the “Competitive Exclusion Principle” from biological networks. We extend these ideas to all structured nonlinear systems. This theory tells precisely which networks can have robust solutions or steady states. Our theory helps one to recognize which nodes are playing a crucial role in the robustness of a structure without knowing what the exact weights of the links are. Our approach will allow ecologists to ask what

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the essential interactions are in an ecosystem that allow the system to be robust. When a structure is fragile, that suggests the modeler needs to add some links. Our methods tell how many links must be added and where they should be added to make a structure robust.

1 Introduction

Mathematical modeling is a mainstay of scientific progress. The fluctuations of physical and biological systems, and their equilibria, are often expressed by equations. These equations come with parameters that are not precisely specified. Our focus in this article is what a mathematical model can tell us when the parameters are difficult to measure, or otherwise inaccessible to the researcher.

In the 1930's, Georgii Gause carried out experiments on two competing strains of Paramecium, *P. aurelia* and *P. caudatum*, that dined on a common banquet of nutrients. He found that under certain environmental conditions, *P. aurelia* outcompeted *P. caudatum* and drove the latter to extinction. Under certain other environmental conditions, the reverse occurred, and *P. aurelia* was driven to extinction. But he found it impossible to find conditions under which both strains coexisted, and was puzzled by the strangeness of this outcome. The notion that two or more species that compete for the same finite resource cannot coexist in a single ecological niche is now known as the Competitive Exclusion Principle (CEP). In fact, this idea was already present in Darwin's writings, that one of the competing species in an ecological niche eventually would either be wiped out or driven genetically to a different niche.

Figure 1 shows a simple mathematical version of CEP, considered originally by Volterra [1]. Species x_1 and x_2 affect the population growth of the prey species x_3 , and vice versa. We could pose a differential equation of the form

$$\begin{aligned} \frac{1}{x_1} \dot{x}_1 &= f_1(x_3) \\ \frac{1}{x_2} \dot{x}_2 &= f_2(x_3) \\ \frac{1}{x_3} \dot{x}_3 &= f_3(x_1, x_2) \end{aligned} \tag{1}$$

that governs the equations of the three species. To search for an equilibrium, set the left sides of the equations to zero, yielding the system in Figure 1(a). The first two equations share one unknown, x_3 . In other words, x_3 is overdetermined. That is, while there may be a solution of these equations with positive x_1, x_2, x_3 , small changes in f_1 and f_2 will cause the solution to disappear, for most choices of f_1 and f_2 that continue to depend only on x_3 . The solution would then be non-robust, in the sense that it is unlikely to be observed in a real-world situation.

The example represented by Model 1 is a mathematical illustration of the Competitive Exclusion Principle. If on the other hand we do find the two populations x_1 and x_2 coexisting in reality, then we may reasonably conclude that our proposed network in Figure 1(c) is incorrect.

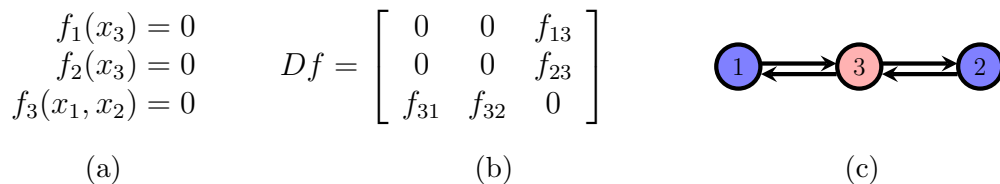


Figure 1: **A fragile family of systems motivated by Competitive Exclusion Principle.**

(a) A system of equations describing the equilibrium. For example, f_1 in the first equation is allowed to depend on x_3 , but not x_1 or x_2 . This fact is represented in the two other parts of this figure. (b) The structure matrix of the Jacobian of the differential equation. (c) The directed graph of the system. Systems of this form cannot have a robust solution so any solution that exists is fragile. The graph is not cycle coverable, and the determinant of S is 0 for all choices of values for the unspecified partial derivatives $f_{ij} = \frac{\partial f_i}{\partial x_j}$ in Df . The coloring of (c) illustrates a “bottleneck”, the obstruction that prevents the graph from being cycle coverable; see Sec. 3. The “bottle” nodes 1 and 2 are blue and the “neck” node 3 is red here and throughout the paper.

One way out of this dilemma is to postulate the existence of a second prey species, shown as x_4 in Figure 2. As we will discuss below, this provides robustness to an existing solution. In fact, we will show that for any solution of the system in Figure 2(a), almost all small perturbations of f_1, f_2, f_3, f_4 that respect the system structure also support a solution. Thus, such solutions are not unlikely to be found in naturally-occurring circumstances.

Notably, the robustness in the network shown in Figure 2(c), and the non-robustness shown in Figure 1(c), are determined not by the knowledge of precise parameters in the functions f_i , but by properties of the network. These properties can be expressed algebraically or geometrically. To be precise, define a **structured system** to be a system of equations where, as in Figures 1(a) and 2(a), only certain variables are allowed to appear in particular equations. These restrictions can be visualized graphically by assigning a graph to the equation. In the graphs in Figures 1(c) and 2(c) there is one node for each equation of the system. There is an edge “ $j \rightarrow i$ ” from node j to node i if f_i is allowed to depend on the x_j . An algebraic way to visualize a structured system is by the **structure matrix** of partial derivatives, as shown in Figures 1(b) and 2(b). Structured systems are common in linear control theory and in other fields [2, 3].

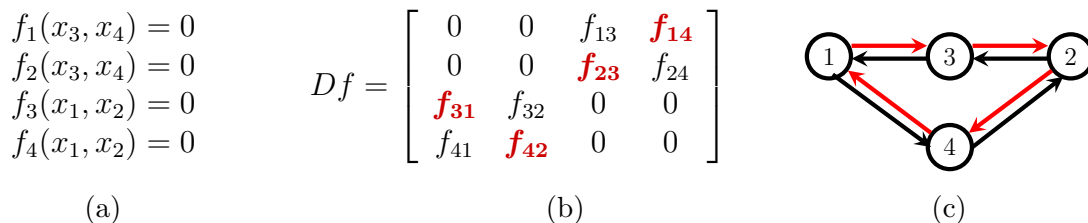


Figure 2: **A robust family of systems.** Almost every system of this form will have “robust” solutions; see Sec. 2. The shaded f_{ij} in (b) and shaded edges (red in the online version) in (c) constitute an example of a cycle cover $(1) \rightarrow (3) \rightarrow (2) \rightarrow (4) \rightarrow (1)$ that passes through all nodes in the graph. Hence the graph is cycle coverable.

In general, we will consider a system of equations

$$F(X) = 0 \tag{2}$$

where $X = (x_1, \dots, x_N)$, $F(X) = (f_1(X), \dots, f_N(X))$, and where f_i is allowed to depend on x_j only if there is a directed edge in the graph from node j to node i . If $F(X_0) = 0$, then X_0 is called a solution. We will call a solution of (2) that persists for tiny changes in F (again, that respect the graph structure) a **robust** solution. A solution will be called **fragile** if it is not robust. Throughout this paper F is a continuously differentiable function (*i.e.*, it is C^1) on some open region in \mathbb{R}^N .

We will show that the criterion for having a robust solution is that the structure graph is “cycle coverable”. A **cycle** is a closed path of directed edges in a graph with no node occurring more than once. Two cycles are **disjoint** if they have no nodes in common. We say a graph G is **cycle coverable** if there is a collection of pairwise disjoint cycles that together cover all the nodes. The cycle cover consists of the paths shown in red in Figure 2(c). In contrast, Figure 1(c) has no cycle cover, and we do not expect to see a physical solution.

The cycle covering criterion for robustness of solutions can be viewed as a generalization of the Competitive Exclusion Principle to more complex contexts. As an example of the more general obstructions to robustness that flow from this characterization, consider the system of equations represented by the graph in Figure 3(a). This graph is an illustration of a generalization of the CEP that says a food web with two trophic levels, with no intraguild communication, cannot be robust if the numbers of nodes in the two levels are not equal. We leave it to the reader to discover the reason that a cycle cover is impossible in Figure 3(a), although this will follow easily from our results in Section 3. In Figure 3(b), one intraguild interaction is added to the top level, allowing a cycle cover, and therefore robust solutions.

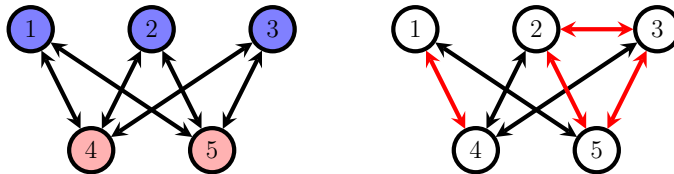


Figure 3: Generalization of the Competitive Exclusion Principle for two trophic levels. (a) The graph represents the structure allowed for a system of equations. Solutions are robust if and only if there exists a cycle cover. No cycle cover exists in this graph, and all solutions are fragile. More generally, if there are no intraguild interactions, the number of species in each level must be the same to allow robust solutions. (b) Adding the interaction between species 2 and 3 allows a cycle cover, and therefore robust solutions.

Although this graph-based criterion may be challenging to verify in complicated networks, there are equivalent characterizations that may be simpler to apply in specific situations, including Figure 3(a). For a set of graph nodes B , define the forward set B^{\rightarrow} to be the set of graph nodes that are pointed to by a node in B . We call (B, B^{\rightarrow}) a **bottleneck** if the number of nodes in B is greater than the number in B^{\rightarrow} . We show that a graph has a cycle-covering if and only if the graph has no bottlenecks. The bottleneck in Figure 1(c) is the pair of sets $B = \{1, 2\}$, shaded in blue, and $B^{\rightarrow} = \{3\}$, shaded in red. Figure 2(c) has no bottleneck. In Figure 3(a), B is the top level of three nodes, and B^{\rightarrow} is the lower level of two nodes.

A more complex ecological model is shown in Figure 4. A quick perusal of the network should convince the reader that establishing whether or not a cycle cover exists in the graph might be

daunting. However, a bottleneck exists with the two-node bottle $B = \{6, 7\}$ and with $B^\rightarrow = \{15\}$ as the neck. Thus we will find that one of these equivalent characterizations of robustness may be easier than the other, depending on what is known about the network. We study this network in more detail in Sec. 4.

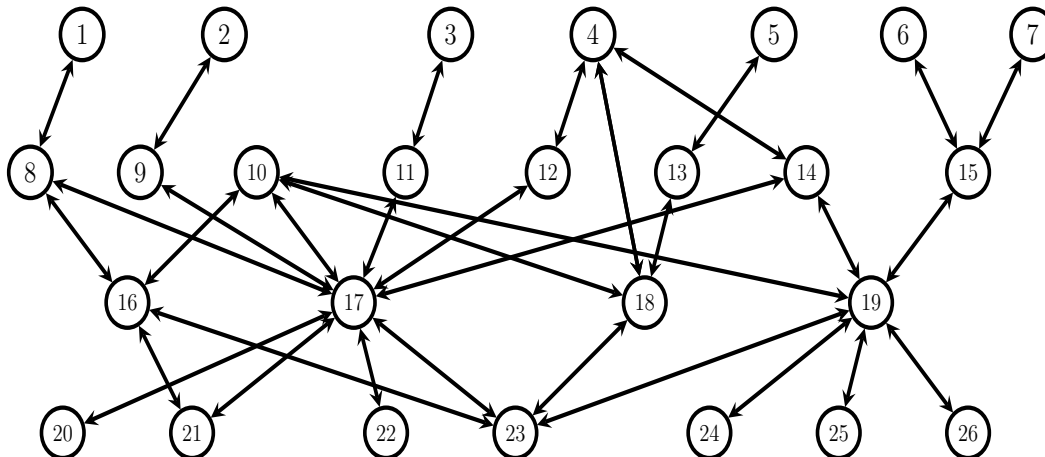


Figure 4: A network model adapted from Solé and Montoya [4]. Each node represents the population density of a different species. Solutions of the structure system of 26 equations in 26 unknowns associated with this graph cannot be robust, since a bottleneck exists with nodes 6 and 7. Several other obstructions to robustness exist. See Sec. 4 for a more complete discussion.

A third equivalent criterion for robustness, that is algebraic in nature, is that the structure matrix be nonsingular for almost every realization of matrix entries. For example, the 4×4 matrix in Figure 2(b) has full rank for almost every choice of entries. In contrast, the 3×3 matrix in Figure 1(b) is rank deficient for every choice of entries. We show the equivalence of these alternative characterizations in this article, and develop strategies to find bottlenecks and show how connections may be added to the system to alleviate them.

Our overarching goal is to provide tools to explain why some networks have robust steady states and others have fragile steady states. Differential equations and graph theory have been used by scientists in studying a vast group of networks [5, 6, 7, 8, 9, 10].

Mason [11] pioneered the discussion of disjoint cycle coverings or “nontouching feedback loops” for linear systems. He says for example “The useful fact is that the determinant of a complete flow graph is equal to the product of the determinants of each of the nontouching parts in its loop subgraph,” but he does not relate the existence of a cycle covering to the existence of a solution. Later, in the context of ecological networks Yorke and Anderson [12] introduced cycle coverability as a criterion for the existence of solutions of systems of linear equations, but only for the case where the matrix is anti-symmetric.

Bottlenecks, called “dilations” in a slightly different context, were studied for structural observability and controllability by Lin [13], and extended by Liu et al. [14, 15]. It is well known that a graph of a linear system is cycle coverable if and only if the rank of its $N \times N$ structure matrix is N [16, 17]. However, this fact does not tell us which nodes are the key nodes or which edges are essential connections in the robustness of the graph. If a graph is not cycle coverable, what is the smallest number of edges that must be added and where must they be to make a fragile structure robust? We answer these questions in Section 3.

Even though there is an extensive literature available on studying linear system of equations using graphs and matrices, the interactions between variables in many applications of interest are nonlinear. In this article, we focus on what is true generically for structured systems of nonlinear equations.

The concept of genericity that we rely on for this discussion is “almost every” in the sense of prevalence [18, 19, 20], a mathematical version of almost every that is appropriate in infinite-dimensional function spaces. It has been used previously to establish the properties of typical representatives in various contexts, such as attractor reconstruction and bifurcation analysis.

In Section 2, we investigate robustness for solutions of structured systems of equations. Section 3 discusses the concept of bottlenecks in the graphs of these systems, and the equivalent characterizations of robustness. We discuss applications to ecological networks in Section 4.

2 Nonlinearity and robustness in structured systems

Ecological models such as Model 1 have long been studied for insight into food webs among species, and more generally to represent the various interactions between members of a community. Mathematical treatments began in the early 20th century with Lotka-Volterra interactions, meaning that the effect of agent j acting on agent i has form $\dot{X}_i = a_{ij}X_iX_j$ for some parameter a_{ij} . These are sometimes referred to as linear interactions, since the right-hand side of $\dot{X}_i/X_i = a_{ij}X_j$ is linear, which leads to a linear system of equations for the equilibrium state.

By the middle of the 20th century, such a linear response was considered reasonable when studying small fluctuations about an equilibrium, but unrealistic for systems in general, where population saturation, predator interference, and other effects play important roles. For example, Holling in 1959 suggested replacing $a_{ij}X_j$ above with the approximation $a_{ij}X_j/(1 + b_{ij}X_j)$ [21], which was further modified by Beddington in 1975 to the approximation $a_{ij}X_j/(1 + b_{ij}X_j + c_{ij}X_i)$ [22]. The type of the functions to be included depends on the situation and should always be considered as an approximation of the population biology. There are many possible forms of equations and we want conclusions about robustness that do not depend on the form of the equations, conclusions that depend only on the graph. In particular, we extend the study of cycle covers and robustness of solutions to the context of “almost every nonlinear system compatible with the graph” in the sense of prevalence.

A property P of members of a function space such as $\mathcal{F}(G)$ is called **prevalent** if there is an m -dimensional subspace E , called a **probe**, such that for every $f \in \mathcal{F}(G)$, the function $f + e$ has property P for almost every e in the sense of Lebesgue measure on R^m . Prevalence is a strengthened version of the topological concept of dense. That is, prevalent in a function space implies dense, but also has a measure-theoretic flavor. We use it due to the lack of a convenient concept of full measure in general function spaces. In a finite-dimensional measure space, a property is prevalent if and only if it holds except for a set of measure zero.

As a first illustration of the usefulness of this definition, we show that non-robust solutions are rare in the sense of prevalence. For the system of equations (2), the matrix $DF(X) = [\frac{\partial f_i}{\partial x_j}(X)]$ denotes the Jacobian of F at X . In the biological literature $DF(X)$ is called community matrix or the matrix of interactions. If $DF(X_0)$ is nonsingular, then the Implicit Function Theorem says that a solution always exists for sufficiently small changes in F [23].

Proposition 1. (Fragile solutions are rare.) Let E be a space of C^1 functions from \mathbb{R}^N to \mathbb{R}^N . For almost every F in E , $F(X) = 0$ has no fragile solutions.

Proof. Sard’s theorem [24] implies that for any C^1 map $F : \mathbb{R}^N \rightarrow \mathbb{R}^N$, the image under F of the points X where $DF(X)$ is a singular matrix has measure zero in \mathbb{R}^N . Thus for almost every C in \mathbb{R}^N , $F(X) = C$ has no fragile solutions. The proof of prevalence uses the probe space of constant functions. For every F , $F - C = 0$ has no fragile solutions for almost every C . \square

For any directed graph G of N nodes such as those in Figures 1(c) and 2(c), we define the $N \times N$ **structure matrix** $S(G)$. This matrix has unspecified real number entries S_{ij} when there is a directed link from node j to node i ; otherwise $S_{ij} = 0$.

We say F **respects the structure graph** G if equation i depends on variable j only if there is a directed edge from node j to node i . Let $\mathcal{F}(G)$ denote the set of functions that respect the graph G . As an extreme example, the identically zero function respects every graph. Denote by $\mathcal{L}(G)$ the subspace of all linear functions (or matrices) that respect G .

Example 1. As an application of Proposition 1, let E be the space of functions that respect a graph G . All constant functions respect all graphs. As Lemma 3 will show, if the graph G is cycle coverable, there may be many robust solutions, but Proposition 1 shows that fragile solutions are rare. If G is not cycle coverable, then almost every function F has no solutions, so it has no fragile solutions. In either case, almost every F has no fragile solutions.

We have seen that robustness can fail for two reasons: either there is a solution that is not robust, or there is no solution at all. Next, we address how the properties of the structure matrix can tell us when the robust solutions actually exist. For lack of a convenient reference, a proof is provided in Section 6.

Lemma 1. Let r be the maximum of the $\text{rank}(A)$ for all matrices in $\mathcal{L}(G)$. Then almost every A in $\mathcal{L}(G)$ has rank r .

We call the rank r given by Lemma 1 the **generic rank** of the graph G , denoted by $\text{GenRank}(G)$. Equivalently write $r = \text{GenRank}(S(G))$ or $\text{GenRank}(S)$ for the generic rank of the structure matrix $S(G)$. “Almost every” in the lemma means almost every with respect to Lebesgue measure on the finite-dimensional vector space $\mathcal{L}(G)$. For lack of a convenient reference, a proof is provided in Section 6.

Our goal in this section is to extend Lemma 1 to a version that is relevant for nonlinear systems of equations (2). As a special case, if $\text{GenRank}(G) = N$, we will show that it is a prevalent property of the system that the Jacobian of the system of equations is a nonsingular matrix at almost every X in \mathbb{R}^N .

Theorem 1 (Structure Graph Theorem). Let G be a graph for which the structure matrix has generic rank r .

- (I) For almost every $F \in \mathcal{F}(G)$, $DF(X)$ has rank r for all X except on a closed set of measure zero.
- (II) If $r < N$ and $F \in \mathcal{F}(G)$, then $F(\mathbb{R}^N)$ has measure zero. Hence for each $F \in \mathcal{F}(G)$, Eq. (2) has no robust solutions. For almost every F , there are no solutions.

The proof of the theorem (in Sec. 6) uses $\mathcal{L}(G)$ as the probe.

Corollary 1. Let G be a graph for which the structure matrix has generic rank r .

- (CI) If $r = N$, for almost every $F \in \mathcal{F}(G)$ and almost every $X_0 \in \mathbb{R}^N$, each solution of the equation $F(X) - F(X_0) = 0$ is isolated and robust.
- (CII) If $r < N$, for almost every $F \in \mathcal{F}(G)$ and almost every $X_0 \in \mathbb{R}^N$, there is an $(N-r)$ -dimensional surface \mathcal{M} consisting of all the solutions X of the equation $F(X) - F(X_0) = 0$; more specifically, the surface \mathcal{M} is a manifold without boundary.

Sketch of proof. Part (CI) follows from part (I) of the Theorem 1.

To prove part (CII), notice that part (I) of the Theorem 1 implies that for almost every $F \in \mathcal{F}(G)$ and almost every $X_0 \in \mathbb{R}^N$, $\text{rank}(DF(X_0)) = r$, the generic rank. Choose such an F and X_0 . Let \mathcal{M} be the set of X such that $F(X) = F(X_0)$. Notice that \mathcal{M} is a closed set.

Because the rank is constant near X_0 , we can apply the Constant Rank Theorem III.4.2 and its corollary III.5.8 in [25]. Hence, there is a differentiable change of coordinates near X_0 and a differentiable change of coordinates for C near $F(X_0)$ such that in these coordinates, $F(X) = F(X_0) + DF(X_0)(X - X_0)$ for X close to X_0 , *i.e.*, F is linear plus a constant. Hence locally, the linear theory tells us (i), the image of the neighborhood in \mathbb{R}^N of X_0 is r dimensional, and (ii), that near X_0 , \mathcal{M} is a surface of dimension $N - r$.

Following Sard [26], we define the set

$$A_\rho = \{C : \text{there exists an } X \text{ such that } F(X) = C \text{ and } \text{rank}(DF(X)) \leq \rho\}.$$

Sard's 1965 paper says A_{r-1} has dimension at most $r - 1$, and that since A_r is r dimensional, "almost every" C in A_r is not in A_{r-1} .

Hence for almost every X_0 , every X for which $F(X) = F(X_0)$ satisfies $\text{rank}(DF(X)) = r$. We can furthermore assume X_0 is such a point. At each of its points \mathcal{M} is locally an $N - r$ dimensional surface, so it is a surface without boundary in the domain of F , *i.e.* a closed manifold without boundary. \square

The $N - r$ manifold \mathcal{M} mentioned in the above proof can be unbounded like a plane or bounded like a sphere, but it cannot be like a disc with boundary.

We can think of the above corollary as a generalization of the following linear result, whose proof is in Sec. 6. Above we have discussed structured matrices that are square, but below we discuss more general structured matrices and vectors.

Lemma 2. Consider the linear system $AX = b$, where the entries of A and b are structured according to an $M \times N$ structure matrix S_A and $M \times 1$ structure vector S_b , respectively. Then the set of entries (a_{ij}, b_k) for which the system has a solution is either measure zero or full measure.

An example of a structured system $AX = b$, where the set of (a_{ij}, b_k) for which the system has a solution is measure zero, is the system of two equations $a_1x = b_1, a_2x = b_2$; here $M = 2$ and $N = 1$. An example of full measure is the system of one equation $ax = b$; here $M = 1$ and $N = 1$. In both foregoing examples $x \in \mathbb{R}$.

3 Bottlenecks and cycle coverability

In this section, we show that for a directed graph G representing a structured system, G is cycle coverable if and only if it does not have a bottleneck, which is true if and only if the structure

matrix $S(G)$ does not have full rank. Together with Theorem 1, this comprises a characterization of robust solutions of structured systems. We begin with a lemma that connects cycle coverage with generic rank. See theorem 3.1 in [17, 16]. For the convenience of the reader, we provide a proof in Sec. 6.

Lemma 3 (Cycle Lemma). A graph G with N nodes is cycle coverable if and only if the generic rank of $S(G)$ is N .

By Lemma 3 and Corollary 1 we conclude if a solution of 2 is robust, then the structure graph corresponding to it is cycle coverable.

Next, we show the equivalence of the properties in Lemma 3 with the nonexistence of a bottleneck. In addition, the Bottleneck Theorem stated below provides more detail on bottlenecks that exist in a graph, and show how that helps diagnose and repair a bottleneck.

Let B be a set of nodes in graph G . The **forward set of B** , denoted by B^\rightarrow , is the set of all nodes g in G for which there is an edge starting at a node in B and ending at g . For $m > 0$, we say a pair of sets of nodes B and B^\rightarrow is a **m -bottleneck** if B has **exactly m nodes more** than B^\rightarrow .

We refer to B as the **bottle** (and usually color its nodes blue) and $K = B^\rightarrow$ as the **neck** (usually colored red). We refer to the nodes in B as **bottleneck nodes**. The word ‘‘Bottleneck’’ connects the B in bottle to the K in neck. Some nodes can be in both the bottle and the neck. These nodes are colored half blue and half red as in Figure 7(b).

A system that has a bottleneck will sometimes have many. Let m_{\max} be the largest value m for which there is a m -bottleneck. Let (B, B^\rightarrow) be a m_{\max} -bottleneck where B has as few nodes as possible. We call such a bottleneck a **minimax** bottleneck. It turns out that there is only one minimax bottleneck.

In the proof of the Bottleneck Theorem (stated below), the bottle B we construct is the minimax bottle. The nodes that are colored blue in Figure 6(b) are a bottle of a 6-bottleneck for both Figures 6(a) and 6(b). Adding node 1 to B creates a bigger bottle of a 6-bottleneck for Figure 6(a). Then it is not a minimax bottle. The Bottleneck Theorem below is a key to why some systems have no robust solutions.

The set of nodes comprising the minimax bottleneck is not always obvious from the graph. The concept of null nodes, described next, allows us to exactly locate the bottleneck.

Definition 1 (Null node). For a matrix A , we say a vector X is a null vector if $AX = 0$. The kernel of A , denoted $\ker A$, is the set of all null vectors of A . For a graph G with structure matrix $S(G)$, the graph nodes (coordinates) can be divided into two groups: coordinates that take the value zero for every vector in $\ker(A)$ for almost every matrix $A \in \mathcal{L}(G)$, and coordinates that are nonzero in some kernel vector of A for almost all A . (Recall that $\mathcal{L}(G)$ is the set of matrices that respects $S(G)$.) Lemma 4 of Section 6 implies that each node belongs to one of the two groups. We will call the latter set of nodes the set of **null nodes**, and denote the set by B_{null} .

Intuitively, null nodes can be thought of as those corresponding to coordinates which are nonzero in at least one kernel vector for a matrix A which is obtained by replacing nonzero entries of the structure matrix $S(G)$ by random numbers (and could be discovered this way in a practical situation). Write $b(G)$ for the number of null nodes of the graph G . The dimension of the null space of A , for almost every A respecting $S(G)$, is $N - r$, where r is the generic rank of $S(G)$ from Lemma 1. Clearly $N - \text{GenRank}(S(G)) \leq b(G)$.

The following result says that the minimax bottleneck has bottle B_{null} and neck $B_{\text{null}}^\rightarrow$.

Theorem 2 (Bottleneck Theorem). Let $S(G)$ be the structure matrix of a graph G with N nodes.

(I) If $\text{GenRank}(S(G)) = N$, then G has no bottlenecks. Assume $\mathbf{m}^* = N - \text{GenRank}(S(G)) > 0$. Then the minimax bottleneck is an \mathbf{m}^* -bottleneck. Also, there is an \mathbf{m} -bottleneck if and only if $0 < \mathbf{m} \leq \mathbf{m}^*$.

(II) The bottle of the minimax bottleneck is the set of null nodes B_{null} .

An algorithm for making a graph robust. Let $\mathbf{m}^* = N - \text{GenRank}(S(G))$. If $\mathbf{m}^* > 0$, then find the minimax bottleneck. We can then reduce \mathbf{m}^* by one by adding an edge from any bottle node to any node that is not in the neck. When this process is repeated \mathbf{m}^* times, the generic rank becomes equal to N .

Remark 1. Computer algebra packages give us a computational means of determining the null node set B_{null} . See Example 2 below to see typical output from Matlab and Maple. The package computes a basis for the null space. When symbolic entries are used in the input matrix, for each null node, the software returns non-zero symbolic formulas for at least one of the basis vectors, and it always returns zero for the nodes which are not null nodes. The software has considerable freedom in choosing a basis and some of the basis vectors can have zero coordinates for some of the null nodes.

Example 2. We show how to use Matlab or Maple together with Thm. 2 to find the minimax bottleneck, and how to eliminate the bottleneck so that the system has robust solutions. Consider the network represented in Figure 5c

In Matlab

```
syms 'f%d%d' [5 5] % write this to define a 5 by 5 symbolic matrix
S=[0, 0, 0, f14, f15; 0, 0, 0, f24, f25; 0, 0, 0, f34, f35; f41, f42, f43, f44, 0;f51, f52, f53, 0, f55];
null(S) % This command calculates a basis for null space of S
```

In Maple

```
with(LinearAlgebra):#call linear algebra package
S=Matrix(5,5, S=[0, 0, 0, f14, f15, 0, 0, 0, f24, f25, 0, 0, 0, f34, f35, f41, f42, f43, f44, 0, f51, f52, f53, 0, f55]):
NullSpace(S) # this command calculates the basis for null space of S
```

$$\text{output: } \left\{ \begin{bmatrix} \frac{f_{42}f_{53}-f_{52}f_{43}}{f_{52}f_{41}-f_{51}f_{42}} \\ -\frac{f_{53}f_{41}-f_{51}f_{43}}{f_{52}f_{41}-f_{51}f_{42}} \\ 1 \\ 0 \\ 0 \end{bmatrix} \right\} \quad (3)$$

The result declares that the null space is one dimensional. Therefore, there exists a one-bottleneck. The nodes 1,2, and 3 are the bottle of the bottleneck, since components 1,2, and 3 of the nullvector can be nonzero. By looking at the outgoing edges of these three nodes, we find that the bottleneck is $S = \{1, 2, 3\} \rightarrow S^{\rightarrow} = \{4, 5\}$.

To repair this bottleneck, it suffices to connect one of the nodes of the set $\{1, 2, 3\}$ to one of the nodes from the same set. Any of the nine possible added directed edges will destroy the bottleneck. As a result, the graph with the single added edge will have a cover, and by Theorem 2, the structure matrix $S(G)$ has rank $N = 5$. The resulting network will have robust solutions, according to Theorem 1.

4 Ecological Networks

One of the key challenges confronted by ecologists is to understand how interactions between species impact community structure, species coexistence, and biodiversity [27, 28, 29]. Ecologists attempt to respond to such questions by visualizing a complex ecological community as a network [30, 31, 32], mathematically represented as a directed graph, as in Figures 1 and 6.

Our initial motivation for this investigation was to determine which ecological networks have one or more robust steady-states. In most ecological networks, each species may be directly influenced by many other species [33], though some of those influences might be quite weak. There has been no general criterion in the ecological literature for determining when a robust steady state exists.

The results in this article allow investigators to determine which edges of the graph are essential for robustness. Ecologists have been unable to address such questions since there has been no criterion in the ecological literature for whether a network is robust. They will now be able to create artificially reduced, or “knock-out”, versions of networks *in silico*, with fewer edges, to test whether a network is fragile or robust when various edges are removed.

When there are N species in an ecological network, their interactions can often be modeled as

$$\frac{1}{x_i} \frac{dx_i}{dt} = -c_i + f_i(x_1, \dots, x_N), \quad i = 1, 2, \dots, N \quad (4)$$

where $x_i > 0$ is the population density of the i^{th} species, c_i is a constant, and $f_i(x_1, \dots, x_N)$ expresses how the growth rate of the i^{th} species depends upon the network [5]. We say X is a **steady state** if all species remain at a constant level, *i.e.*, $\frac{dx_i}{dt} = 0$ for all i .

In a graph representing biological networks, each node represents a species. An arrow $j \rightarrow i$ from species j to species i means species j “directly influences” the density of species i . Many edges are bi-directional. For example an edge which represents interactions between predator-prey is bi-directional. However, other edges may be better represented as uni-directional. The mere presence, or even the scent, of a top predator may have a major effect on a second predator species while the second predator has an almost negligible direct impact on the top predator. For that reason, our results concern directed graphs, allowing both uni-directional and bi-directional influences.

The Competitive Exclusion Principle (CEP) is a statement that two predators that do not interact directly with each other and depend on the same resource cannot coexist. More generally it asserts that if there are more predator species than resource species, then there is no robust steady state.

In other words, if they are coexisting in a natural environment, then some other factor is involved and the ecologist may want to figure out what that factor is. If the steady-state of the network has equations of the form in Figure (1a), then there is no robust steady state. Figure (1c) is a graphical equivalent of (a). We now know that having no robust steady state is equivalent to saying (b) is not coverable by Thm. 1.

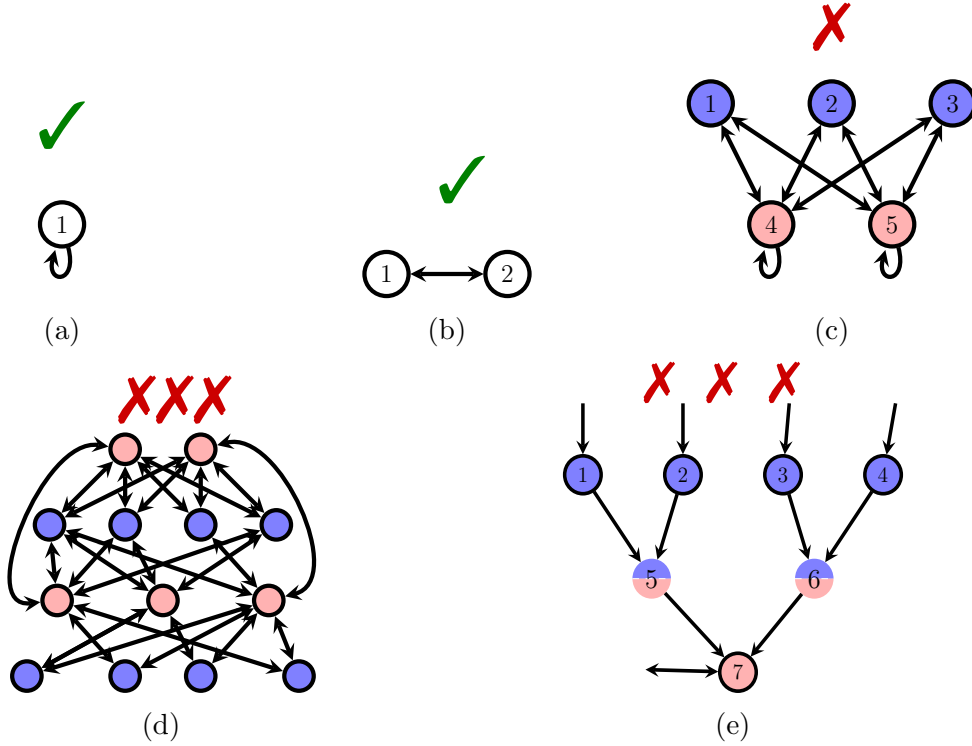


Figure 5: **Examples of robust and fragile graphs.** In each figure, a green checkmark above a graph indicates it is robust, *i.e.*, it has a robust steady state or solution for almost all choices of F that respect the structure of the graph. A red X-mark indicates that every F that respects the graph is fragile; such F have no robust steady states. The number of X-marks is the minimum number of edges that must be added before the graph can be robust. (a) One-node graph, robust. (b) Two-node graph, robust. (c) The blue nodes are a bottle, and the red nodes are the neck. There is a 1-bottleneck. (d) The three X-marks mean there is a 3-bottleneck. (e) Whenever possible, the reader should imagine these graphs as part of a larger network. For a forward bottleneck, edges coming to the nodes of the bottle from nodes in the rest of the graph are allowed without changing the bottleneck, provided they do not come from bottleneck nodes. The bottle and the neck are unchanged. This figure shows a minimax 3-bottleneck that contains smaller bottlenecks, such as the bottles $\{1, 2\}$ or $\{3, 4\}$, or $\{1, 2, 3, 4\}$, or $\{5, 6\}$. Each supports nullvectors. Together these six nodes are the bottle of the forward minimax bottle.

The ecologist S. A. Levin [34] described a biological network that has the graph Figure (1c), but where there is only one predator species (node 3), that is shared by two prey species (nodes 1 and 2). He found again that there can be no robust steady state. Note that the equations and graphs are the same for Levin's case and the CEP, even though the cases are somewhat different. If species i is a predator and j is a prey, increasing the prey will increase the predator, *i.e.* $f_{ij} = \frac{\partial f_i}{\partial x_j}(X) > 0$, but increasing predator will decrease the prey, that is $f_{ji} = \frac{\partial f_j}{\partial x_i}(X) < 0$. Hence for the CEP, f_{12} and f_{32} are positive while f_{21} and f_{23} are negative. For Levin's case, the signs are reversed.

We can extend Levin's insight to all other combinations that correspond to the same graph.

For the graph represented in Figure 1, there are additional possibilities. Two of the species 1 and 2 might be mutualistic, with both terms positive, or antagonistic with both negative. Every choice of positive (+) and negative (-) is a case where there is no robust steady state. There are 2^5 different choices of these terms if we equate cases that are left-right symmetric, corresponding to the structure matrix

$$S = \begin{bmatrix} 0 & 0 & \pm \\ 0 & 0 & \pm \\ \pm & \pm & \pm \end{bmatrix} \quad (5)$$

Our formalism can further be applied to more general graphs, including those that *are* robust. Every edge can be assigned a sign, positive or negative, and each choice for all the edges yields different biology.

Here we note the distinction between stability and robustness for an equilibrium of a dynamical system. McGehee and Armstrong [35] analyzed the CEP from the point of view of both stability and robustness for some special cases. Robust solutions may or may not attract nearby trajectories; an unstable equilibrium will not be observed as a rest state in a natural system. Some combinations of the signs in (5) may cause stability and other instability, but they all share the same structure matrix, which excludes robust equilibria for all combinations of signs.

A substantial research effort has aimed at discovering what stabilizes ecological networks. Some have found ways to promote robustness [36, 37], but there is no gold standard for assessing robustness. Gross et al. [36] suggested two universal rules: Food-web stability is enhanced when (i) “species at a high trophic level feed on multiple prey species”, and (ii) “species at an intermediate trophic level are fed upon by multiple predator species.” Robert T. Paine [38] showed that eliminating one keystone species (in this case, starfish) can cause the ecosystem to collapse. These rules suggest adding edges might enhance the robustness of the ecological network, but it is not the full story.

Figure 5(d) represents an ecological network supporting interactions between species in four different trophic levels. In this figure each blue node species on each level is connected *only* to the species in the adjacent trophic level, though some edges connect red nodes with other red nodes. Let N_1, N_2, N_3, N_4 denote the number of species in each of these “trophic” levels, listing from the bottom to the top.

According to the theory in Section 3, this type of trophic graph cannot be coverable unless the total number of species in the odd-numbered levels, $N_{\text{odd}} = N_1 + N_3$, equals the total of species in the even-numbered levels, N_{even} . Otherwise, let B consist of all the species either in the odd-numbered layers or in the even-numbered layers, whichever is numerically greater. Then B is the bottle of a bottleneck, and B^\rightarrow is the neck, consisting of the remaining species. Here $N_{\text{odd}} = 8 > N_{\text{even}} = 5$, so by the Bottleneck Theorem, at least 3 edges must be added.

Figure 6(a) is a representation of an ecological graph from Figure 1 in Solé and Montoya [4], though equilibria are not discussed there. Our results show that their graph is fragile. In fact, there is a 6-species bottleneck. It should be noted that for this network, quantity alone is not the answer. In order to repair the bottleneck, added edges must be carefully targeted. As an example, Figure 6(b) is made by adding 22 bi-directional (green) edges to Figure 6(a), adding edges throughout the network, but the resulting network, Figure 6(b) is not yet robust. Our theory suggests where the edges must be added to make a system robust.

Write B for the set of blue nodes and B^\rightarrow the red nodes. Since $\#(B) = 12$ and $\#(B^\rightarrow) = 6$, B is a 6-bottleneck so the graph cannot be robust. At least six forward edges starting in B and not ending in B^\rightarrow must be added before the graph becomes robust.

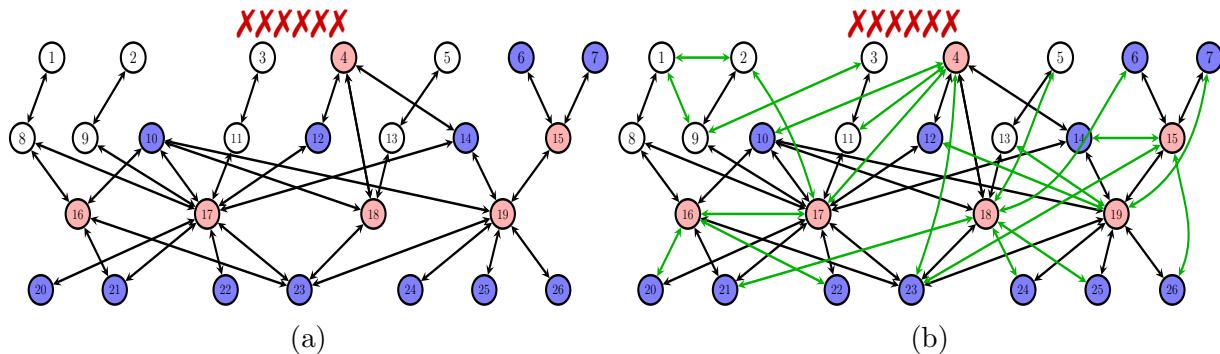


Figure 6: **A bottleneck makes a network fragile.** The six X 's mean six species must be eliminated before it becomes robust – unless carefully chosen edges are added. (a): This graph is reproduced from Figure 1 of Solé and Montoya [4]. Let B denote the 12 nodes shaded blue. Then the forward nodes B^\rightarrow consists of 6 nodes shaded red. Hence B is a 6-species bottleneck. At least six edges that increase the set B^\rightarrow must be added to make the graph robust. (b): 22 bi-directional edges have been added, shown in green, adding at least one edge to every node, and edges between every pair of layers, and edges within each layer except the lowest. These make no difference to the robustness. B is still a 6-species bottleneck.

It is a common occurrence in biological networks that the densities of some species are dependent on an intermediate species, which can be incorporated implicitly. For example, consider the structured equations given in Figure 7(a). These steady state equations demonstrate that the densities of species x_3 and species x_4 both depend on total number of $x_1 + x_2$. The graph give in Figure 7(a) is cycle coverable. That means for almost every $F \in \mathcal{F}(G)$, the structure system is robust. But, the phrase “almost every F ”, means there can be exceptions. The structure system given in Figure 7(a) is such an exception. This type of implicit structure is not supported by our theory. Hence, when we introduce an intermediate species, we first rewrite the explicit structure by introducing a new variable and we are forced to add a new constant c_5 . For example, in Figure 7(b) we add the variable $x_5 = x_1 + x_2$ and the constant, c_5 . The structure graph in Figure 7(b) is not cycle coverable and it agrees by our theory that reports the given structured equation in Figure 7(b) does not have a robust solution.

The general rule is that anytime a function $g(x_1, \dots, x_N)$ occurs in two or more different equations, we can introduce a new variable x_{N+1} and a new equation $x_{N+1} - g(x_1, \dots, x_N) = 0$. The new expanded system and the graph can be analyzed using our results.

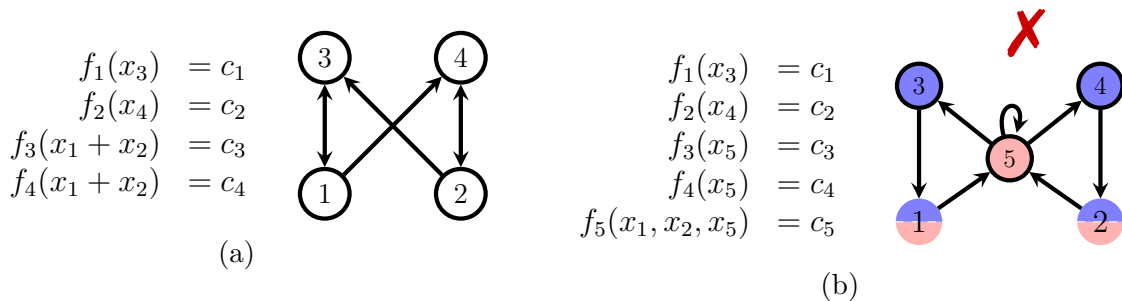


Figure 7: **An example with a forbidden implicit structure.** Suppose we want to consider only equations of the form in (a). Its structure graph is cycle coverable, but there are no robust solutions since we have two equations that involve the expression $x_1 + x_2$ that occurs more than once. Such a restriction is not allowed in our formulation of structured systems. Here $x_1 + x_2$ is over-determined since it must satisfy 2 equations. There cannot be a robust solution for almost any choice of f_3 and f_4 . If the c_3 and c_4 equations are satisfied, a small change in either constant results in no solutions for almost any choice of f_3 and f_4 . We convert the system in (a) into an (explicit) structured system in (b) by adding the variable x_5 and an extra equation, $x_1 + x_2 - x_5 = c_5$. This requires the addition of the constant, c_5 . In (b) there is a bottleneck so there are no robust solutions. Nodes 1,2,3, and 4 constitute a (forward) bottle of a 1-bottleneck. The forward minimax bottle however consists of nodes 1 and 2. Nodes 3 and 4 are a backward minimax bottle. This example was motivated by the systems represented by Akhavan and Yorke [9].

5 Discussion

We show in this article how the basic lesson of the Competitive Exclusion Principle of ecology can be extended to a general concept that applies to all systems of N equations in N unknowns that respect an underlying structure. Our interest was in proving what the structure itself implies about robustness of solutions in the generic case, regardless of the specific values that coefficients of the equations may take.

In particular, we proved the equivalence of three ostensibly different views of structured systems, including cycle coverage, rank of the structure matrix, and the existence of topological obstructions to robust solutions, called bottlenecks. Depending on what is known about the network model, or class of models, one or another of the views may be most informative. These results have immediate implications to possible graph structures, for example precluding robust solutions in strictly trophic food webs without intraguild interaction, unless strict constraints on the number of species in each guild are satisfied. These constraints are direct generalizations of the CEP. Interestingly, they may have extensive implications for systems in general, outside ecology.

The Bottleneck Theorem is an extended version of the Competitive Exclusion Principle. If the generic rank of a structure matrix is not maximal, then there must exist a (minimax) bottleneck. Suppose there is a bottleneck. One could think of the bottle as being a set of predator species and the neck as prey species. Hence, there are more predator species than prey species, and these predators depend directly only on the preys and not on each other. The Bottleneck Theorem says the correct generalization of the Competitive Exclusion Principle is not about predators and preys. It says that if a collection of species depends purely on m^* fewer species, there can not be

a robust steady state. That is a statement about the equations of nature. That generalizes to a statement about the nature of (structured) equations: if a collection of equations depends upon m^* fewer variables, then there is a m^* -backward bottleneck, so for every F that respects the graph G there are no robust solutions, and for *almost every* F that respects the graph G there are no solutions, not even fragile solutions.

Our results depend on the notion of “almost every” structured system in the sense of prevalence. That means that each equation that is allowed to depend on a given variable, according to the structure matrix $S(G)$ that is imposed, is allowed to do so independently of other equations. In other words, there are no other hidden constraints among the dependencies allowed in $S(G)$. One could pose such constraints, and consider the effects on the robustness results, but we leave that investigation in general to future work.

6 Proofs

This section collects proofs of the results stated above. We will make liberal use of Fubini’s Theorem.

First we mention some notations that we will use herein.

$S = S(G)$ denotes the $N \times N$ structure matrix of a graph G .

$E(G)$ denotes the number of edges in G , correspondingly, number of nonzero entries in $S = S(G)$.

Fubini’s Theorem (special case). Let Z be a subset of the Euclidean space $\mathbb{R}^{N_1} \times \mathbb{R}^{N_2}$.

(L_Z) : Z has measure zero

if and only if

(L_X) : the intersection of Z with each translate $\{X\} \times \mathbb{R}^{N_2}$ has measure zero for almost every $X \in \mathbb{R}^{N_1}$.

The above happens if and only if

(L_Y) : the intersection of Z with the translate $\mathbb{R}^{N_1} \times \{Y\}$ has measure zero for almost every $Y \in \mathbb{R}^{N_2}$.

Proof of Lemma 1.

Let r be the maximum of the rank of A for $A \in \mathcal{L}(G)$. Choose $M \in \mathcal{L}(G)$ to have rank r . The matrix M has some collection of r rows and r columns such that the determinant denoted \det_r of the restricted matrix M_r has non-0 determinant. For any matrix $A \in \mathcal{L}(G)$ write A_r for the restriction to those columns and rows, and write \det_r for the corresponding determinant. If $\det_r A_r \neq 0$, then $\text{rank}(A) = r$. Let $Z = \{A \in \mathcal{L}(G) : \det_r A_r = 0\}$. Let $\mathcal{P}_0 \subseteq \mathcal{L}(G)$ be the set of matrices A for which $\text{rank} A < r$. We will prove \mathcal{P}_0 has measure zero. Note that $\mathcal{P}_0 \subseteq Z$, so it suffices to prove Z has measure zero in $\mathcal{L}(G)$.

Consider the one-dimensional subspace $E_0 = \{\lambda M : \lambda \in \mathbb{R}\}$ of $\mathcal{L}(G)$. We examine translates $A + E_0$ and show that each such translate, i.e for each A in $\mathcal{L}(G)$, $A + E_0$ intersects Z in a finite set.

For each A in $\mathcal{L}(G)$, $\det_r(A_r + \lambda M_r)$ is a degree r polynomial in λ . It equals $\lambda^r \cdot \det_r(\frac{1}{\lambda} A_r + M_r)$. It is not identically zero since for large λ , $\det_r(\frac{1}{\lambda} A_r + M_r)$ is approximately $\det_r(M_r)$, which by assumption is non 0.

By the Fundamental Theorem of Algebra, such a polynomial can be zero for at most r values of λ . Hence, each line $A + E_0$ intersects Z in at most r points, a finite set. Hence, Z is essentially a surface (with turning points and singularities) whose dimension is 1 less than that of $\mathcal{L}(G)$. Therefore Z has measure zero with respect to Lebesgue measure on $\mathcal{L}(G)$. Hence, almost every matrix in $\mathcal{L}(G)$ has rank r . \square

Alternative proofs are available in algebraic geometry, but our goal here has been to provide intuition concerning the geometry of Z .

6.1 Proof of Theorem 1

Proof of part(I).

For each F , let $Z = \{(X, A) : \text{rank}(DF(X) + A) < r\}$.

For each X , let Z_X be the intersection of Z with $\{X\} \times \mathbb{R}^{E(G)}$.

For each A , let Z_A be the intersection of Z with $\mathbb{R}^N \times \{A\}$.

Note that Z , Z_X , and Z_A are closed sets.

Write $\mathcal{P} = \mathcal{L}(G)$, which can also be written $\mathbb{R}^{E(G)}$. Recall \mathcal{P} is a finite-dimensional subspace of $\mathcal{F}(G)$. Write $\mathcal{P}_0 = \{A \in \mathcal{P} : \text{rank}(A) < r\}$.

To conclude prevalence, recall the meaning of \mathcal{P} in our definition of prevalence. To prove the Theorem 1, part (I), according to the Fubini Theorem it is sufficient to show that Z_X is of measure zero for almost every $X \in \mathbb{R}^N$.

To prove (L_X) , let $\sigma : \mathcal{P} \rightarrow \mathcal{P}$ be the translation given by $\sigma(A) = A + DF(X)$. Then $(X, A) \in Z_X$ if and only if $\sigma(A) \in \mathcal{P}_0$. Since σ is a translation, mapping Z_X onto \mathcal{P}_0 , σ preserves measure, proving the claim since \mathcal{P}_0 has measure 0 by Lemma 1, and thus proving Theorem 1, part (I). \square

Proof of Theorem 1, part(II). Let dX denote a volume element at the origin with volume denoted $|dX|$ so we can write $X + dX$ for the volume translated to X . For $U \subseteq \mathbb{R}^N$,

$$\text{Volume}(F(U)) \leq \int_U |\det DF(X)| \cdot |dX|$$

If $DF(X)$ has rank less than N , then $\det DF(X) = 0$. It follows that the set $F(\mathbb{R}^N)$ has measure 0. \square

6.2 Proof of Theorem 2

In the proofs below $A = (a_{ij})$ is in $\mathcal{L}(G)$. Thus, the a_{ij} 's are required to be zero for certain i, j in the structure matrix.

Proof of Lemma 2. Let t denote the number of unspecified entries of b . Rearrange the structure matrices S_A, S_b so that the first t positions of S_b are allowed to be nonzero and the remaining $N - t$ are zero. Define A_1 to be the top t rows of A and A_2 the last $N - t$ rows of A . Hence, $AX = b$ can be rewritten as follows.

$${}_{N-t} \begin{bmatrix} A_1 \\ A_2 \end{bmatrix} X = \left. \begin{bmatrix} b_1 \\ \vdots \\ b_t \\ 0 \end{bmatrix} \right\} {}_t \quad {}_{N-t}$$

By Lemma 1, the rank of A is constant for almost every (A_1, A_2) respecting A . Hence, for such A , $\dim(\ker(A))$ is constant. Since $\ker(A) = \ker(A_1) \cap \ker(A_2)$, $\dim(\ker(A_1) \cap \ker(A_2))$ is also constant. $\dim(A_1(\ker(A_2))) = N - \dim(\ker(A_1) \cap \ker(A_2))$ is a function of the entries a_{ij} that takes a fixed integer value on a full measure set of a_{ij} . If this fixed value is t , then there is a solution for almost every A and every b . If the fixed value is less than t , almost every b is not in the image of A , so there is no solution for almost every (A, b) . \square

Proof of Lemma 3. The existence of a cycle covering for G is equivalent to the existence of N edges $\{v(1) \rightarrow u(1), \dots, v(N) \rightarrow u(N)\}$ in G such that the sets $\{u(1), \dots, u(N)\}$ and $\{v(1), \dots, v(N)\}$ are both equal to $\{1, \dots, N\}$. That is equivalent to there being a matrix $M = (m_{ij}) \in \mathcal{L}(G)$ such that $m_{ij} = 1$ when $j \rightarrow i$ is one of the edges and otherwise $m_{ij} = 0$. Since M has exactly one non-0 entry in each row and in each column, M maps all of coordinate basis vectors e_i to all of the coordinate basis vectors. Hence it has rank N . By Lemma 1, the structure matrix has generic rank N . \square

Now we give a formal definition of null nodes, that shows that Def. 1 is well-defined. For each integer j , let S_j be the set of matrices $A \in \mathcal{L}(G)$ such that for all X in $\ker(A)$, the coordinate $x_j = 0$. The set S_j is a subset of an $E(G)$ dimensional space. Any nonsingular matrix that respects the graph (if there are any) is automatically in S_j .

Lemma 4. For each integer $1 \leq j \leq N$, either S_j or its $\mathcal{L}(G)$ -complement S_j^c is measure zero.

Then we recognize node j as a null node if S_j is measure zero. In other words, such a node has nullvectors in $\ker(A)$ with coordinate $x_j \neq 0$ for almost every $A \in \mathcal{L}(G)$.

Proof of Lemma 4. Recall that for each integer k , S_k is the set of matrices A such that $G(A) = G$ and for all X in $\ker(A)$, the coordinate $x_k = 0$. The set S_k is a subset of an $E(G)$ dimensional space, where $E(G)$ denotes the number of edges in the structure matrix. Lemma 4 claims that for each integer $1 \leq k \leq N$, either S_k or its complement S_k^c is measure zero.

Without loss of generality, set $k = 1$. The proof proceeds by noting that a matrix A is in S_1^c if and only if there exists an X in $\ker A$ with nonzero first component x_1 . Hence,

$$\begin{aligned} a_{11}x_1 + \dots + a_{1N}x_N &= 0 \\ &\vdots \\ a_{N1}x_1 + \dots + a_{NN}x_N &= 0 \end{aligned}$$

with $x_1 \neq 0$, which is equivalent to

$$\begin{aligned} a_{12} \frac{x_2}{x_1} + \dots + a_{1N} \frac{x_N}{x_1} &= -a_{11} \\ &\vdots \\ a_{N2} \frac{x_2}{x_1} + \dots + a_{NN} \frac{x_N}{x_1} &= -a_{N1} \end{aligned}$$

having a solution. According to Lemma 2, this occurs for either a measure zero or full measure subset of the a_{ij} . \square

Lemma 4 can be illustrated explicitly for 2×2 structure matrices A . Let

$$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix},$$

where some of the entries may be 0 in the structure matrix. The reader should understand that each set $\{\dots\}$ below is a subset of $\mathcal{L}(G)$. Without loss of generality, we describe set of matrices S_1 as follows

$$S_1 = \{a_{11}a_{22} - a_{12}a_{21} \neq 0\} \cup \{a_{12} = 0 \text{ and } a_{11} \neq 0\} \cup \{a_{22} = 0 \text{ and } a_{21} \neq 0\},$$

and accordingly, its complement is

$$S_1^c = \{a_{11}a_{22} - a_{12}a_{21} = 0\} \cap \{a_{12} \neq 0 \text{ or } a_{11} = 0\} \cap \{a_{22} \neq 0 \text{ or } a_{21} = 0\}.$$

If the structure matrix allows all entries of A , then (S_1^c) is of measure zero, and so S_1 has full measure.

On the other hand, if the structure matrix requires $a_{11} = a_{21} = 0$, the roles are reversed. In that case S_1 is of measure zero and so S_1^c has full measure.

Proof of Theorem 2, Part (I). Assume there is a \mathbf{m} -bottleneck (B, B^\rightarrow) . Therefore B and B^\rightarrow have b and $b - \mathbf{m}$ nodes, respectively, where $b > 0$. The $N \times b$ submatrix S_B of S consisting of the b columns represented by the nodes of B has $b - \mathbf{m}$ nonzero rows, the rows corresponding to nodes of B^\rightarrow . Thus, the kernel of S_B is at least \mathbf{m} -dimensional, which implies the same about the kernel of S , and so $\text{GenRank}(S) \leq N - \mathbf{m}$. Moreover, the structure matrix can be written as the following

$$S = \begin{bmatrix} b & N-b \\ 0 & \star \\ \star & \star \end{bmatrix} \begin{matrix} N - b + \mathbf{m} \\ b - \mathbf{m} \end{matrix} \quad (6)$$

where we have renumbered the nodes so that B consists of the first b columns and where we have situated the $b - \mathbf{m}$ nonzero rows at the bottom of the matrix for simplicity (the nonzero rows could be anywhere in S).

Conversely, let $\mathbf{m}^* = N - \text{GenRank}(S) > 0$. We will show that S must have form (6) with $\mathbf{m} = \mathbf{m}^*$, with the proviso, as above, that the bottom $b - \mathbf{m}^*$ nonzero rows could occur anywhere in S . Let $B = \text{Null}(S)$ be the set of nodes j such that S_j is measure zero guaranteed by Lemma 4. For a node j in B , $x_j \neq 0$ for some $x \in \ker(A)$ for almost every A that respects S .

If B is the empty set, then the intersection of the S_j is a full measure set, i.e. for almost every A respecting the structure S , $\ker(A) = \{0\}$, a contradiction to S being rank deficient. Thus B is nonempty, and $b = |B| > 0$. Note that if j is in the complement B^c , then $x_j = 0$ for every vector x in $\ker(A)$, for every A not in the measure zero set $T = \bigcup_{j \in B^c} S_j^c$. We use this fact below.

Consider matrices A that respect the structure matrix, and are not in the set T . Renumber the nodes such that $B = \{1, \dots, b\}$. Let A_B denote the submatrix of first b columns of A . Since A is not in T , $x_{b+1} = \dots = x_N = 0$ for x in $\ker(A)$, so we can assume $\ker(A) = [U, 0, \dots, 0]$, where U is a dimension \mathbf{m}^* subspace of \mathbb{R}^b , and the space U^\perp is $b - \mathbf{m}^*$ dimensional. For almost every A satisfying S , the rows r_1, \dots, r_N of the submatrix A_B must all be in U^\perp , and satisfy the following

two properties, proved below: (1) the nonzero rows of A_B are linearly independent, and (2) no set of p columns of A_B contains all of the nonzero entries of p or more nonzero rows. Property (1) forces all but $b - \mathbf{m}^*$ of the rows of A_B to be zero rows in the structure S . Thus the first b columns of A have at most $b - \mathbf{m}^*$ nonzero rows. Let K be the set of indices of $b - \mathbf{m}^*$ rows which include the nonzero rows. Then (B, K) is an \mathbf{m}^* -bottleneck. The set K is shown as the last $b - \mathbf{m}^*$ nodes in (6), but they could be any of the rows of A .

Finally, we verify (1) and (2). If $b = 1$, (1) is true because if any entry in the (single) column of A_B is nonzero, the first component of vectors in $\ker(A)$ is zero for almost every A , a contradiction to the definition of B . For $b > 1$, we induct on b . Let $0 = \sum c_i r_i$ be a dependency of rows of A_B , where all $c_i \neq 0$. If the union of the coordinates appearing in the rows of the r_i does not include all b coordinates, use the induction hypothesis. If they include all b coordinates, clearly no such dependency exists, for almost every A . To verify (2), suppose there are columns c_{i_1}, \dots, c_{i_p} and p such rows. By (1), the rows are linearly independent, and their entries are restricted to p columns. Therefore, any vector $x = (u, 0, \dots, 0)$ in $\ker(A)$ must be zero in entries u_{i_1}, \dots, u_{i_p} . This contradicts the fact that i_1, \dots, i_p are null nodes. \square

Proof of Theorem 2, Part (II). Note that B_{null} is the \mathbf{m}^* -bottleneck used above in the first part of the proof, where \mathbf{m}^* is such that $\text{rank}(S) = N - \mathbf{m}^*$. No bottleneck exists with larger \mathbf{m} , by Part (I). Also, B is minimal because no node can be deleted without the bottleneck becoming an \mathbf{m} -bottleneck for $\mathbf{m} < \mathbf{m}^*$, due to property (2) above. Therefore B_{null} is the minimax bottleneck. \square

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