USING HIERARCHY AND DIRECTIONALITY TO STUDY THE STRUCTURE AND DYNAMICS OF DIRECTED COMPLEX NETWORKS

by

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ABSTRACT

A huge range of vitally important systems from social to biological and from economic to technological can be represented as complex networks hence it is crucial to understand the dynamics and structure of these networks. Many real-world interactions are also intrinsically directed and hence best represented by directed networks. Directed networks admit unique features such as the fact that the edges may align with a global direction. We use the recent methodology of Trophic Analysis to show how the directional hierarchy in directed networks affects the structure and dynamics on these networks. In this work, we review the range of techniques used to quantify hierarchy in directed networks. We show how hierarchy relates to the emergence of strongly connected components in real networks. We relate hierarchical structure to the performance of directed Hopfield-like networks and the ability of a network to be influenced by a small number of nodes. We further analyse how hierarchy can arise in networks by studying a fitness-based generative model and how the properties of the generative model relate to the structures measured via Trophic Analysis. This thesis furthers our understanding of how the behaviour of directed networks relates to their hierarchical organisation and global directionality.

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LIST OF PUBLICATIONS

This thesis is based on the following published peer-reviewed work, incorporated via the University of Birmingham alternate thesis format guidance:

- Niall Rodgers, Peter Tiňo, and Samuel Johnson. “Network hierarchy and pattern recovery in directed sparse Hopfield networks”. In: *Physical Review E* 105.6 (June 2022), p. 064304. ISSN: 2470-0045. DOI: 10.1103/PhysRevE.105.064304. URL: https://link.aps.org/doi/10.1103/PhysRevE.105.064304
- Niall Rodgers, Peter Tiňo, and Samuel Johnson. “Strong connectivity in real directed networks”. In: *Proceedings of the National Academy of Sciences of the United States of America* 120.12 (2023). ISSN: 10916490. DOI: 10.1073/pnas.2215752120
- Niall Rodgers, Peter Tiňo, and Samuel Johnson. “Influence and influenceability: global directionality in directed complex networks”. In: *Royal Society Open Science* 10.8 (Aug. 2023). ISSN: 2054-5703. DOI: 10.1098/rsos.221380. URL: https://royalsocietypublishing.org/doi/10.1098/rsos.221380
- Niall Rodgers, Peter Tiňo, and Samuel Johnson. “Fitness-Based Growth of Directed Networks with Hierarchy”. In: *Journal of Physics: Complexity* (Aug. 2024). ISSN: 2632-072X. DOI: 10.1088/2632-072X/ad744e.

In all of the above work I was first and corresponding author, wrote the manuscripts, conducted the numerical simulations and analytics and conceived much of the research direction. While my co-authors, my PhD supervisors, provided a supervisory role, guidance on the research direction and editing. Edited and typeset versions of the above work can be found in the respective journals. Versions of the above work are also available on arXiv.

The literature review of this thesis is written such that a standalone extended version with some additional contribution can be submitted to the arXiv and for potential publication. This is expected to occur around or after the time of thesis submission and examination.

CONTENTS

CHAPTER

1

INTRODUCTION

The world we inhabit is shaped by the interactions of large complex systems spanning a vast range of fields and scales. From ecosystems to economies, the internet to infrastructure and other diverse domains from social networks to brain networks. These systems are made up of a large number of interacting elements where the complexity of studying them arises from the irregular but structured interactions between the elements of the system. Such systems can be heterogeneous with varying importance and function of the individual elements. Additionally, these systems may exhibit complex non-linear responses to stimuli and varying amounts of feedback. Despite the diverse range of applications and scales many of these systems share features and structures which can be illuminated by the field of network science. In this framework, the system under investigation can be represented by a generic mathematical object, such as a graph or network, allowing the behaviour of many diverse complex systems to be understood by studying the structure and dynamics of these mathematical objects.

In this work, inspired by the fact that many real-world complex systems with directed interactions, such as food-webs, social or economic networks [5, 6, 7, 8], exhibit some degree of linear hierarchy and global directionality, we study how hierarchy affects the structure of a directed networks, how this type of structure can emerge and how this structure affects dynamics on networks. In particular, we use the technique of Trophic Analysis [8], a technique to measure hierarchy in networks, to study these phenomena and demonstrate its utility for understanding directed complex networks.

1.1 Network Science

The field of modern network science, in which this thesis resides, emerged roughly around the turn of the century. It is a distinct field in its own right, while being extremely interdisciplinary, with applications being found and inspiration taken from across many disciplines of science [9]. The field grew from a few key early results into a maturing field with institutes and groups dedicated to network science research [9]. However, it is still relatively new on the scale of scientific disciplines and it is interesting to note that the author of this thesis is approximately the same age as the field of network science. One of the key breakthroughs of early network science was to show how relatively simple network features were present in a wide array of real-world systems and to highlight the consequences of these features for the dynamics of these systems. Over the years, it has been shown that a huge number of scientific fields and concepts can be studied via the language of network science [10, 9]. This can include food-webs, economic and financial networks, social networks, the Internet, Wikipedia, artificial and biological neural networks, metabolic networks, genetic networks, transportation networks, infrastructure networks and many more possible examples.

The field of network science formed in the synthesis of already existing ideas from graph theory, statistical physics, sociology and computer science. However, a key fact that allowed it to emerge as a distinct field was the time period. More widespread computing resources allowed more people to study large networks and analyse their structure, which is not practical by hand for almost any real system. While the popular emergence of the internet allowed the sharing of datasets and the structure of the web and early social networks provided new objects to study and inspiration to study the structure of networks.

One of the foundational results of early network science was the concept of the small-world network model [11], with the paper proposing it [11] having been cited tens of thousands of times. This model of undirected networks expresses the idea that many complex networks have local clustering but that the length of a path between any two nodes is significantly less than the number of nodes in the network. This is something that is very commonly observed in many diverse real-world systems such as in social networks through the “six-degrees of sepeartion” phenomena. The idea, well known in popular culture, that any two people are connected in a small number of steps relative to the potentially billions of users of a social network. This effect can also be found in collaboration networks in both film and science where the Bacon number measures the number of connections required to reach the actor Kevin Bacon in film collaboration networks and the Erdős number which measures the number of connections from the mathematician Paul Erdős in co-authorship networks.

Again, despite the number of people involved in these systems being very large most people in the system have a Bacon or Erdős number which is very low. Similarly, it is also possible to traverse between any two Wikipedia pages in a small number of steps by clicking through links present on the page due to this affect. The fact that a relatively simple observation [11] explains phenomena observed in many diverse systems shows the goals and explanative power of network science which motivates the continued growth of the field.

Another of the key observation made in the early years of modern network science was the concept of the scale-free network [12]. Where again, the proposing paper has been cited tens of thousands of times and highlights a relatively intuitive concept which was thought to be present in many systems. However, there has been more recent doubts regarding the ubiquity and universality of this phenomena [13, 14]. A scale-free network is defined as a system where the degree of the nodes follows a power-law distribution [12]. This means that the majority of nodes, by number have a small number of connections but there a few nodes which have a very large number of connections, orders of magnitude greater than the modal or median value. Even if in practice, some systems do not fit the mathematical definition [13, 14] it captures a key feature of network science, that in the systems of study there may be a huge imbalance in the importance of certain nodes in the system. In online social networks, there are users with millions more followers than a more standard user. In transport networks, hub stations and airports have much more connections than smaller local sites. In citation networks, a small number of papers receive a very high number of citations compared to most other papers published. The wide range of importance individual elements of a system can take is a key feature of network science. The importance of this feature to network dynamics and stability is also something we frequently observe in everyday life, when news or memes go viral after being shared by large accounts or an issue at a key train station causes disruption across the network.

One of the most well studied and important problems in network science is determining methods to find which nodes are the most important in these heterogeneous systems, known as the centrality of a node. This could be a simple measure like the number of connections a node has, degree centrality, or take into account other aspects of the network structure [10]. For example, a node is likely to be more important if it is also connected to nodes which are also important which is the idea behind Eigenvector centrality [10]. Many different centrality measures exists [10] which serve a particular niche and quantify importance in a way suited to an application. One of the most impactful discoveries related to network science was that of PageRank centrality [10, 15]. This algorithm which has been now widely used in network science was originally designed to rank websites. It was developed by the founders of Google and helped in the creation of the search engine which has changed how we interact with the world. This clearly demonstrates the impact and relationship that the networks have with the modern world.

Another well known facet of network science is the concept of community structure. This is the idea that a network can be decomposed into groups where the nodes in each group are more densely connected within the same group compared to nodes outside of the group, with early work on the concept again being cited thousands of times [16]. The study of the impact of communities on network dynamics and algorithms to detect community structure has since become widely studied field within network science [17]. Clearly, community structure is very important to many aspect of network science and impacts on everyday life. How beliefs propagate in society is shaped by the online communities in which people interact. While how diseases spread is shaped by the community structure of the social networks that we inhabit. Community detection algorithms can also reveal features of the nodes which relate to the group formation answering questions related to sociology and inequality. Community structure is again something which is very intuitive and can be observed in everyday life across a range of settings.

1.1.1 Importance of Directed Interactions

Despite the widespread success of network science, directed networks are still an understudied area compared to undirected networks [18], with much of the research focusing on generalising previous results on undirected networks to the directed case. Directed networks are an important field of network science as many real-world systems such as social networks, ecosystems, economic networks and many more feature intrinsically directed interactions. There are several reasons which explain the relative understudy of directed networks compared to the undirected case [18]. Many real-world systems may be well modelled by undirected networks, hence if you work on these systems there is less motivation to consider the directed case. As directed networks feature an asymmetric adjacency matrix some calculations can become more difficult as the matrix has a complex spectrum. Notions of connectivity become more difficult to describe in a directed network since there now distinct values of in and out degrees. This makes it more difficult to quantify the importance of a nodes. There is also the additional concept of strong and weak connectivity, when considering if there is a path between all the nodes in a network or not we need to consider if we respect the directionality of the edges or not. Directed networks may feature components which are reachable only in one direction, a concept which may complicate notions of dynamics, influence and stability. As such directed networks are more complex than a simple of extension of an undirected network to an asymmetric adjacency matrix [18]. Directed networks have properties unique to the directed case such as varying levels of normality, how close the adjacency matrix is to commuting with its transpose [18, 8, 19, 20]. In this thesis, we study one such feature of directed networks. Principally that nodes in a directed network may be given a local ranking corresponding to their position in the one-dimensional flow hierarchy created by the fact that the edges align with some global directionality. To study this phenomena we employ and study the technique of Trophic Analysis [8] which was originally devised to study the directional organisation present in food-webs and study their stability [5].

1.2 Outline of Thesis

This thesis utilises the method of Trophic Analysis [8] which is used to to study the hierarchical organisation and global directionality present in many directed networks. In this work, we present a series of results which use this methodology to study the structure and dynamics of these systems, using the most recent definition of Trophic Analysis put forward in [8]. This thesis is presented using the Alternative Thesis Format laid out in the University of Birmingham regulations and as such papers are presented in the published form, leading to duplication of some background sections.

In Chapter 2, we present a review of the different ways hierarchy has been understood and quantified in the literature and introduce Trophic Analysis and the relevant background for this work. This review provides the first summary of all the applications of Trophic Analysis as well as highlighting the methodologies closely related to this technique. In addition, it highlights the broad range of methods used to quantify local hierarchy across scientific disciplines as well as detailing the global measures of network structure which relate to the Trophic Incoherence. This review provides a high-level overview of the vast range of techniques which can be used to quantify hierarchy in directed networks while also relating the idea of network hierarchy to global organisation of the network, something which as far as we are aware was not present in the recent literature at the time of the PhD. A standalone extended version of this review is intended to be submitted to the arXiv pre-print server and for potential publication.

In chapter 3, we present the paper “Strong Connectivity in Real Directed Networks” [2], which was written during my PhD. This work highlights how Trophic Analysis can be used to analytically predict the emergence of large strongly connected components in real directed networks. It demonstrates how a network being strongly connected implies that there should be edges which do not follow the hierarchical ordering. This fact is then exploited to derive the main result of the work and show that in some systems the strongly connected component may rely on only a small number of edges. In the appendix, we demonstrate the importance of the strongly connected component for various dynamics.

In chapter 4, we present the paper “Influence and Influenceability: Global Directionality in Directed Complex Networks” [3] written during my PhD. In this work, we explore various concepts related to network influence and relate them to Trophic Analysis. We show how the ability to use hierarchy to influence the state of various dynamics by targeting a small number of nodes at the bottom of the hierarchy depends on the global directional organisation of the network. This is shown for models of opinion and synchronisation. We further show how hierarchy can be used to predict the most prevalent strategies in networks representing generalised rock-paper-scissors games. We also show how many structural quantifiers of network influence and spectral features can be understood via Trophic Analysis.

In chapter 5, we present the paper "Network hierarchy and pattern recovery in directed sparse Hopfield networks " [1]. This was the first paper written during during my PhD. This work studied the dynamics of directed sparse Hopfield-like networks. This first work provided the foundations which allowed the later insights of my PhD to be made. In this work, we show how the pattern recovery performance of networks depend on the trophic incoherence and the location in the hierarchy the pattern is presented at. The motivation for this work was the observation that biological neural networks operate in an intermediate incoherence regime between the layered architecture of deep neural networks and the incoherent structure of a recurrent neural network based on a complete or random graph. We also highlight the network features which lead to networks with higher pattern recovery performance at a given trophic incoherence.

In chapter 6, we present the paper "Fitness-Based Growth of Directed Networks with Hierarchy" [4]. This was the one of the last projects of my PhD and attempts to explain the ubiquity of hierarchy in real systems using a simple generative model to explain this. This model combines degree-based preferential attachment with interactions between node fitness variables. In this work, we analyse the utility and limitations of using Trophic Analysis to infer the properties of this model. As well as highlighting a range of features of this model, in particular that the interplay of the different types of preferential attachment can lead to a wide spectrum of networks structures with a wide range of global directionality. We also link this work to the study of real systems and attempt to quantify under which conditions Trophic Analysis can reveal underlying information about the properties of the nodes.

In chapter 7, we review the results presented in this thesis, discuss the progress made in evolving our understanding of hierarchy in directed networks by this work and the common themes explored in each of the chapters. We also give an outlook on general trends within network science and the explore the potential future development of Trophic Analysis.

CHAPTER

2

LITERATURE REVIEW

2.1 Introduction

In this review, we highlight the technique of Trophic Analysis, a technique which is used to quantify the linear flow hierarchy and global directionality found in directed complex networks as well as review the literature surrounding hierarchy and directionality in directed networks. We review how the concept of hierarchy is understood in the networks literature. We give an overview of the wide range of techniques and methodologies used to quantify hierarchy. In particular, we highlight the techniques which are closely related to Trophic Analysis and point out the connections between these methodologies. We list all the areas where Trophic Analysis has been applied to highlight the array of applications for which hierarchy can be a useful tool. Additionally, we briefly review the global network measures which have been linked to Trophic Analysis and where they have been applied. In this review, we cannot hope to cover in detail the vast array of ideas and concepts of hierarchy that have been used to study complex networks. However, we hope to give some insight into the range of techniques and approaches available and connections between methodologies. This review presents the first time the applications of Trophic Analysis have been detailed in this way and presents the most up to date list of applications of this technique as of mid 2024. It also provides a starting point to understand the range of techniques used in this area which may be of use to a researcher who begins working on network hierarchy.

2.1.1 Distinct Notions of Hierarchy

In network science and general usage “hierachy” and “directionality” can refer to many distinct notions and ideas. In this work, we refer to hierarchy as a flow hierarchy. This means that the hierarchical structure is derived from the fact that it may be possible to label the nodes such that many of the edges generally point in the same direction in a one dimensional space. Then how strict the hierarchy is can be related to how many of the edges point upwards a specific distance in this space. This is a natural type of hierarchy for many systems. For example, in a food-web where there is a clear flow of energy up the hierarchy from plants to herbivores to carnivores. Additionally, this kind of hierarchy is natural in supply chain networks, where for example a rare earth metal goes into a processor which goes into a consumer electronic device. There can however be many different facets and details of how a flow hierarchy is understood, quantified and what types of networks are considered hierarchical [21]. However, since early in the field of network science [22] “hierarchy” and “hierarchical” has also been used to refer to different network features related to modular structure, clustering, the building of a network from groups of smaller structures or other concepts related to degree [23]. Some of these types of concepts may be referred to as “nested hierarchy” [24, 25, 26]. This kind of organisation is important in varied applications and found in many undirected networks [22, 27]. This is a well used vocabulary and concept with various definitions and methodologies which use the terminology of “hierarchy” to refer to various network features and structures which are distinct from flow hierarchy [27, 28, 24, 29, 26, 30]. We will not discuss the details of this type of hierarchy in this work, since we focus only on the type of flow hierarchy related to ranking and directionality present only in directed networks. However, we note the unfortunate overlap in terminology between the concepts, which can lead to confusion when searching the literature. It was considered whether we should use a new set of terminology when discussing Trophic Analysis but we feel the phrasing is too natural and has become too ubiquitous to introduce new terminology.

2.2 Trophic Analysis

Trophic Analysis is a technique for measuring the flow hierarchy and global directionality present in directed complex networks first proposed in [5] and redefined in [8] to be more widely applicable. It is a method which pairs the calculation of local hierarchy, trophic level, with a measure of global ordering, trophic incoherence. In the following, we present the method and detail the wide range of areas where it has been applied. Trophic Analysis has the key feature that the rankings are very explicitly tied to the global directionality parameter which means that the local rankings are closely tied to a global understanding of the network structure. It is also designed to be interpretable and simple to calculate to promote its use in applications.

In this work, we use the following convention to define the adjacency matrix which represents a directed unweighted complex network,

$$A_{ij} = \begin{cases} 1 & \text{if there exists an edge } i \to j, \\ 0 & \text{otherwise .} \end{cases} \quad . \tag{2.1}$$

Each node i then has an in-degree $k_i^{in} = \sum_j A_{ji}$ and an out-degree $k_i^{out} = \sum_j A_{ij}$. Weighted networks can easily be defined by multiplying the value by the strength of the edge. Aspects of Trophic Analysis are invariant to transposing the adjacency matrix, so some features may be unchanged if the convention is altered. However, care must be taken with what is considered the “bottom” and “top” of the hierarchy as this can flip. The problem of adjacency matrix convention is a general issue in directed networks and care must be taken with it when comparing methodologies. Particular care should be taken when using real networks, for example if you take a directed social network should the edges point towards people you follow or be reversed to account for the direction that the information and content flow?

2.2.1 Original Definition

The original definition of Trophic Analysis was proposed in 2014 [5] in order to study ecosystem stability and understand questions related to May’s paradox [31]. May’s paradox arose in the 1970s when results from the mathematical study of random matrices suggested that as a random matrix system grows in size it is expected that the leading eigenvalue of the matrix should also grow rendering the ecosystem related to this matrix unstable, however this is not what was observed in ecology with large ecosystems being more stable [5]. Trophic Coherence provided a possible explanation to this question by arguing the ecosystems were stable due to the fact that the interactions are not random and that the constraint that the ecosystems are flow hierarchical systems, where most of the edges point in the same direction, leads to increased stability (in this specific framework). This paper provided the first insight (in terms of the trophic analysis framework) that the hierarchical structure and directionality present in real systems could have an impact on the stability, formation and dynamics of these systems. It also proposed a two part measure: the local node position in the hierarchy, trophic level, and the global measure of the hierarchical structure, trophic coherence.

The trophic level of a node, position in the hierarchy, was initially defined [5] as follows:

$$s_j = 1 + \frac{1}{k_j^{\text{in}}} \sum_{ij} A_{ij} s_i. \tag{2.2}$$

Where the 2014 trophic level of a node, s_i, depends on the sum of the trophic level of its in-neighbours weighted by in-degree plus a constant factor. This is how the concept of trophic level is defined in ecology and where the name arises from. This is defined only when there are basal nodes (nodes of zero in-degree) which are given trophic level equal to 1. This makes sense for an ecological system as the basal nodes correspond to organisms such as plants which do not consume other species and are at the bottom the food chain. However, this limits the application of the method to only systems with basal nodes. This limitation was a motivating factor in the formulation of a new definition [8]. The original global trophic incoherence was measured using the incoherence parameter, q, [5] defined as

$$q = \sqrt{\frac{1}{\sum_{ij} A_{ij}} \sum_{ij} A_{ij}(s_j - s_i)^2 - 1}. \tag{2.3}$$

Where q is the standard deviation of the trophic difference distribution and provides a measure of the hierarchical organisation of a network. This can also be written as

$$q = \sqrt{\frac{1}{\sum_{ij} A_{ij}} \sum_{ij} A_{ij}(s_j - s_i - 1)^2}. \tag{2.4}$$

by exploiting the result that the average of the level difference, $s_j - s_i$, between nodes in a network in this definition of trophic level is always equal to 1 [5, 6, 18]. Writing it in this form, equation 2.4 highlights the similarities between this definition and the updated definition which we cover in the next section. Being equal to zero when the level difference is exactly $+1$ across every edge and growing when the value deviates from this. $q = 0$ represents a coherent network with a perfect layered hierarchical structure while for large values of q it is expected that the networks will have less hierarchical structure and more cycles and feedback [6]. In this definition of Trophic Level assigning nodes to a level is equivalent to solving the matrix equation

$$\Lambda' s = z', \tag{2.5}$$

where $\Lambda' = \text{diag}(z') - A$ and $z'_i = \max(k_i^{\text{in}}, 1)$ [18]. Λ' is only invertible, leading to unique solution, when there are basal nodes (nodes of in-degree zero) which is expected given the constraints of this method [18]. The matrix formulation and its similarity to the updated formulation which can handle basal nodes [8] show how the updated definition [8] can thought of as a symmetrised version of the original definition and how the writing the original formulation in this way prompted the discovery of the updated definition [8], section 2.2.2.

2.2.2 MacKay Definition of Trophic Analysis

Trophic Analysis was redefined in 2020 [8] to the current definition used in this work. This new definition removes the constraint that basal nodes are required making it useful for more systems. In this framework, Trophic Analysis is presented as an optimisation problem. Where the local position of a node in the hierarchy trophic level, h_i, comes from finding the set of trophic levels which minimise equation 2.6, which when evaluated at the minimum value is the global measure of directionality, the trophic incoherence, F. The expression for trophic incoherence is given by as

$$F = \frac{\sum_{ij} A_{ij}(h_j - h_i - 1)^2}{\sum_{ij} A_{ij}}. \tag{2.6}$$

As equation 2.6 is quadratic in the trophic level it can be minimised by taking the derivative and solving a linear equation for the trophic level given by

$$\Lambda h = v. \tag{2.7}$$

Where v is the degree imbalance vector defined as $v_i = k_i^{\text{in}} - k_i^{\text{out}}$ and Λ is defined as

$$\Lambda = \text{diag}(u) - A - A^T \tag{2.8}$$

with u being the vector of the sum of the in and out degrees of each node, $u_i = k_i^{\text{in}} + k_i^{\text{out}}$. It should be noted with this approach that the matrix Λ is not invertible as it has a zero eigenvalue and that the solution to equation 2.7 is invariant upon addition of a constant vector. This can be resolved by setting the level of one of the nodes so that the equation can be solved directly or by solving iteratively or via any other method that does not require computing the inverse of Λ. Iteratively solving the equation is the preferred approach for large sparse systems and allows Trophic Analysis to be a useful tool even when the networks are very large. As the equation for the trophic levels, equation 2.7, is invariant upon addition of a constant vector and adding a constant vector to h does not change the incoherence, equation 2.6, a convention needs to be defined to select the solution. We choose to work in the convention where the lowest trophic level in the network is set to zero by adding the constant vector which achieves this.

The goal of minimising equation 2.6 is to select trophic levels so that the differences in trophic level across an edge are exactly $+1$ as far as possible. This means that in a network with perfect trophic hierarchy, $F = 0$, the trophic levels are all integers where the trophic differences between nodes are exactly $+1$. The would be observed in a graph with strict hierarchy like a directed path. As cycles, or any other motif which contributes to the incoherence, are introduced the network becomes more incoherent. Food-webs are generally very low incoherence as they have few cycles and most edges point up in the same global direction up the trophic hierarchy. A directed cycle will have $F = 1$ and the same trophic level for every node as there is no hierarchy which can be measured by this method.

The minimised value of equation 2.6, trophic incoherence, is bound between zero and one [8]. With real networks existing somewhere on this spectrum. Erdős–Rényi random graphs are generally quite incoherent although the value depends on the sparsity of the graph. These graphs are not maximally incoherent as the degree imbalance present creates some structure which is measure by Trophic Analysis. Whereas graphs which are $F = 1$ are balanced in terms of in and out degrees at each node [8]. It is also possible to speak in terms of coherence measured with $1 - F$ instead of incoherence. So high coherence graphs are low incoherence and high incoherent graphs are low coherence. Additionally, in this definition of trophic analysis, using the standard unweighted form of trophic incoherence, the mean level difference across edges in the network can be written as $\bar{z} = 1 - F$ [8]. This shows how maximally directed networks have $F = 0$ as the average level difference is exactly one with any deviations from this leading to edge differences of a differing lengths in trophic level space. Some works have chosen to quantify directionality in terms of "trophic directedness" defined as $\sqrt{1 - F}$, [20].

2.2.3 Extension to Weighted Networks and Arbitrary Height Differences

The definition put forward in [8] was also extended to weighted networks with the option of setting a different target height difference using a different definition of incoherence, F_w, given by

$$F_w = \frac{\sum_{ij} W_{ij}(h_j - h_i - \tau_{ij})^2}{\sum_{ij} W_{ij}\tau_{ij}^2}. \tag{2.9}$$

This leads to the same set of equations for trophic level, $\Lambda h = v$, as previously apart from with the vector u being replaced with the sum of the weighted degrees and and the imbalance vector being replaced by $v_j = \sum_j w_{ij}\tau_{ij} - w_{ji}\tau_{ji}$ [8]. This definition is useful as it shows trophic incoherence is not sensitive to transposing A as this is equivalent to setting $\tau_{ij} = -1$ for all edges. The extension to weighted networks is useful for applications as it means Trophic Analysis can be used when the systems is most appropriately represented by a weighted network. Setting τ_{ij} to any positive constant value for all edges does not change the hierarchy which is found and merely has the affect of rescaling all the levels and differences. In this work, and most work using Trophic Analysis, the choice is made that $\tau_{ij} = 1$ for all edges and that the target trophic difference is $+1$. There may be situations where another choice is more appropriate reflecting some aspect of the system being studied but when looking at generic networks the choice of $+1$ is simplest to work with.

2.2.4 Applications of Trophic Analysis

Trophic Analysis has been widely applied to study many different network phenomena and we present a summary of the known applications of Trophic Analysis, broken down by the definition used. The intuition behind the results found in the original definition of levels [5] and general trends are expected to hold in the MacKay definition, however with the levels and incoherence values rescaled. Some analytical results such as [6] transfer between definitions very well and can be adapted to the MacKay definition [8].

Original Definition

The concept of Trophic Analysis, as with when it was conceived, has been useful to understand the structure of ecological networks. It was used to study the concept of 'niche-width' in [32] and the prevalence of motifs in ecological networks in [33]. However, Trophic Analysis has also been widely applied outside of ecology. It has been used to study various network dynamics such as spreading processes [34], including in airport networks [35], and impact of the structure of an organisation on how it can be influenced and controlled [7]. In [18] it was highlighted how varying trophic structure affects the stability of majority vote type dynamics leading to distinct behaviours depending on the trophic incoherence.

Trophic Analysis has also been used to analyse infrastructure networks and has been used in the study of the resilience of both rail [36] and water networks [37]. It has also been found to be a useful tool when studying socioeconomic bubbles [38], in particular when studying the behaviour of Reddit discussions around meme stocks. Trophic Analysis was also used to the global directionality present in directed networks which represent pollution spread [39]. Additionally, trophic coherence has also been used to quantify the stability of regional economies [40].

Trophic Analysis has also been used to study general network structural properties such as in [6] where it was shown that the spectral radius, the largest eigenvalue of the adjacency matrix, could be written as a function of the trophic incoherence under certain assumptions and approximations. This result holds well in large data-sets of real networks [6] and highlights the potential importance of the trophic incoherence as the spectral radius can be related to the behaviour and stability of various network dynamics. This work was also extended to the specific case of bipartite networks which arise in the study of production processes [41].

This technique has also been used to study neural network design [42] where artificial neural networks were represented as Directed Acyclic Graphs (DAGs) and the relationship between the trophic incoherence of the structure and the network performance as investigated. It was also attempted to extend the original definition of trophic analysis to networks without basal nodes by defining forward and backwards levels [43] which can be calculated via the pseudo-inverse of a graph Laplacian, however this lacks the simpler definition of trophic incoherence used in [8] and the equivalence with the approaches of [44, 45]. A useful feature of the original variant of trophic level was demonstrated in [46] where it was shown that the trophic levels in this definition, given the appropriate conditions hold, can be accurately found using a low-rank approximation for the adjacency matrix.

MacKay definition

This definition is more recent at the time of writing, so has been much less widely applied than the previous definition. However, it has still seen some usage and is hoped to be more widely used in the future. In network science, it has been used to relate the directional structure to the entropy production rate of several dynamical processes defined on networks [20]. In [20] trophic incoherence was also related to the parameters of a network generative model based on preferential attachment with a tunable probability of edge reciprocation. It has been used to study societal systems, for example to study the structure of the United Nations Sustainable

Development Goals (SDGs) [47, 48, 49]. In biological systems, it has been used to analyse the behaviours of models of epilepsy on networks by providing insight into the impact of the network structure on seizure dynamics [50]. While in [51] Trophic Analysis was used to study the impact of depression treatments on the hierarchical structure of networks derived from functional magnetic resonance imaging data. Additionally, it has been used to study the hierarchy of historical network of Islamic scholars and to infer missing temporal information associated with hadith transmission using the network hierarchy [52]. Trophic Analysis has also been incorporated into attempts to evaluate linear hierarchical and periodic structures in directed networks [53] by linking the measurement of these structures to the likelihood of certain random graph models.

2.3 Methods Related to Trophic Analysis

As Trophic Analysis is a natural way to measure hierarchy and directionality in directed networks and the trophic incoherence penalty function can easily be minimised due to it being quadratic, there are several independently proposed measure of network hierarchy which are defined in similar ways and capture similar structures [8, 54]. For example, SpringRank proposed in [44] which views the ranking problem as minimising the energy of a network of directed springs. In addition to the method of Helmholtz-Hodge decomposition used in [45] which is based on a large body of work linking this decomposition to least squares minimisation based rankings. The fact that there are multiple similar techniques to understand this structure in directed networks highlights the fact that it is important and many people are interested in trying to understand the global directional organisation and hierarchy present. Additionally, convergence of multiple research groups to similar methodologies makes sense as the quadratic penalty term is simple to solve for and all the related methods rely on this structure. A comparison between the ranking methodologies to Trophic Analysis, SpringRank and Helmhotz-Hodge Decomposition can also be found in [54] and in Portuguese in the thesis [55].

2.3.1 SpringRank

The problem of minimising the Trophic Incoherence of a given network can also be interpreted as minimising the energy of a network of directed springs. The methodology of SpringRank comes directly from the observation that ranking of nodes can be achieved by minimising the energy of some Hamiltonian representing a network of directed springs. SpingRank has a very similar minimisation problem to that found in Trophic Analysis apart from that it is not normalised in the same way and that a regularisation term may also be included to enforce a unique solution by breaking the invariance of solutions of the minimisation problem to the addition of constant vector. This is defined as

$$F_s = \frac{1}{2}\sum_{ij} A_{ij}(h'_j - h'_i - 1)^2 + \frac{\alpha_{\text{reg}}}{2}\sum_j h'^2_j. \tag{2.10}$$

Where α_{reg} is a small regularisation parameter. In the original paper proposing SpringRank [44] a different convention is used for the adjacency matrix so some terms are modified by taking their transpose, also noted in [54]. This can be minimised and leads to an equation for ranks in SpringRank, h', which is equivalent, depending on the adjacency matrix convention, to the equation used for trophic level up to the regularisation term,

$$(\Lambda + \alpha_{\text{reg}}\mathbb{I})h' = v. \tag{2.11}$$

This can be solved in the same way as for the trophic level however without the need to define a convention for the lowest level node as the regularisation term, which can also be considered a Gaussian prior on the ranks, means the equation has a unique solution. The regularisation term forces the levels to be centred around zero and can be thought of as connecting all the nodes to weak springs with resting position at the origin whereas the approach of adding a constant vector can be thought of as translating the whole network of springs to the desired position. When the regularisation parameter is negligibly small we should see the same structure as is found with Trophic Analysis up to convention for the adjacency matrix and centring of the levels. The linear structure again makes the ranks simple to solve for and methodology applicable to large systems. One difference between SpringRank and Trophic Analysis is that Trophic Analysis equally emphasises the levels and incoherence parameter, using the normalised trophic F to derive analytic results [8, 2], while the Hamiltonian ground state energy is not used in this way in SpringRank as far as the author is aware. However, the ground state energy per edge, which is similar in concept to F, is used as part a statistical test to determine if the hierarchy is significant, see [44] for details.

Applications

SpringRank has been widely used to study the structure of academic hiring networks and the hierarchical nature of interactions between academic institutions [56, 57, 58, 59] as well in social settings like endorsement networks [60]. SpringRank has also been used to form a ranking from pairwise comparisons of different approaches to network community detection [61]. SpringRank has been extended by modifying the minimisation problem to create a ranking mechanism designed for temporal networks where the current ranks take into account how the nodes ranked at previous times [62]. This kind approach is useful for ranking systems which change in time and this approach could be adapted and combined with an incoherence like parameter which also measures how the directionality of the system changes with time. Other changes to the SpringRank function have been proposed such as in [63] where the minimisation problem was formulated as a Huber loss in order to be more robust to outliers in the data and change the impact they have on the ranking which may be appropriate in some settings.

2.3.2 Helmholtz-Hodge Decomposition

Trophic analysis is also very similar to a technique for analysing ‘circularity’ [45, 54] based on Helmholtz-Hodge decomposition. Hodge Laplacians on graphs are a well studied field [64] which cannot be adequately summarised here. The work of [45] is based on a large literature of work which has linked to the problem of computing a ranking to Hodge decomposition, the Hodge Laplacian and least squares minimisation [65, 66, 67, 68, 69, 70, 54].

The equivalence between Trophic Analysis and Helmholtz-Hodge Decomposition [54] of the type used in [45] is described in [8] which we restate here. Helmholtz-Hodge decomposition is the decomposition of a vector field into one part which is divergence free and another part which can be written as a gradient. This is done by taking flows, f_{ij}, and conductance terms,w_{ij}, which take values depending on the way nodes i and j are connected. f can then be split into two parts $f = f^P + f^C$. Where $f^P_{ij} = w_{ij}(\phi_j - \phi_i)$ and f^C can be balanced.

After some substitution, see [45], minimising the following

$$\sum_{ij} w_{ij}^{-1}((f_{ij} - w_{ij}(\phi_i - \phi_j))^2, \tag{2.12}$$

allows the potential, ϕ_i, to be solved for which is the version of rank or level in this methodology.

The minimisation can be shown to be equivalent in form to trophic analysis extended to weighted networks with arbitrary target heights [8], for non-normalised incoherence, with the choices

$$h_i = -\phi_i \tag{2.13}$$

and

$$\tau_{ij} = \frac{f_{ij}}{w_{ij}}. \tag{2.14}$$

Where again we have the property that the minimised incoherence equivalent is invariant upon setting $\tau'_{ij} = -\tau_{ij}$, the transposing of the adjacency matrix and the addition of a constant vector to the level equivalents.

Helmholtz-Hodge decomposition, sometimes referred to as HodgeRank [71, 70], using a broad range of notations and definitions has been widely used to study many systems. It has been used to study economic networks [45], neural networks [72], social representation theory [73, 71], to analyse economic time series in [74], to asses video quality from the pairwise comparisons [70] and in [75] to study flows in bank transactions where the rankings obtained were compared to the bow-tie structure found in directed networks. However, being such a large research area an exhaustive list of all areas where it has been applied as is possible for Trophic Analysis is outside the scope of this work. In addition, variants have been defined such as in [76] where HodgeRank is extended to deal with outliers when ranking visual properties. The idea of extending HodgeRank using a variant of Huber Loss [76] has also been seen in a SpringRank variant [63], highlighting the similarity of the techniques as a similar extension was independently arrived upon. Many of the formulations of least squares based rankings [77] share a strong similarity with the minimisation problem found in Trophic Analysis and various works have studied the properties of least squares rankings and this minimisation problem in detail [77, 78].

2.3.3 Others

Several other similar methodologies have also been detailed in the literature. One methodology which is equivalent to Trophic Analysis based on energy minimisation was proposed in [79] as a tool for drawing and visualising directed graphs with hierarchical structure where the levels would be used as the y-coordinate when drawing the graph. A different hierarchy measure is proposed in [79] where the amount of hierarchy in the system is quantified by the difference between the maximum and minimum level divided by the graph diameter, distance between the two furthest apart nodes, which can be used to determine the appropriate graph drawing framework [79].

A ranking method of similar methodology to SpringRank and Trophic Analysis was also found independently in [80]. In this work, rankings were derived from a model of competing nodes where ‘results’ of the interactions are normally distributed based on the rank difference of the nodes. The maximum likelihood estimate of the ranks for this model then corresponds to minimising the energy of a network of directed springs [80] which is again similar to the other methods presented in this section.

2.4 Other Approaches to Ranking Problems

The problem of finding a ranking of a set of elements to find hierarchy given some pairwise comparisons or a network is a very well studied problem across as range of scientific disciplines and as such there is a very wide literature of techniques designed to find rankings [81]. Some examples of historic discussion on how to construct a ranking from pairwise comparisons can be found in the early psychology literature [82] and the proposal of the widely used Bradley-Terry-Luce model [83, 84] where ranks are constructed based on the idea that the ranks can be used to compute the probability that an element of the system "wins" over another during a pairwise comparison. The Bradley-Terry-Luce model and variants are still very widely used and is one of the founding models in the field of ranking a set of pairwise comparisons, it was compared to SpringRank in [44] and an overview of the many ways it can be derived is given in [85].

The key difference between Trophic Analysis and much of the ranking literature is that Trophic Analysis emphasises the trophic levels, ranks, in conjunction with the Trophic Incoherence which highlights how globally directed the network is which can be used to understand how the ability to rank nodes relates to the global network properties [3, 2, 8] and how important the hierarchy is to the system [4]. Another important thing to note, shown in [81, 44], is that when a clear hierarchy exists then it can be picked out with many ranking techniques and that the results correlate with each other [81]. So the choice of ranking methodology may come down to performance, simplicity, interpretability and relationship to other networks properties. For example, a reason why a method like SpingRank is successful is that it can be extremely simply summarised as "the ranks correspond to the minimum energy state of a network of directed springs" compared to other methods which may have more complex implementation and interpretation.

Ranks can be constructed in a multitude of ways. In some early ranking literature they where constructed from the difference in number of wins and loses, which is equivalent to degree imbalance, [86]. This [86] makes sense for a system like a tournament where every element interacts with every other but not in a sparse complex network.

There are a host of techniques found to solve the ranking problem that have been proposed in the literature. There is the ranking methodology of [81] which employs Singular Value Decomposition (SVD) as part of the ranking method. There is the technique of SerialRank [87] based on serration methods. SyncRank relates the problem of ranking to the problem of group synchronisation, over the group of planar rotations, SO(2), by mapping the rank differences to angular differences [88]. Which then allows the construction of a hermitian matrix from which an angular synchronisation problem can be expressed, solved and mapped back to the ranking solution [88].

A set of rankings can also can found by using a Graph Neural Network (GNN) [89]. In [89], a loss function is constructed which relates to minimising the number of upsets in the ranking. This methodology [89] compares favourably to many other ranking methodologies. However, in many of the test cases used to evaluate the GNN the second best performing method according to the metric used is SpringRank, which highlights the good performance of the computationally simpler and interpretable method which is equivalent to Trophic Analysis and Helmholtz-Hodge decomposition.

There are also methods like PageRank [90, 15] which rank nodes by perceived “importance”. These are not designed to extract hierarchy in the same way as the other methods described but they may also detect some aspects of hierarchical structure. Particularly as PageRank is based on the behaviour of random walkers with random jumps which would explore the network hierarchy if it existed. Ranking methods which are based on random walks such as Rank Centrality have also been proposed [91]. With random walk based methods being further studied in [92] where a faster process was found along with a message passing interpretation. Ranking can also be constructed by using the spectral properties of a variant of the Laplacian matrix known as the dilation Laplacian [68]. The problem of finding a ranking has also been viewed in the context of preference aggregation from different sources, such as in [93] where a Multinomial Preference Model was used to aggregate preferences into a consensus ranking.

There is also an element of the literature derived from ranking problems found in computer science which relates the problem of creating ranks from pairwise comparisons to the field of matrix completion [94, 95, 96, 97, 98, 99], with a summary given in and references found using the review of [81]. Matrix completion attempts to solve the following problem: given a matrix with a mixture of observed and unobserved entries how can we use the observed values to infer the unobserved entries. In terms of pairwise comparisons and ranking, this would be: given a set of observed pairwise comparisons how can we predict the outcome of the unobserved pairwise comparisons and from this work out the hierarchy of interaction between the elements of the system. There are also ranking methods designed from ranking players as they interact with each in games over time such as ELO in chess [100] or TrueSkill in online video games [101].

2.4.1 Network Science Methods

There are also a large number of approaches to study and quantify hierarchy in networks [102], with a summary of some given in [103]. Global reaching centrality [25] measures hierarchy through the number of nodes which are reachable from a given node. This allows a local measure of hierarchy, how large the out-component of each node is, and a global measure of hierarchy, an average of how much the out-component of each node differs from the maximal possible value. It has been studied analytically in the case of random graphs [104]. It has been used to study the emergence of hierarchy in social settings [105, 106], hierarchy in metabolic networks [107], network robustness [108] and the structure of organisations [109], with variations of this method used to study hierarchy in scientific publishing [110]. The measure of global hierarchy based on reaching centrality works well in many cases. However, it can lead to examples of networks where what looks like a perfect global hierarchy is not measured, examples given in [102].

The level of a node in the hierarchy can sometimes simply be measured as the distance of a node from the "root" node, a node of zero in-degree at the bottom of the hierarchy as was done in [111], where the importance of reverse edges to network dynamics was highlighted. This type of approach is quite common, as in [112] hierarchy was also studied in various network models by defining hierarchy as distance from nodes of zero in-degree [112]. This is similar to the idea of the original trophic level [5], although with a specific method to deal with cycles [112]. These hierarchy measures also lend themselves to interpretation related to network control as in [113] where the number of nodes of zero in-degree was related to network control. Global directionality has also been studied in network science by simply measuring the fraction edges which are unidirectional and the fraction which are bidirectional [114], with the relationship between this quantity and the spectral properties of the adjacency matrix was studied in [114].

Ranking can also be computed through a technique known as 'agony' [115, 116], originally proposed in [117], where a penalty is only applied to edges which go backwards against the ordering and there is no penalty for edges which go too far up in the hierarchy as in trophic incoherence [8]. It allows a ranking to be computed and a global directionality to be measured from the value of this penalty function [115]. However, the minimisation of the this function can be computationally difficult. Depending on the form of the penalty function, it may become equivalent to the Feedback Arc Set problem which is the problem of finding the minimum number of edges which need to be removed to make a graph acyclic, which is NP-hard [115, 118]. This kind of approach of trying to find a ranking by minimising the number of connections which violate the ranking has been of interest to the literature for a long time [119]. 'Agony' is a useful technique but the choice to not apply penalties to the forward edges, as in Trophic Analysis or SpringRank, means the hierarchical structure it finds does not have the idea of distinct 'layers' in the same way which may be important when the ranking of the nodes represents a node characteristic where it is important that edges do not go too far upwards. Additionally, since the minimisation function used in Trophic Analysis can be differentiated the computation of the ranking is simple. Flow hierarchy has also been studied by computing the fraction of edges which are not involved in a cycle [120] and by trying to reorder the adjacency matrix so it is upper triangular [121].

Hierarchy can also be quantified by using the distribution of random walkers in a network [122], where the position of nodes in the hierarchy is calculated using the stationary distribution of the random walkers and the global hierarchy is measured by the coefficient of variation (ratio of standard deviation and mean) of this distribution [122]. A three part measure of hierarchy in networks was proposed in [21] where the space of hierarchies was defined using measures of graph orderability, feedforwardness and treeness [21]. Directed networks have also been studied with the ‘bow-tie’ framework where the network is viewed as being composed of a giant in-component, giant strongly connected component, giant out-component plus other smaller contributions [123] which can be extended further by concepts such as “tendrils” and “tubes” [124]. Clearly these ideas are strongly tied to network hierarchy as many of the measures of network hierarchy detect the features which contribute to this structure, for example “root” nodes or nodes with large out-components or nodes of low trophic level would be expected to be in the giant in-component if it exists. ‘Bow-tie’ structure has been linked with hierarchy via the Helmholtz-Hodge potential in transaction networks [45].

Hierarchy can also be measured and viewed as related to how the results of pairwise comparisons can be predicted [125]. In [125] extensions of Bradley-Terry model are studied and the hierarchical structure is understood by measuring the prevalence of complete upsets based on ‘luck’ that are not predicted by the hierarchy and the ‘depth of competition’ parameter which relates to the span of the skill range of a game. Additionally, in [125] the accuracy of many hierarchy measures including SpringRank was tested on an edge direction prediction task, on a variety of data-sets relative to the Bradley-Terry. It was found that the best performing measure varied as the data-set changed but also that in terms of accuracy the difference in the performances were relatively small [125]. This again highlights that if a hierarchical features are present in a real system it may be adequately detected by many methods. Hierarchy has further been linked to the idea of network control in [126] where the position of a node in the hierarchy of a directed acyclic graph was linked to its ability to control the system [126]. As directed acyclic graphs have no cycles they can be perfectly ordered, which allows the connection to control made in [126], something which is more difficult to do in the case where the network contains cycles. The problem of finding a ranking in a digraph was shown to be relatable to continuous spin systems in [127] where system proprieties were computed using a belief propagation algorithm.

Hierarchy can also be measured by the approach of [128] where the network hierarchy is inferred via an ordered stochastic block model. This Bayesian approach to infer hierarchy has a number of advantages. It can measure the hierarchy at the same time as community structure, so can be used to study both features simultaneously. As the approach is Bayesian it allows the significance of the hierarchy to measured [128]. In addition, this approach can be degree corrected meaning that it does not detect hierarchy which is caused by local degree imbalance in unstructured random graphs as observed in Trophic Analysis and SpringRank [128]. Furthermore, this method can be accessed through the popular `graph-tool` library [129] lowering the barrier to entry of its usage. For the reasons listed above this is one of methodology which we would most highly recommend be used in applications.

2.4.2 Fields with Distinct Notions of Ranking

There are some fields which may already have ingrained ideas of hierarchy, longstanding terminology for this or specific features that should be taken into account when quantifying the structure. For example in social networks, a ranking can be built which takes into account that reciprocated and unreciprocated connections play different roles in social networks and it is likely that unreciprocated edges point up in the ranking [130]. Of course, hierarchy is well known in ecology as it is where Trophic Analysis takes inspiration from and where the phrase “trophic level” meaning the ranking of a species in a food-web is well known. This relates to the idea that species have a ‘niche profile’ and consume species in a set range below them in this ‘niche’ space [131, 132, 32]. These concepts have a long history in ecology which cannot be adequately covered in this work, see the introduction of [32] for a brief summary and further reading.

Rankings and hierarchy also naturally occur in economics. In this field hierarchy can be referred to as “upstreamness”, which is a scaled measurement of distance along an economic flow. For example, in a production network where raw material inputs are at one end and consumer products are at the other end of the scale [133]. Other measures for measuring ranking have also been described in economics such as SinkRank [134] which was proposed to study the ranking in interbank payment networks by measuring distance from absorbing nodes in Markov chains. This is strongly related to the many measures of hierarchy based on weighted distance from sink or source nodes. The total number of research areas where notions of a graph based hierarchy has been applied is vast and includes diverse fields such as the study of Digital Twins [135]. Hierarchy could be applied to any area where directed graphs are relevant and as such it is not possible to list all possible applications in this review.

2.4.3 Network Embedding Perspective and Magnetic Laplacian

Trophic Analysis can also be throughout of as embedding the nodes along a one-dimensional axis with position determined by the minimisation of Trophic Incoherence. However, many methods exists for determining a network embedding and many features of a network can be illuminated by assigning the nodes a position in a given space. In particular, the network geometry framework [136] has recently been extend to directed networks where reciprocity, a quantity which is related to flow hierarchy, was studied in networks where the connection probability is derived from the placement of a node in a circular topology. Similarly, directed networks have also been studied by using complex phases to represent periodic circular hierarchy via the proprieties of the Magnetic Laplacian [137, 53, 138]. There have been multiple applications of this type of framework including as part of a GNN methodology [139], to understand community structure [137, 138], to quantify periodic hierarchy [53] or as a visualisation tool [140]. It has also been proposed that directed network structures could be analysed using the Magnetic Laplacian framework in combination with a ranking method [54] such as HodgeRank [54]. This could mean embedding the nodes in a two dimensional space where node position is given in polar coordinates with the radial part derived from the flow hierarchical ranking and the angular part derived from the Magnetic Laplacian [54] which can capture more structure than either method alone.

Graph embedding is widely studied field with a wide range of approaches used [141], a detailed discussion of which is outside the scope of this work. However, we highlight a small sample of various embedding approaches for directed graphs which have been put forward and are designed to capture some elements of the directionality, asymmetry, and ordering present in directed graphs [142, 143, 144, 145, 146]. Other recent work has demonstrated the evolving ways the structures found in directed networks can be understood, such as in [147], where renormalisation methods were extended to directed networks with varying reciprocity.

2.5 Global Quantities Related to Trophic Incoherence

In this section we detail the global quantities which have been related to Trophic Incoherence and explain the network features they relate to. These connections are analytical approximations which hold in real networks. Highlighting this phenomena shows how trophic analysis could be incorporated into the wider literature and shows how previous results could be interpreted in terms of the network directionality.

2.5.1 Spectral Radius

One useful aspect of Trophic Analysis is the fact that the trophic incoherence can be linked with the of spectral radius of unweighted networks, largest eigenvalue of the adjacency matrix, via an analytical approximation [6, 8]. This eigenvalue, which is guaranteed to be real and positive by the Perron–Frobenius theorem [148], can be related to many network properties and is important for network stability and robustness. The link to Trophic Incoherence can be made [6] due to the fact that the spectrum of the adjacency matrix is related to the number of cycles in a network [6, 8]. The fact that the spectral radius can be related to trophic incoherence means that the large body of work which depends on the spectral radius could be viewed in terms of the trophic incoherence.

Trophic Incoherence was related to the spectral properties of matrices when it was first used to study ecosystem stability [5] however the first explicit analytical link between trophic incoherence and spectral radius was made in [6] using the original definition of levels. In this work [6] a loop parameter, τ, was constructed which was a function of the trophic incoherence and branching factor, a network property which depends on the degree distribution. The sign of the parameter τ was able to predict if the network was in a regime of a large or very small number of cycles. Using this parameter it was possible to analytically estimate the spectral radius of real networks using the branching factor and trophic coherence. In [8], this work was modified and adapted to the MacKay definition of Trophic Analysis where it was shown that the scaled spectral radius,

$$\rho_s = \frac{\rho}{||A||_2}. \tag{2.15}$$

Where ρ is the largest eigenvalue of A, which is real and positive by the Perron–Frobenius theorem, and $||A||_2$ is the 2-norm of A, equivalent to the largest eigenvalue of $A^T A$ [8], can approximately be written as a function of the trophic incoherence,

$$\rho_s \approx \exp\left(\frac{1}{2}\left(1 - \frac{1}{F}\right)\right). \tag{2.16}$$

This demonstrates how the global directionality as measured by Trophic Incoherence is more than simply a measure of how easy it is to rank the nodes and is strongly related to the structural properties of a directed network. The spectral radius is clearly very important. If a dynamical system is defined using the adjacency matrix then the stability of that system may depend on the spectral proprieties of A and in particular the size of the largest eigenvalue [8]. For example, in ecology where the stability of a food web depends on the largest eigenvalues of the Jacobin matrix which is related to the connectivity structure [5, 149]. The logarithm of the spectral radius can represent a topological entropy [150] which is related to the robustness of a network, as this entropy is correlated with the decay rate of fluctuations [150]. Furthermore, it has been argued [150] that some biological networks may evolve in ways which maximise this entropy. Topological entropy expressed in this way can also be used in Symbolic Dynamics [151] to study the properties of dynamical systems which can be represented as directed graphs. Network synchronisation is a well studied field [152] and it has been shown that the critical coupling for synchronisation of a network of directed Kuramoto oscillators [153] depends on the inverse of the spectral radius. However, it has been highlighted in [154] that in networks which are non-normal, a property related to trophic incoherence, standard techniques for studying stability and synchronisation such as the Master Stability Function may fail [154]. The spectral radius is again important in the study of epidemics on networks [114] where the mean-field epidemic threshold for SIS models can also be shown to be related to the inverse of the spectral radius [155]. This dependence of a threshold on the inverse of the spectral radius is common in many dynamics [156]. The importance of edges or sets of edges has also been inferred by the impact their removal has on the value of the spectral radius [157, 158], something which could be understood by viewing the removals as modifying the trophic incoherence and the fact that certain edges have a different penalty to the trophic incoherence [8, 2]. Given that the spectral radius is such a fundamental property of a matrix it appears in many diverse settings, for example being important in the weighted networks used in machine learning [159], we cannot give a complete account into the possible systems it could be used to analyse. However, the results of [6, 8] provide a possible reinterpretation of wide range of results in terms of networks hierarchy.

2.5.2 Non-normality

Directed networks with hierarchical structure can also be viewed as having non-normal adjacency matrices [18, 8, 20]. A real non-normal matrix, such as the adjacency matrix of a directed network, A, is one where the matrix does not commute with its transpose,

$$AA^T \neq A^T A. \tag{2.17}$$

However how non-normal a real matrix is, how far A is from commuting with its transpose, can be quantified and related to the behaviour of the systems which depend on these matrices [160]. Non-normality can affect many systems [160] including condensed matter physics, machine learning, acoustics, the behaviour of numerical methods and fluid mechanics, [160, 161, 162, 163, 164].

The concept of non-normality in networks was first linked to trophic coherence in [18]. Where it was observed that in the original definition of trophic coherence [5] it could be shown using the loop exponent, τ, which related trophic coherence to the expected number of cycles in a network that coherent networks are also likely to be non-normal. Networks which are more normal have a higher prevalence of reciprocal connections and are more similar to undirected graphs while non-normal networks have few reciprocal connections and are much more likely to have a strong hierarchical structure. When the MacKay definition of trophic incoherence was proposed in [8], it was also shown how non-normality could be approximately linked analytically to this definition of Trophic Incoherence. When matrix normality is measured via the parameter, ν, given by

$$\nu = \frac{\sum_i |\lambda_i|^2}{||A||_F^2} \tag{2.18}$$

where $||A||_F$ is the Frobenius norm of A which can be written as $||A||_F = \sqrt{\Sigma_{ij}|a_{ij}|^2}$ and λ_i are the complex eigenvalues of A. It was shown in [8] that this can approximately be expressed in terms of trophic incoherence

$$\nu \approx \exp\left(1 - \frac{1}{F}\right). \tag{2.19}$$

This result makes use of several approximations but generally holds well in real networks [8]. Additional results have backed up the correlation between normality and incoherence using related measures of non-normality [20] or measuring quantities related to non-normality like the pseudospectral radius [3]. The relationship between network properties derived from Trophic Incoherence and properties related to the network normality can however be non-liner and complex [20] despite the relationships found in real networks [8] and generated networks [20]. Examples can be found of small networks which break the trends seen, being incoherent but non-normal in the unweighted case or coherent but normal in the weighted case [20]. These results [20] highlight that care must be taken and that the two metrics do measure different aspects of network structure, even if there is a strong approximate relationship between them observed in real systems.

The importance of non-normality in the study of directed networks has been shown by recent work [165, 19, 38, 166, 167, 3, 168, 154, 20] where it has been highlighted how non-normality can be linked to the behaviour of network dynamics. Additionally, similarly to how it has been shown that coherent networks are common in nature [18, 8, 20] it has been found that non-normality is also commonly found in real-world systems [19, 165, 8, 20] as would be expected given the link between coherence and non-normality.

The links to normality and the spectral radius separates Trophic Analysis from a standalone ranking procedure and shows how local hierarchy is derived from the global organisation of the network. It also motivates several branches of future work. Can other network quantities be explicitly related to Trophic Analysis? While from the other side can phenomena which involve non-normal networks or the spectral radius be studied using Trophic Analysis?

2.6 Discussion on Trophic Analysis and Literature

As can be inferred from the preceding sections, there are a large number of ways to characterise hierarchy and directionality in directed networks. This demonstrates the importance of these features in directed networks but also presents a difficulty for researchers. Given the wide range of approaches, notations and terminology used for similar concepts, differing aims of various methodologies and what is meant by "hierachy". It is very difficult to provide answers to a question such as "What is the best method to understand hierarchy and directionality?". Since the answer to this question depends on many factors. What do you consider when you mean hierarchy and directionality? What do you think the ranks or levels you find will relate to? Do you want to quantify if the ranking is significant compared to a null model or some other global measure? How interpretable should the methodology be and what is the ease of explanation to people outside the field? What computational resources do you have available and how many networks and what size do you need to study? How widely used is the methodology and will it be understood by your audience? What level of accuracy is required, how it is measured and does the improvement in accuracy gained merit the cost associated with changing framework? How much certainty do you have in the underlying network data? As can be seen this is not a set of questions which have general answers. An advantage will be held by methods which are easy to implement or alternatively already implemented in easy to access software packages. Although, it is also true that in many cases that if you consider ranking something very simple, like a directed path graph, different methodologies will give the same answer or in real settings answers which are correlated with each other [81] so the impact of the methodology choice may be hidden by this feature.

Additionally, there are various things that should be considered when ranking algorithms are used in the real-world. It has been noted, particularly in social settings, [169] that there are certain challenges with the application of ranking algorithms to real systems [169]. Network ranking algorithms may be biased by certain features of the network architecture, the ranking method may have variable usefulness as it is used in different domains while the optimal methodology may also change [169]. Furthermore, in social settings if actors in a system know that they are being measured with a ranking algorithm this may influence their behaviour [169]. A discussion of some of the philosophical points which underpin the field of ranking and specific considerations which should be taken into account when ranking sports teams is given in [85]. There may also be situations where even though a ranking algorithm can be applied it is more appropriate to focus on other simpler metrics which show the key features of the data. This is the case in [170] where SpringRank [44] could potentially have been applied to study a network of online dating interactions but other metrics were chosen to better highlight interaction rates between groups and for the results to be understandable to the widest possible audience. Additionally, a place in the ranking may not necessarily directly relate to the skill or talent of the object being ranked and luck can play a role in where an element in placed in the ranking [171].

In this work we cannot provide the answer on which methods to understand directionality and hierarchy in directed networks is optimal in every potential setting but give some general arguments about the utility and constraints of using Trophic Analysis to study directed networks.

2.6.1 Trophic Analysis

The benefits of Trophic Analysis comes from the connection between the local hierarchy, trophic levels, and the global parameter, Trophic Incoherence as it explicitly connects the existence of hierarchy to the global directionality. This separates it from the global measures it can be linked to analytically, like the non-normality and spectral radius, which do not have explicit local interpretations. Whilst the link to the global parameter aides the interpretation of the hierarchy as it is easier to understand the importance of hierarchy to the system, which would not be the case with a hierarchy measure alone. Trophic Analysis is also simple to calculate requiring only the solution of a linear equation. Additionally, it links into the wider literature by the range of methods which use similar formulations to understand hierarchy, section 2.3. The fact the method is simple to calculate may aide its use in applications as the barrier to entry and understanding the methodology is lower. As it is related to SpringRank it is may be surmised that results found in terms of SpringRank can be likely expressed in terms of Trophic Level and the performance metrics of SpringRank give an idea of how Trophic Level would likely perform [89].

Caveats of Trophic Analysis

There are however certain situations which Trophic Analysis is not an appropriate tool and other methods may need to be used. One difficulty with many of the hierarchy measures is how to extend them to networks with negatives edge weights. The challenges of hierarchy measurement in signed networks was discussed in [172]. However, in general it is not clear how to extend a method like Trophic Analysis to cases where there are negative edge weights such as in a network where negative edges represent inhibitory neurons. It is not clear how a negative edge should be ranked and how it would contribute to the hierarchical structure in our framework. There may be future work in studying how features of directed signed networks like reciprocity or frustration [173] link to potential hierarchical structure if a suitable framework is constructed. In Trophic Analysis, it is assumed that edges represent one type of interactions whereas in some real systems [174] hierarchy may come about as a results of multiple types of edge interaction. For example, differing types of dominance or subordination interactions in animal or social networks as was assumed in the framework of [174]. Another concept which is not addressed by Trophic Analysis alone if the fact that hierarchy and community structure can both be present simultaneously [175, 128]. This may need to be taken into consideration when analysing the structure of some real-world systems, with the interplay between the phenomena addressed in [175, 128].

There are also some views of directionality which mean that incoherence is not the appropriate tool to measure it. If the view is taken that a graph which is acyclic is maximally directional then trophic incoherence fails to fully capture this idea. As although all graphs which are $F = 0$ are acyclic it is possible to create acyclic graphs which are not minimally incoherent. This can be done by having a graph which is acyclic but where the edges go upwards across multiple levels and hence large deviation from trophic difference $+1$. Another caveat with Trophic Analysis is since F roughly measures the average penalty per edge there are many structures which can have the same F yet be organised in very different ways. For example, a homogeneous network where the edges which contribute to the incoherence are equally distributed around the network behaves very differently a network where this is not the case. An example of this type of structure is if you took a directed path graph and at the end of the path placed an incoherent structure like a complete graph or a cycle. It is then possible to get any value of F, apart from exactly zero or one when both components are finite, by varying the size of each component. Several consequences arise from this example, one being that since F acts like an average penalty it is possible that if the network is very large and the deviations are inhomogeneous it can be very coherent but still have a sizeable number of cycles or large spectral radius. F is also invariant under transposing the network so care needs to be taken with definitions which relate to which nodes are at the bottom and top of the hierarchy and the direction that influence flows in the network.

Another facet of Trophic Analysis and associated methods to be aware of is that in some circumstances the trophic level [3] or SpringRank [128] may correlate with the degree imbalance, difference of in and out degree of a node. This is most commonly found in directed Erdős–Rényi random graphs. These are not maximally incoherent as although they are formed without hierarchical structure the degree imbalance contributes to generating some incoherence as it is a term in the equation for calculation of trophic level. This behaviour may not be desired as in some interpretations of hierarchy it may be your view that a maximally random structure like an Erdős–Rényi graph should also be maximally incoherent. However, the view can also be taken that in some circumstances the degree imbalance is an important feature which can contribute to the dynamics [3] so it makes sense for Trophic Analysis to identify it. It can also be argued that $F = 1$ are not expected to be formed randomly and that a more complex formation rule is required to form the structures required to have balanced degrees and form a completely incoherence structure with no ordering which can be found by Trophic Analysis. Overall, the caveats associated with Trophic Analysis do not impact the usefulness of it and related measures [44, 45] however they are something to be aware of.

2.7 Conclusion

In conclusion, we have presented the methodology Trophic Analysis which is used to study the flow hierarchy and global directionality in directed networks. We have highlighted the vast range of ways hierarchy and ranking can be understood and measured in the literature. We detailed the wide ranges of domains where Trophic Analysis has been applied and described the other closely related methodologies. We have also highlighted how Trophic Incoherence can be linked to various other network properties such as the spectral radius and non-normality. We have also highlighted the equivalence between Trophic Analysis, SpringRank and Helmholtz-Hodge Decomposition. The equivalence between these methodologies means that results found using one method would be expected to hold in another of the methods. Additionally, these methods are relatively simple to compute and simple to interpret as the rankings can be interpreted as minimising the energy of a network of directed springs.

CHAPTER

3

STRONG CONNECTIVITY IN REAL DIRECTED NETWORKS

This chapter is based on

- Niall Rodgers, Peter Tiňo, and Samuel Johnson. "Strong connectivity in real directed networks". In: *Proceedings of the National Academy of Sciences of the United States of America* 120.12 (2023). ISSN: 10916490. DOI: 10.1073/pnas.2215752120

The supplementary information from this paper has been included in the appendix of this thesis so all references to supplementary information or SI in this chapter refer to the appendix of this work.

Relationship of Work to Thesis

This paper represents an important contribution of this thesis as it is where we apply Trophic Analysis to study the structure of real directed networks and analytically link the information captured via Trophic Analysis with structural properties of the network. Inspired by the work of [8, 6] it shows how Trophic Analysis can be a used to reinterpret aspects of network structure in terms of hierarchy. This work was conducted in the middle of my PhD and the second paper produced. The insights gained when working on the dynamics of Hopfield-like networks, chapter 5, were vitally important for making the connection between the hierarchical structure and strong connectivity. This chapter also complements the results of the third paper of my PhD, chapter 4, where we show that additional structural properties of networks are related to the hierarchical structure. This work also marked the transition from using `Python` to `Julia` for the computational part of this PhD which lead to speed improvements in the network generative process which were useful throughout the whole thesis. This work highlights that many distinct types of real networks exhibit hierarchical structure and the unique role that edges which break the ordering play in the directed networks which provided the motivation and initial ideas to start working on the final work of my PhD, chapter 6, on fitness-based generative models of networks which give more control over this structure.

Abstract

In many real, directed networks, the strongly connected component of nodes which are mutually reachable is very small. This does not fit with current theory, based on random graphs, according to which strong connectivity depends on mean degree and degree-degree correlations. And it has important implications for other properties of real networks and the dynamical behaviour of many complex systems. We find that strong connectivity depends crucially on the extent to which the network has an overall direction or hierarchical ordering – a property measured by trophic coherence. Using percolation theory, we find the critical point separating weakly and strongly connected regimes, and confirm our results on many real-world networks, including ecological, neural, trade and social networks. We show that the connectivity structure can be disrupted with minimal effort by a targeted attack on edges which run counter to the overall direction. This means that many dynamical processes on networks can depend significantly on a small fraction of edges

Significance Statement

Many real-world systems are connected in a complex directed network, such as food webs, social or neural networks. Spreading and synchronisation processes often occur in such systems, and understanding the percolation transition (formation of a giant connected component) is key to controlling these dynamics. However, unlike in the undirected case, this had not been understood in directed networks with realistic non-random architectures. We provide a universal framework in which the percolation threshold for networks to be strongly connected (every node to be able to reach every other) can be analytically predicted on any real-world network, and verify this on a diverse data-set. This explains why many real, dense networks are not strongly connected, in contrast to random-graph theory.

3.1 Introduction

Understanding the connectivity structure of a directed network is crucial in many different contexts. Can every node be reached in a communications network or one way street grid? How will a disease spread or will a dynamical system be stable and resilient to perturbation? Whether a network will be connected has been well studied in the case of undirected networks through percolation theory, however, this is less well understood in directed networks, and hence real-world systems, which are often directed [176, 18]. We demonstrate through understanding the global directionality and hierarchical organisation of directed networks through a method known as Trophic Analysis [8] that it is possible to construct a phase diagram which predicts if real networks are strongly connected using only the average degree and the incoherence parameter which measures the global directionality going beyond previous understanding based on directed random graphs [177]. The notion of global directionality provided by trophic analysis enables us to talk meaningfully of “forward" and “backwards" edges and gives us an insight into the directed network which is not possible without this. It is the backward edges that break the overall hierarchical structure. This hierarchical structure can be found in almost all real-world networks, not just networks with obvious hierarchy such as food webs where the hierarchy is number of steps from the nodes of zero in-degree such as plants. Global directionality, Trophic Incoherence, has been linked to network non-normality [8] which has been shown to be ubiquitous in real directed systems [19, 165]. We use the insight that the strong connectivity is driven by edges which break the hierarchical ordering to apply percolation theory [178] to these “backwards” edges and an analytical estimate of the number of such edges derived from the global directionality to analyse the connectivity structure and predict the threshold for the emergence of a giant strongly connected component. This provides an insight beyond degree [177] and explains why, even if they have high mean degree, highly structured networks like food-webs often have very small strongly connected components. We extend our understanding of strong connectivity to real networks beyond previous results on directed random graphs [177] which do not capture the complex structures of real-world systems. We demonstrate the role the “backwards” edges have in controlling the strong connectivity by conducting a targeted attack on these edges. This removes the strongly connected component while maintaining the weak connectivity. We show the vital role that strong connectivity plays in dynamics, in the supplementary information, by comparing the spread of an infection using SIS dynamics; synchronisation of coupled Kuramoto Oscillators and how a new state establishes itself in the Majority Vote and Voter Models before and after the targeted attack. These dynamics demonstrate the role of hierarchy in the dynamics as the global directionality and “backwards” edges drive feedback and how their removal creates an asymmetry the ability of nodes to interact with each other dependent on their position in the hierarchy.

3.2 Background

Trophic Analysis is a technique which is used to calculate the global directionality and the hierarchy in directed complex networks [8]. Complex networks are graphs which represent real-world systems. Graphs are sets of vertices (nodes) and edges (links) which represent connections between elements in the system. Graphs are topological objects as they do not need to have a distance scale, they merely represent whether elements are connected. A directed graph is one in which the connections between elements go in only one direction. This is very common in real-world systems [18] which can be intrinsically directional like a prey-predator food web interaction or following a profile on social media. In complex networks it is common to represent a graph via an adjacency matrix. For a graph consisting of N nodes the adjacency matrix, A, is defined such that

$$A_{ij} = \begin{cases} 1 & \text{if there exists an edge } i \to j \\ 0 & \text{otherwise} \end{cases} . \tag{3.1}$$

As a result, the topology of the graph can be represented by the non-zero entries of this matrix. This form is preferred for studying complex networks as it is convenient for computer simulations, defining dynamical systems on the network, and network properties can easily be accessed from the properties of this matrix. In a directed graph this matrix is not necessarily symmetric, $A_{ij} \neq A_{ji}$, since the interactions are only in one direction. Undirected graphs always have symmetric adjacency matrices. Adjacency matrices can also be weighted to capture the strength of an interaction. However, for simplicity we focus here on the unweighted case. An undirected graph is connected if and only if for any pair of distinct nodes there exists a path connecting them. In directed graphs the notion of connectivity is more complex. A directed graph is weakly connected if there is a path between all pairs of vertices when edge direction is ignored. A digraph is strongly connected if for every pair of nodes i and j, there is a directed path from i to j and another from j to i (in other words, every node is reachable from every other node).

It is common for real-world directed networks to be weakly connected, but many are not strongly connected. In such cases, the extent to which a network approaches strong connectivity can be quantified by the size of its largest strongly connected component (i.e. the largest subgraph which is strongly connected). Later on, when we talk about predicting strong connectivity in real networks from a classification problem perspective, we use the more general definition of α-strong connectivity, which requires the largest strongly connected component to be larger than α times the number of nodes ($0 < \alpha < 1$). In our analysis, we set $\alpha = 0.9$.In an undirected graph, each node has a degree, corresponding to the number of edges connected to it. In a directed graph the in-degree of a node i is the number of edges which point to it $k_i^{in} = \sum_j A_{ji}$ and its out-degree is the number of edges pointing to other nodes, $k_i^{out} = \sum_j A_{ij}$. If the adjacency matrix is transposed the in- and out-degrees swap. [1]

3.2.1 Trophic Analysis

Trophic Analysis first arose in the study of food webs [5]. The hierarchical organisation of the network, as measured by a property called trophic coherence, was proposed as a solution to May's paradox regarding the stability of food webs [31]. The name arises from the trophic

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[1] This is a point to take care with as many authors have opposite conventions for defining the adjacency matrix. Note also that the mean in-degree is always equal to the mean out-degree, so we can refer simply to the mean degree of a digraph.

level of a species in ecology [179]. This definition relies on the existence of basal nodes, that is, nodes with in-degree zero. A new definition was then proposed in [8] which removed this constraint and made it applicable to any directed network. We follow the new definition [8],although most previous work used the original convention [5]. Trophic Analysis has been used to study many aspects of directed networks, including the structure of food webs [33]; spreading processes such as epidemics or signals in neural networks [34]; resilience of infrastructure networks [36, 37], control of organisations [7], and networks in economics and finance [8].

Trophic Analysis is composed of two parts: the node level information, Trophic Level, and the global information, Trophic Incoherence [8]. Trophic level gives a measure of where a node sits in the hierarchy of a directed network. For example, in a food web plants would be the low trophic level nodes and carnivores the high trophic level nodes, as energy flows up the food web from low to high trophic level. This can however be generalised to any directed network. Trophic levels are calculated by solving the $N \times N$ matrix equation given by

$$\Lambda h = v, \tag{3.2}$$

where h is the vector of trophic levels and the "imbalance" vector is the difference between in- and out-degrees: $v : i = k_i^{in} - k_i^{out}$. Λ is the Laplacian matrix,

$$\Lambda = diag(u) - A - A^T, \tag{3.3}$$

where u is the sum of in- and out-degrees, $u_i = k_i^{in} + k_i^{out}$, A is the adjacency matrix and A^T its transpose. These are all quantities which can be simply evaluated from the adjacency matrix. Note that equation 3.2 cannot be solved by inverting Λ since this matrix is singular. However, one can use other methods, such as LU decomposition, and for large networks the equation can be solved iteratively. Moreover, equation 3.2 is invariant under the addition of a constant vector to h. We therefore follow the convention that the lowest level node takes the value $h = 0$ [8].

Trophic Incoherence measures the global directionality of the network [8], based on the distribution of level differences across edges. If the network is maximally coherent, the edges only connect to nodes exactly one level above them and the network is perfectly hierarchical and globally directed. If the network is highly incoherent then the edges connect without respect to the levels and there is no global directionality. This is quantified via the trophic incoherence parameter F which is defined as

$$F = \frac{\sum_{ij} A_{ij}(h_j - h_i - 1)^2}{\sum_{ij} A_{ij}}. \tag{3.4}$$

This equation measures, averaged over the system, the square of the deviation in level difference of destination to source vertex from 1 across the edges of the graph. This equation is bound between 0 and 1 [8]. Networks with $F = 0$ are perfectly coherent, they have distinct integer levels in which all nodes are placed, and they are acyclic. When $F = 1$ every node has the same level and the network has no hierarchy. Examples of $F = 1$ networks are directed cycles. Networks which have $F = 1$ are perfectly balanced ($k_i^{in} = k_i^{out}$ for all nodes i), and are therefore unlikely to come about from a fully random process. For example random graph models such as the Erdős-Rényi model [180, 6] lead to networks where F is around 0.95, depending on sparsity. The trophic levels can be thought of as the set of values, h, which minimise F [8] for a given A. This leads to equation 3.2. It is also possible, equivalently, to speak in terms of Trophic Coherence, which can be defined as $1 - F$. When we say "top of the hierarchy" we mean the nodes with high trophic level, and when we use the phrase "bottom of the hierarchy" we mean nodes of low trophic level.

The definition of h as a measure of node hierarchy has been proposed independently more than once. For example, SpringRank [44] uses a physical argument to arrive at the same minimisation function as Trophic Analysis, but without the same quantification of the global directionality [8]. It is also possible to use a Helmholtz-Hodge decomposition to construct the idea of levels and "circularity" [45, 181], which leads to a different set of terms to quantify hierarchy and directedness, and it can be shown that this method is equivalent to

Trophic Analysis [8].

Generated Networks

When we require numerically generated networks to better sample the full range of Trophic Incoherence and degrees we the use the same variant of the generalised preferential preying model as [1], which was based on work from [34]. This model allows the Trophic Incoherence of a generated network to be approximately controlled. This is done by a taking an initial network structure and adding edges with a probability which is proportional to the level difference between the nodes, in a way which is determined by a “temperature” parameter. This probability is defined as

$$P_{ij} \propto \exp\left[-\frac{(\tilde{h}_j - \tilde{h}_i - 1)^2}{2T_{\text{Gen}}^2}\right], \tag{3.5}$$

where $\tilde{h}_i$ is the temporary trophic level assigned during the generation. T_{Gen} is the generation temperature used to control the incoherence. At high T_{Gen} edges are added without respect to the level structure so it produces an incoherent network similar to a random graph, while at low temperature the edges are only added when the level difference is near one, producing a very coherent network. Details of how to efficiently sample the possible edges and generate networks in this way can be found in [1].

3.3 Results

3.3.1 Fraction of Edges going against the Hierarchy

It is possible to analytically estimate the number of edges that go “backwards” – i.e. against the hierarchy. We define a backwards edge as one where the difference between the trophic level of the target vertex minus that of the source vertex is non-positive. As we go on to see, these edges are important as they determine the strong connectivity of the network, because they are needed to induce a path back down the hierarchy. This fraction of edges is useful in further calculation of strong connectivity.

The first part of this derivation is to assume that the edges follow an approximately Gaussian distribution in trophic level differences [6], where the mean is the mean level difference, $\bar{z}$, and the standard deviation is given by $\bar{z}\eta$ [8]. We assume that the level differences follow a Gaussian distribution as this assumption was used to derive the results linking trophic coherence to spectral radius [6], which also hold for the new definition of trophic levels and coherence [8, 1]. In addition, we have observed that for many real networks (some examples given in the supplementary material) the distribution of level differences can be well approximated by a Gaussian. Other formulations of hierarchy make similar assumptions, for example when SpringRank was first introduced [44] it was assumed that the ranks followed a Gaussian distribution, and shown that adding a quadratic regularisation term is equivalent to a Gaussian prior on the ranks.

The mean level difference can be computed from the Trophic Incoherence,

$$\bar{z} = 1 - F, \tag{3.6}$$

which was derived in [8] by writing the function for Trophic Incoherence as function of the mean and standard deviation of the level differences and then minimising it. The parameter η which which is the standard deviation scaled by the mean trophic level difference can also be expressed in terms of F [8] by similarly writing F as a function of the standard deviation and mean level differences

$$\eta = \sqrt{\frac{F}{1 - F}}. \tag{3.7}$$

Note that equations 3.6 and 3.7 hold for any digraph, and are not dependent on the assumption of Gaussian differences.

Assuming that the edge level differences, $x_{ij} = h_j - h_i$, follow a Gaussian distribution leads to the probability distribution,

$$p(x_{ij}) = \frac{1}{\bar{z}\eta\sqrt{2\pi}} \exp\left[-\frac{1}{2}\left(\frac{x_{ij} - \bar{z}}{\bar{z}\eta}\right)^2\right]. \tag{3.8}$$

The fraction of edges which do not go in the same direction as the hierarchy is the integral of this distribution from negative infinity to 0. The cumulative distribution of a Gaussian is well known and the result can be written in terms of the error function as

$$\overline{\beta(F)} = \frac{1}{2}\left[1 + \operatorname{erf}\left(-\frac{1}{\sqrt{2}}\sqrt{\frac{1-F}{F}}\right)\right], \tag{3.9}$$

where we have substituted for $\bar{z}$ and η in terms of F. Hence, $\overline{\beta(F)}$ can be regarded as the expected fraction of backwards edges under the assumption of Gaussian-distributed trophic differences. This equation can be understood by looking at the limiting cases where F equals 1 or 0. When F approaches 1 the error function goes to zero and then half the edges go against the “hierarchy", as every node approaches the same level and hence there is an equal likelihood of going forwards or backwards. When $F = 0$ the error function goes to negative 1 so the expression cancels and no edges go backwards, which makes sense as the network is fully coherent. Due to the fact that edges of level difference zero are counted as backwards the approximation breaks down in the extreme case of a perfectly balanced network such as a directed cycle or undirected graph, as all the edge differences are zero. Hence the measurement labels all the edges as backwards, whereas the approximation limits to half the edges going backwards.

This prediction holds well in real networks, as shown in figure 3.1, with some small deviations. This is likely because of the assumption that the distribution of edge differences is Gaussian. The relationship between F and the number of backwards edges looks almost linear but the non-linearity at low F is important: it is possible for a network without backwards edges not to be maximally coherent, since certain feed-forward motifs generate some incoherence [8].

All the real networks used in this paper and the original sources can be found in the supplementary information, for convenience we cite the online sources in the main text. This includes all the networks used in [6], plus a sample of networks from [182]. This data set includes metabolic networks, neural networks, trade networks, food webs and social networks. The number of backwards edges could also provide a rough estimate of the upper bound on the size of a feedback arc set, the number of edges which need to be removed to make the graph acyclic [183]. The link between hierarchy breaking edges and a heuristic to approximate the cycles has been made before [183] with different measures of the hierarchical ordering, including PageRank [184], however these lack an analytical estimate of the expected number of backwards edges. The probability of a path going backwards was also used to derive various expressions in the “coherence ensemble” of random graphs [6]. However, none of these works established the link to strong connectivity and the emergence of a giant strongly connected component, which follows.

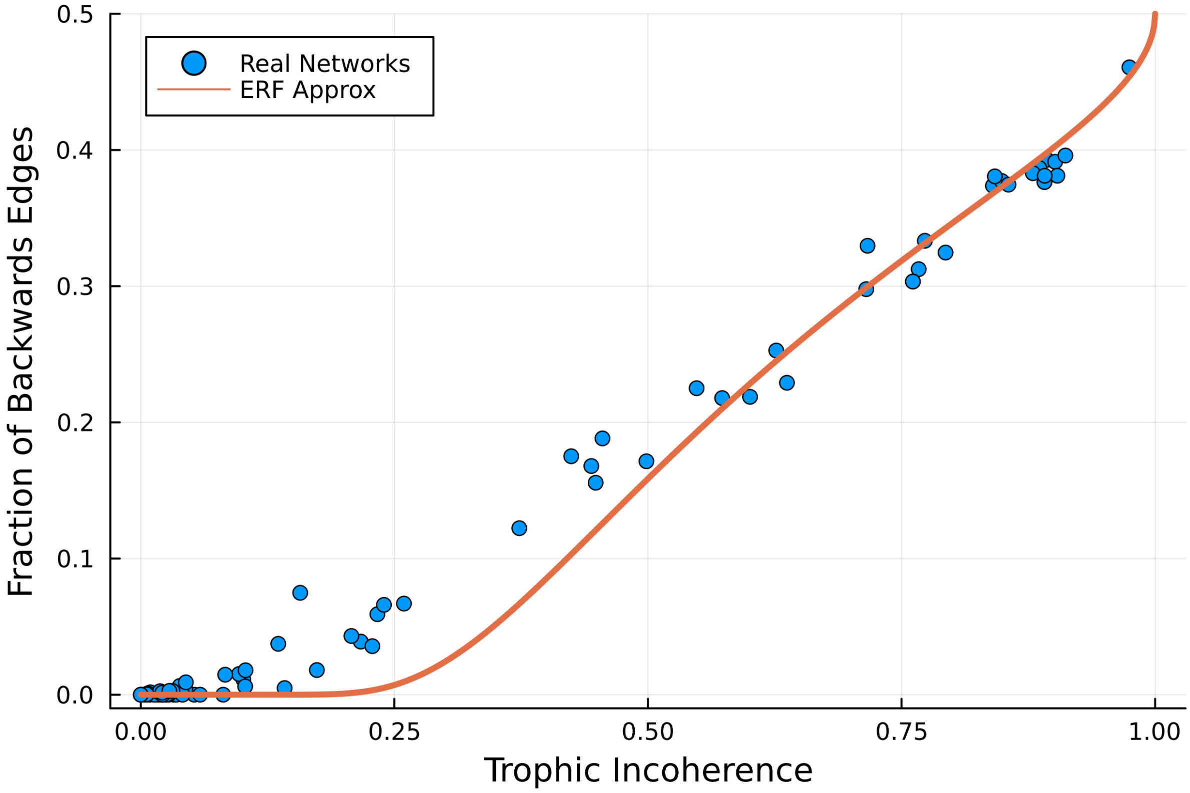


Figure 3.1: Number of backwards edges in various real networks (symbols) and the prediction of equation 3.9 (line), against trophic incoherence F. Data from [185] and [182] (original sources in SI Appendix).

3.3.2 Derivation of Strong Connectivity Critical Point and Phase Diagram

It is possible to derive an estimate of the percolation transition threshold for the emergence of a giant strongly connected component in directed networks using the insight gained from the hierarchical structure. This can be done by observing that if the nodes in a network are ordered in some way, then the edges which break that ordering by going ‘backwards’ are the important edges for strong connectivity. Adding more edges in the forward direction will not make the network strongly connected if it is very strictly hierarchical, as they do not provide a way to move back down the ordering towards the bottom of the network. In this way, the growth of the strongly connected component in a directed network can be thought of as a percolation process on the backwards edges, where the backwards edges connect the layers of the network. This makes it possible to move back down the hierarchy, thereby creating a giant strongly connected component.

This can be expressed using the framework for solving percolation problems set out in [178]. This framework decomposes the percolation process to transitions between l-step neighbourhoods, which in our case can be thought of as steps down the hierarchy. We assume a weakly connected network when the backwards edges are removed, which is a reasonable assumption for real networks as the fraction of backwards edges is usually small and the networks are dense enough so that removal of the backwards edges does not result in the network being disconnected. It is possible to find counter examples to this where the network does become disconnected if the backwards edges are removed (see Appendix 3.6). This, however, only occurs when the backwards edges are calculated once and trophic level is not recalculated after each removal. This is proven in Appendix 3.6, where we also show examples of the maintenance of weak connectivity in real networks, justifying this assumption. We wish to find the percolation threshold for the network to be at least weakly connected by only backwards edges, and hence have a giant strongly connected component.

We define a directed subgraph, $G(V, E_B)$, made up only of backwards edges, where the trophic level difference is less than or equal to 0, of the larger graph $H(V, E)$ containing all the edges from which the trophic levels are calculated. Following the steps laid in out in [178], we introduce the l-neighbourhood of a vertex, y. This is recursively defined as

$$\mathcal{N}_l(y) = \bigcup_{X \in V(\mathcal{N}_{l-1}(X))} \mathcal{N}_1(X), \tag{3.10}$$

where $V(\mathcal{N}_{l-1}(X))$ is the set of all of the vertices within the neighbourhood $\mathcal{N}_{l-1}(X)$. This neighbourhood can be thought of as the nodes reachable in within l steps from vertex y, illustrated in more detail in [178]. The percolation transition can then be understood by analysing the surfaces of these neighbourhoods, which can be defined as the vertex sets

$$V_l := V(\mathcal{N}_l(y)) \setminus V(\mathcal{N}_{l-1}(y)). \tag{3.11}$$

These are the nodes which lie exactly l steps from the origin vertex, y. This origin vertex can in general be any vertex, but in the case of backwards connectivity we choose the vertex with the highest trophic level. Following the work of [178], the system is above the percolation threshold if

$$\lim_{l \to \infty} \mathbb{E}[o(V_l)] > 0, \tag{3.12}$$

where $\mathbb{E}[x]$ is the expectation value of x, and $o(V_l)$ is the number of connected nodes on the surface l. The expectation values are taken using draws from the "coherence ensemble", the set of all unweighted directed networks of fixed trophic coherence, size and degree distribution, used in [6, 18, 8]. Equation 3.12 can be understood to mean that there is a giant connected component if the expectation value of a node being connected is greater than zero as the surface size extends to infinity. This is analogous to the probability of a branching process dying out as the number of steps tend to infinity.

One assumption for our specific case is that in the network of backwards edges the expected number of connected nodes in a surface is simply the number of connected nodes in the previous surface multiplied by the average number of backwards connections. This is

$$\mathbb{E}[o(V_{l+1})] = \beta\langle k\rangle\mathbb{E}[o(V_l)], \tag{3.13}$$

where $\langle k\rangle$ is the mean total degree and β is the fraction of edges which go backwards. This equation can then be solved iteratively assuming that $\mathbb{E}[o(V_0)] = C$, where C is some finite constant representing the number of nodes at the top of the hierarchy. This leads to

$$\mathbb{E}[o(V_l)] = (\beta\langle k\rangle)^l C. \tag{3.14}$$

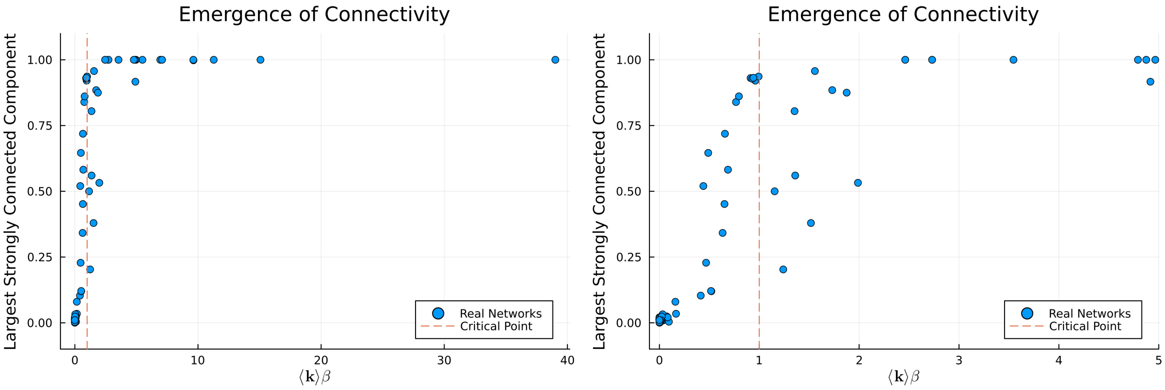
Taking the limit l goes to infinity leads to the result

$$\lim_{l\to\infty}\mathbb{E}[o(V_l)] = \begin{cases} \infty & \text{if} \quad \beta\langle k\rangle > 1 \\ C & \text{if} \quad \beta\langle k\rangle = 1 \\ 0 & \text{if} \quad \beta\langle k\rangle < 1 \end{cases}. \tag{3.15}$$

This means that we expect a giant strongly connected component when $\beta\langle k\rangle > 1$, which means that on average each node has at least one backwards connection. This can also be written directly as a function of trophic incoherence using the expected value of β,

$$\frac{\langle k\rangle}{2}\left[1 + \operatorname{erf}\left(-\frac{1}{\sqrt{2}}\sqrt{\frac{1-F}{F}}\right)\right] > 1. \tag{3.16}$$

This estimate, which uses very little information about the network structure (only the mean degree and trophic incoherence), works well for real networks, figures 3.2a and 3.2b. This result shows how the understanding of hierarchy can allow insights into the connectivity of directed networks. The result relies upon the ability to calculate the hierarchy for any directed network, and the realisation that the backwards nodes shape connectivity and that their number can be linked to the global directionality and analytically estimated. Other measures of hierarchy would allow the number of "backwards" edges to be enumerated numerically but lack the link to global directionality which gives the intuition behind these results.



(a) Full Range of Real Networks

(b) Closer View of Critical Point

Figure 3.2: Fraction of nodes in the largest strongly connected component against $\beta\langle k\rangle$ for several real networks. The critical point, $\beta\langle k\rangle = 1$, is indicated with a vertical line. The panel on the right shows only the networks with $\beta\langle k\rangle \leq 5$. Data from [185, 182] (original sources in SI Appendix).

The equation for the percolation threshold, under the Gaussian edge difference assumption, in terms of F, equation 3.16, can be expressed as an equation for the critical incoherence. This can be written as

$$F_c = \left[1 + 2\left(\mathrm{erf}^{-1}\left(\frac{2}{\langle k\rangle} - 1\right)\right)^2\right]^{-1}. \tag{3.17}$$

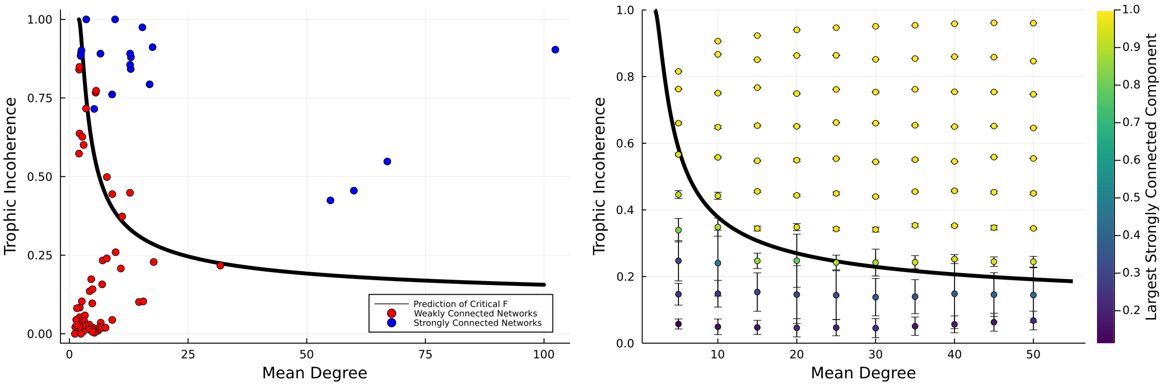
For a fixed $\langle k\rangle$, if F is greater than the predicted value, then we expect the network to be strongly connected. This allows the existence of a giant strongly connected component of a real network to be predicted based only on F and the average degree. The accuracy of this prediction for real networks is demonstrated in figure 3.3a, where the prediction of strong connectivity is formulated as a classification problem. We assume that the positives in our sample are the α-strongly connected networks which have a strongly connected component of at least 90% of the network size, and the negatives are the networks which fall below this value. The confusion matrix for this process reads as True Positive Rate 0.783, True Negative Rate 0.906, False Negative Rate 0.217, False Positive Rate 0.09375. This is quite a good classification rate as we note and demonstrate in figure 3.3a that all the errors lie close to the transition line where we do not expect to be able to classify the networks with a high level of accuracy into the two categories. We note, however, that the classification problem approach is very sensitive to the difficulty of the data chosen. For example, if a data set were selected with very few networks in the intermediate region (say, a single network type, such as food webs), then the results would improve without any change in the method. In our data set we have 64 networks with a strongly connected component below 90% and 23 with a strongly connected component larger than this.

The only regions where the prediction is less good is close to the boundary, however this is not surprising as we are not taking account of any finite size effects or potentially heterogeneous degree distributions, and in particular how the backwards edges are distributed. These results are broken down by network type in the supplementary information.

We can give further insight into the accuracy of the prediction by using numerically generated networks to better sample the parameter space and verify the results in a larger region. This is shown in figure 3.3b. We take 1000 networks where $N = 500$, generated as in [1], where each node has at least in-degree 1 (which would make the trophic level impossible to calculate in the original definition from ecology [5]), and then bin them by Trophic Incoherence and average the size of the strongly connected component. This result agrees well with the analytical prediction, with the networks well above the boundary being strongly connected and a large component forming in the networks around the boundary as expected.

These results, which hold for both real and generated networks and are based on the assumption of Gaussian edge differences, give a good insight into how global directionality determines strong connectivity and the emergence of a giant strongly connected component. Even for very large degree a network is still unlikely to be strongly connected if F is low enough, which demonstrates that more than just information on node degrees is needed for estimating the connectivity of a directed network. Why some real networks lie close to the transition line and properties of networks at this point may be a possible avenue for future work.

The value of this analysis can be highlighted by comparing to the results obtained by taking this real network data set and trying to predict the the emergence of a giant strongly connected component without using the hierarchical structure. This can be roughly estimated using results from [177, 6], where one wold expect the strongly connected component to grow



(a) Real networks

(b) Numerically generated networks.

Figure 3.3: Prediction of strong connectivity using the trophic incoherence (y-axis) and mean degree (x-axis), based on the critical incoherence F_c given by equation 3.17. Panel (a): Real networks from [185, 182] (original sources in SI Appendix). Panel (b): 1000 Networks with $N = 500$ generated numerically as in [1], with varying mean degrees and binned by trophic incoherence. Error bars are one standard deviation.

very quickly and the percolation to occur when the branching factor is greater than 1,

$$\frac{\langle k^{\text{in}} k^{\text{out}} \rangle}{\langle k \rangle} > 1. \tag{3.18}$$

This is demonstrated in figure 3.4, which shows how many networks of very high branching factor nevertheless have a small strongly connected component. The figure represents a closer look at the critical point and networks of very high branching factor can be found in the supplementary information. This demonstrates how the directional organisation is a vital part of the connectivity structure of real networks. Understanding the interplay between global directionality (trophic incoherence) and ordering (trophic level) provides an intuition greater than each individual notion can.

For comparison we also repeat the same classification experiment using the branching factor to predict if a network has a large strongly connected component. The confusion matrix for this process is True Positive Rate 1.0, True Negative Rate 0.219, False Negative Rate 0.0, False Positive Rate, 0.781. This is expected as such a classification technique predicts that almost every network apart from those of very small branching factor is strongly connected, which explains the very high true positive rate, but also the very high rate of false

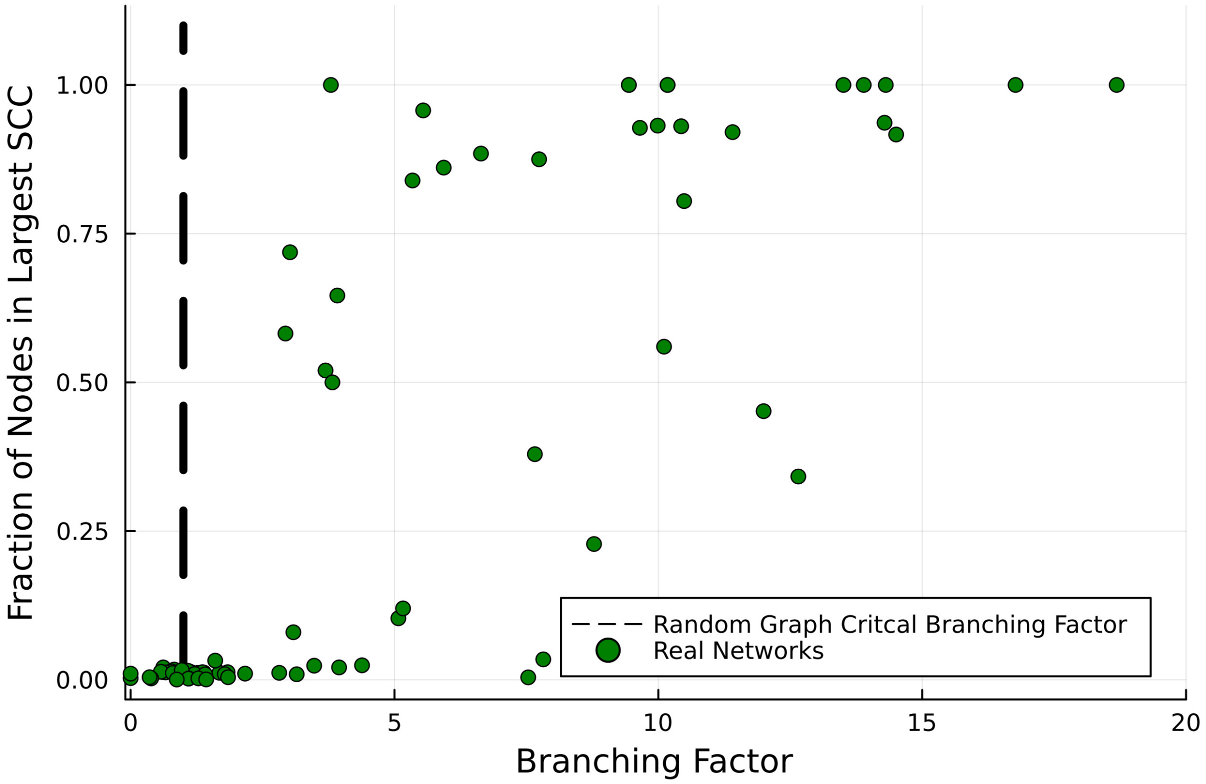
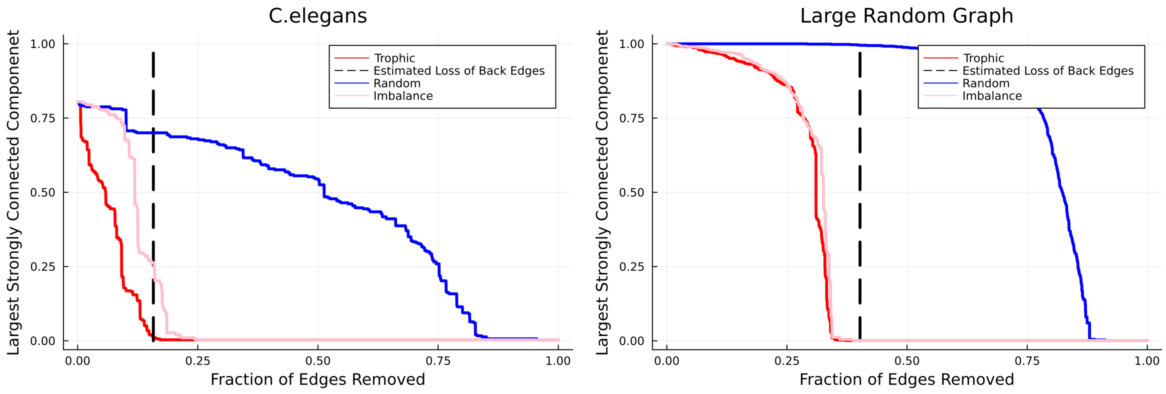


Figure 3.4: Prediction of strong connectivity based on the branching factor for real networks. Contrast with figure 3.2a, based on trophic coherence as presented here. Data from [185, 182] (original sources in SI Appendix).

positives. This further quantifies why in order to understand how strong connectivity arises in real directed networks it is important to factor in the global directionality of the system.

3.3.3 Targeted Attacks on Backwards Edges

To demonstrate how the strong connectivity of a network depends on the edges which break the hierarchy we can conduct a targeted attack on those edges and compare the degradation of the strongly connected component to that observed in a random attack. We remove edges in order of their trophic difference, starting by removing the edges with the most negative trophic difference. This only takes into account the hierarchical organisation; it may be possible to destroy the strongly connected component faster using a different method, for example attacking bottleneck edges or specifically trying to target edges breaking the hierarchy in different components of the network. However, when all the backwards edges are removed all cycles are destroyed and the strongly connected component is guaranteed to vanish. This can be demonstrated in real networks, figure 3.5a, such as the connectome of the worm *C.Elegans*. The point at which we estimate the “backwards” edges to vanish, shown by the dashed line in figure 3.5a, is analytically estimated from equation 3.9 and predicts well the point at which the strongly connected component vanishes completely. We compare the attack using backwards edges with two alternative attack strategies: (1) completely random edge attack, and (2) attack based on the edge degree imbalance differences, $(k_j^{in} - k_j^{out}) - (k_i^{in} - k_i^{out})$. Here we attack the most negative of degree imbalance differences as a proxy for trophic level. The intuition is that we roughly expect nodes of high in-degree and low out-degree to be high level nodes and the inverse to be low level nodes. We observed in the structured network of *C.Elegans* that the backwards edges attack strategy is significantly better than the random attack. The imbalance strategy is better than random but is less successful than the trophic level strategy as it does not encompass the range of structural information captured in the trophic levels.



(a) *C.Elegans* connectome.

(b) Erdős-Rényi graph. $N = 1000$, $\langle k \rangle = 10$.

Figure 3.5: Size of the strongly connect component as edges are removed randomly, in order of trophic level difference, and in order of degree imbalance difference, for real and Erdős-Rényi networks (panels (a) and (b), respectively). The dashed vertical lines represent the point beyond which no backwards edges are predicted by equation 3.9.

Similar results can be found for networks where there is no expectation of this kind of organised structure, like a dense random graph. This is shown in figure 3.5b. The figure shows that even in networks where there is little structure expected there still exists a degree of directional organisation that can be exploited to break down the network, as demonstrated by the comparison of the backwards attack to the random attack.. The number of edges needed to make the network acyclic and have no strongly connected component depends on the total number of backwards edges, which is a function of the trophic incoherence and the mean degree, as in the percolation transition above. This demonstrates that the strongly connected component can be understood by focusing on the backwards edges, which was the intuition that motivated the above derivation.

In the case of a random graph, because it lacks an overall hierarchical structure, the degree imbalances act as a good proxy for trophic level. Hence, an attack on the imbalances performs similarly to trophic level. A similar effect has been shown in [3], where the success of different measures such as imbalance and PageRank were compared to trophic level, as incoherence varied, in predicting strategy choice in generalised rock-paper-scissors dynamics.

One important thing to note about this targeted attack is that it does not generally affect the size of the weekly connected component until all the backwards edges are removed and then it behaves in the same way as a random attack in most real-world cases. For more detail see Appendix 3.6. This could be useful in situations where one wishes to attack the strongly connected component without disrupting the weakly connected component, which would happen if bottleneck edges were attacked, for example. This means that the backwards edges can act as an approximation for the feedback arc set [183]. Trophic level may not perform as well as specialist methods at this task [183], but does provide an analytical estimate of how many edges one would expect to need to remove in any large network, which can be simply calculated from F. It also explains why certain networks are more difficult to render acyclic based on where they lie on the phase diagram.

3.4 Discussion and Potential Applications

There are a wide range of network applications where percolation in networks has been observed to be important [176]. We highlight a few areas where our work may be useful, but this is not necessarily exhaustive. Strong connectivity and percolation can play an important role in city planning as networks of one-way streets must be strongly connected [186].

Trophic analysis can be useful for understanding spreading processes where the network is directed and there is some ordering to the network structure, for instance in ecological settings [187]. A real-world example of this is the spreading of crown-of-thorns starfish on coral reefs [188, 189, 190]. These starfish are a pest which eat coral reefs and can damage ecosystems. Outbreaks are governed by the spread of their larvae by the ocean currents. This process is directed as the larvae move in the direction the ocean flows. This is the kind of process Trophic Analysis could lend itself to as it could be used to understand the global connectivity structure to see if the outbreak is likely to spread across the reef or in a directed manner. It can be used to extend the existing analysis of a region's vulnerability to outbreaks or danger as a starting point beyond simply the size of the out- and in-components [188], by factoring in where reefs sit in the network hierarchy determined by trophic level.

Our work could also relate to the growth of biological neural networks and formation of a giant strongly connected component of cells [191, 192]. These neurons have previously been grown in circumstances where there is limited hierarchical structure and the degree distributions are well known. However, if the cells were exposed to a directed gradient, or in a real-life system are more likely to grow in a particular direction, Trophic Analysis may play a role in explaining this percolation threshold.

Our results may also partially explain the difference in percolation thresholds for dynamical processes on directed networks [193] compared to the undirected case, due to the effect of hierarchical ordering increasing the threshold for strong connectivity. This will be observed even in random graphs, as trophic incoherence does not usually reach one. The percolation of the strongly connected component and the direction of flow and spread of information may also play a role in communication networks and control and decision making in organisations [7].

In general, Trophic Analysis can be used to modify the dynamics by understanding the hierarchical organisation and the effect of localised perturbations, as well highlighting the role of hierarchy breaking edges in driving strong connectivity, feedback and resilience in complex systems. Trophic Analysis is also a useful metric due to the simplicity of the calculation and its interpretability, as the notion of directionality and place in hierarchy is quite simple and intuitive. This makes the method attractive to be employed in many settings as the barrier to entry is relatively low, while still providing good intuition into the structure of a directed network. Additionally, it provides motivation to focus on the intrinsic directional aspects of real-world systems, which are understudied compared to the undirected case [18].

Our results for strong connectivity, though quite robust, are based on a very simple approximation of the percolation of backwards edges. So it may be possible to extend or repeat this result with a different measure of hierarchy or more information about the degree distribution, providing greater accuracy.

3.5 Conclusion

We have shown how, by using Trophic Analysis to study the hierarchical ordering and global directionality of a directed network, it is possible to analytically estimate the number of “backwards” edges which break this ordering and predict the threshold for the network to be strongly connected. From this a phase diagram of strong connectivity in terms of trophic incoherence and mean degree can be derived which holds well for real directed networks. This shows that strong connectivity in directed networks is driven by more than just the degrees, and that hierarchy can play a significant role.

We highlight these results by conducting a targeted attack on “backwards” edges, revealing their crucial role in maintaining a strongly connected component. In the SI, we further illustrate the importance of these edges by implementing several dynamics (voter model, SIS and Kuramoto oscillators) where the behaviour is dictated by the strongly connected component and the trophic level of the initiating node.

3.6 Appendix:Removal of Backwards Edges and Weak Connectivity

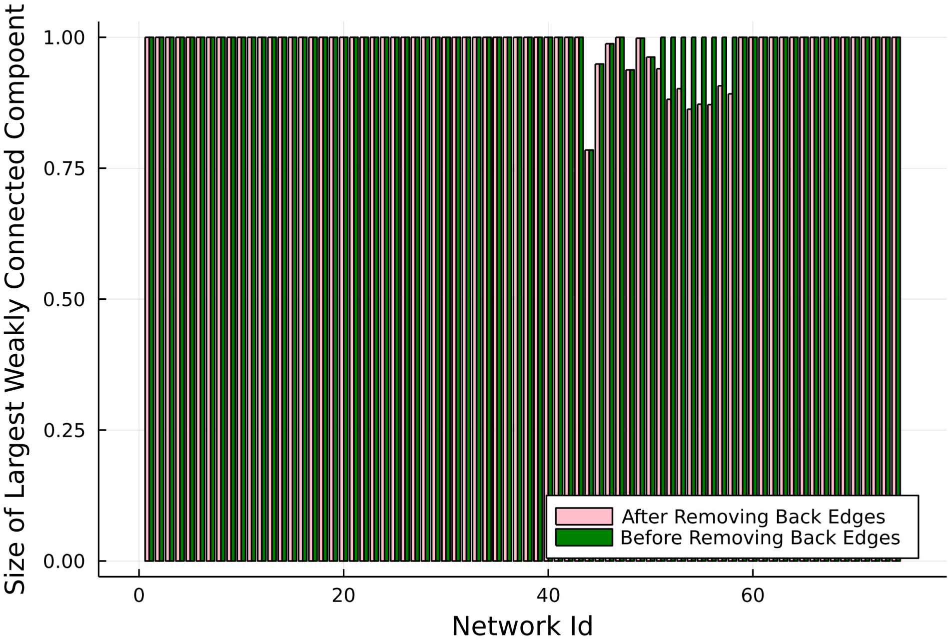


Figure 3.6: Lack of change in the size of the weakly connected component as the backwards edges are removed from real networks [185] (original sources in SI Appendix).

Backwards edges are in general linked to cycles and reciprocal edges this means than in general removing one backwards edge is unlikely to separate a network into distinct components. This explains why the size of the weakly connected component is generally unaffected when the backwards edges are removed in real networks, figure 3.6.

However, there are specific structures composed of interlocked cycles which can cause the network to become disconnected if the trophic level is calculated only once and then all the edges which are initially backwards are removed as shown by the example in figure 3.7 where the backwards edges are highlighted in red. This however is a specific case and does not seem to be found when studying the connectivity of real networks. In addition if the trophic levels were recalculated after the first edge was removed the second edge would then become forwards. This leads to the property that if the trophic level is recalculated then the network will not become disconnected. This is proved below.

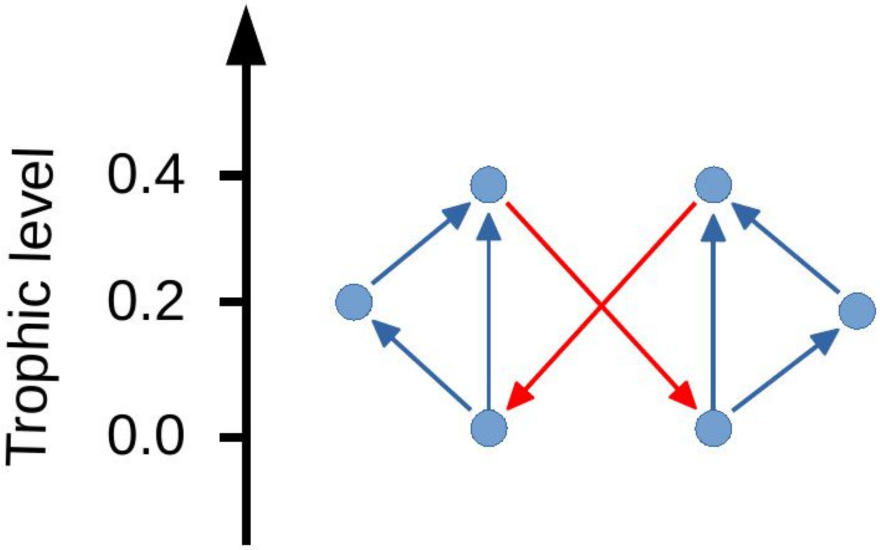


Figure 3.7: Example of network which is connected by two edges which go backwards in Trophic level.

Given an initial graph G(V,E) at each step remove the edge which is most backwards in trophic level and then recalculate the trophic level. Stopping when all the edge differences are non-negative. In order to break the network into separate components via this method there would require a situation where the graph has been separated into two disjoint components joined by a single edge which upon removal would break the graph into disconnected pieces. If the trophic levels are recalculated then it is never optimal for this edge to go backwards in trophic level as the levels of one of the components can be modified by a constant which will not change the global coherence apart from across the joining edge where it will become positive. If the edge is backwards it is always possible to reduce incoherence in this way so the configuration can not exist upon recalculation.

CHAPTER

4

INFLUENCE AND INFLUENCEABILITY: GLOBAL DIRECTIONALITY IN DIRECTED COMPLEX NETWORKS

This chapter is based on

- Niall Rodgers, Peter Tiňo, and Samuel Johnson. "Influence and influenceability: global directionality in directed complex networks". In: *Royal Society Open Science* 10.8 (Aug. 2023). ISSN: 2054-5703. DOI: 10.1098/rsos.221380. URL: https://royalsocietypublishing.org/doi/10.1098/rsos.221380

Relationship of Work to Thesis

This chapter comprises the third paper written during my PhD [3], which was based on ideas generated during the earlier projects. It uses the intuition gained through earlier work on Hopfield-like networks, chapter 5, to highlight how hierarchical structure can affects many different dynamics. As well as demonstrating how other structural features which could not be covered in chapter 3 are also related to Trophic Analysis. This paper relies on the knowledge gained in chapter 5 to be able to further generalise our understanding of Trophic Analysis to more systems. It also provides many potential avenues of future work, as a more detailed study of any of the dynamics covered in this work could form the basis of a future project. This work relates to the chapter on fitness-based generative models, chapter 6, as one can imagine that in real systems nodes which are influential over the state of the system may also have some fitness variable or metadata associated with them which relates to this.

Abstract

Knowing which nodes are influential in a complex network and whether the network can be influenced by a small subset of nodes is a key part of network analysis. However, many traditional measures of importance focus on node level information without considering the global network architecture. We use the method of Trophic Analysis to study directed networks and show that both 'influence' and 'influenceability' in directed networks depend on the hierarchical structure and the global directionality, as measured by the trophic levels and

trophic coherence, respectively. We show that in directed networks trophic hierarchy can explain: the nodes that can reach the most others; where the eigenvector centrality localises; which nodes shape the behaviour in opinion or oscillator dynamics; and which strategies will be successful in generalised rock-paper-scissors games. We show, moreover, that these phenomena are mediated by the global directionality. We also highlight other structural properties of real networks related to influenceability, such as the pseudospectra, which depend on trophic coherence. These results apply to any directed network and the principles highlighted – that node hierarchy is essential for understanding network influence, mediated by global directionality – are applicable to many real-world dynamics.

4.1 Introduction

Influence in directed complex networks and the ability of the networks to be influenced is vitally important in many real-world systems, for example the spreading of opinions and epidemics or the synchronisation of the brain in a seizure [194]. However, when we think of what makes nodes influential, the answer is very disparate and depends on many factors. This question has been of great interest to the network science community and well studied in the case of undirected networks [195, 196]. However, in the directed case insight can be gained by considering properties unique to directed networks. This is necessary as many real-world systems are intrinsically directed and the influence of nodes is strongly tied to the directionality of the edges [197]. Influence can be thought of as how well nodes control the dynamics of a network, how measures of centrality are distributed across the network, how many nodes can be reached from a set of nodes and how sensitive the network is to perturbations. We show that all of these properties can be understood and made intuitive by considering the hierarchical ordering and global directionality of the network as measured through the technique of Trophic Analysis [8, 1, 2].

When the nodes are easily ordered in a hierarchical fashion, as in a food-web, it is clear that the network can be influenced by the nodes at the bottom of this hierarchy and conversely it is very difficult to influence the network from the top of the hierarchy. When there is little hierarchical structure, like in an Erdős-Rènyi random graph, this effect is damped and influence over the network is more evenly distributed. This simple construction, detailed in the background, aides in the interpretation of control over network dynamics, spreading processes, localisation of centrality measures and sensitivity to perturbations. Hierarchical ordering can explain why nodes which locally look unimportant may be able to influence the entire network. This framework may provide an interpretation to observations made about influence in directed networks in a variety of literature settings such as the effect of heterogeneous centrality and directionality in opinion formation in real networks [198], the influence of peripheral nodes on dynamics of directed networks [193] or the asymmetry between paths up and down the network hierarchy [199]. Trophic Analysis pairs a global measure of directionality with a local measure of hierarchy, making it different from a single centrality measure. This allows an intuition surrounding the variability in the importance of a node's position in the hierarchy and how this affects its role in the network. This differs from previous results on the relationship between hierarchy and influence which do not feature this pairing of local and global measures [200, 201]. The fact that centrality measures play different roles dependent on the mesoscale structure of the network has been noted previously in the case of PageRank and clustering [202].

This paper is organised as follows. We first introduce the background and explain the principles underlying Trophic Analysis. We then introduce some dynamics and highlight how global directionality can affect the influence and influenceability of these processes. These are Majority Vote, Kuramoto oscillators, the Voter Model and the frequency of strategies in Generalised Rock-Paper-Scissors games. We then include some results on the relationship between structure and influence in real-world networks and how this can be shaped by hierarchy. We demonstrate the relationship between hierarchy and eigenvector localisation, left and right eigenvector correlation (with specific real-world examples), sensitivity to structural perturbation through the pseudospectra and the size of the out-component of a node. The real network data used in this paper, also used in [6, 2], is available at [185] and contains food-webs, neural networks, social networks and more as well as the original sources of the network data used. This shows how many diverse notions of influence can be investigated in directed networks using Trophic Analysis and how in a wide range of systems the ability to exploit hierarchy to influence a system depends on the global directional organisation.

4.2 Background

Real-world systems formed by many interacting elements can be represented using graphs. These complex networks are sets of nodes or vertices representing the elements of the system while the edges or links represent the interactions or connections between elements. Many real-world systems such as social networks, food-webs, the internet and more have interactions which are intrinsically directional and may represent the influence a node has over another [18]. This structure can be represented through a matrix, A, known as an adjacency matrix where the edges are represented by the non-zero entries of the matrix. For an unweighted directed network of N nodes this $N \times N$ matrix is defined as

$$A_{ij} = \begin{cases} 1 & \text{if there exists an edge } i \to j \\ 0 & \text{otherwise} \end{cases} . \tag{4.1}$$

In the case of directed networks this matrix is not symmetric, unlike the undirected case where edges go in both directions and the matrix is symmetric. Each node i then has an in-degree, $k_i^{in} = \sum_j A_{ji}$, and an out-degree, $k_i^{out} = \sum_j A_{ij}$. The matrix A can also be weighted to show the strength of interactions but here we focus on the simple unweighted case although it is possible to use Trophic Analysis in the weighted regime [8].

4.2.1 Trophic Analysis

Trophic Analysis is a technique to quantify the global directionality inherent in real directed networks [8], and is applicable to any directed network. Trophic Analysis was originally derived from ecology [5] where the original definition linked hierarchy to weighted steps from the basal nodes (vertices of in-degree zero), which is an intuitive way to view hierarchy but cannot be generalised to any directed network without basal nodes like the definition used here and in [8, 1, 52, 2]. Much of the previous work which applied trophic level and incoherence used the previous definition [6, 5, 7, 33, 34]. This was successfully applied in a wide variety of settings including infrastructure [36, 37], the structure of food webs [33], spreading processes such as epidemics or neurons firing [34], and organisational structuring [7].

Trophic Analysis combines two parts: the node level local information, Trophic Level, and a measure of the global network directionality, Trophic Incoherence. Trophic level is a node level quantity which measures where a specific node sits in the network hierarchy. Trophic level is calculated by solving the $N \times N$ matrix equation, first proposed in [8], given by

$$\Lambda h = v, \tag{4.2}$$

where h is the vector of trophic levels for each node and v is the vector imbalance of the in and out degree of each node, where each element is defined as $v_i = k_i^{in} - k_i^{out}$. Λ is the Laplacian matrix:

$$\Lambda = diag(u) - A - A^T, \tag{4.3}$$

where u is the sum of the in and out degrees of each node, $u_i = k_i^{in} + k_i^{out}$, and A^T is the transpose of the adjacency matrix, A. The solution of equation 4.2, which provides the trophic levels of the nodes, is only defined up to a constant vector so we take the convention that the lowest level node is set to trophic level zero. The Laplacian matrix is singular by definition, yet a solution can be found either by choosing a node (say $i = 1$) and setting its value (e.g. $h_1 = 0$); or iteratively, which is convenient for very large networks [8].

In a balanced network, for instance a directed cycle, there is no hierarchical structure so every node has the same level. This is due to the dependence of equation 4.2 on the imbalance vector, $v_i = k_i^{in} - k_i^{out}$, which means that when the in and out-degrees of all nodes are equal the right side of the equation goes to zero. In a network with a perfect hierarchy like a directed line, the nodes are assigned integer levels with steps of one between connected nodes. The level distributions of real networks are more complex and lie somewhere between these extreme cases.

Trophic Incoherence is a global parameter which measures how well hierarchically ordered the network is. It is related to the amount of feedback in the system, and thus to network properties such as the spectral radius, non-normality and strong connectivity [8, 2]. It is quantified via the trophic incoherence parameter F, which is defined as

$$F = \frac{\sum_{ij} A_{ij}(h_j - h_i - 1)^2}{\sum_{ij} A_{ij}}. \tag{4.4}$$

In [8], the authors begin with equation (4.4) (which is the original definition of trophic incoherence [5]) and define the trophic levels, h, as those which minimise F. Hence, the linear form of equation (4.3) and dependence on the imbalance vector comes from the minimisation of the quadratic function in equation 4.4.

Trophic Incoherence measures how far the mean square of the difference in trophic level, h calculated via equation 4.2, between start and end vertices of all the edges differs from one. The equation for Trophic Level, equation 4.2, can be derived by minimising equation 4.4 with respect to h. The Trophic Incoherence takes values between 0 and 1 with real networks found on a spectrum between these extreme values. Networks with a perfect hierarchy are coherent and have $F = 0$. When the network is balanced like a directed cycle then $F = 1$. It is also possible to speak in terms of coherence instead of incoherence by using the quantity $1 - F$. When we talk about hierarchy we refer to the bottom of the hierarchy as nodes of low trophic level and the top of the hierarchy as the nodes of high trophic level. In a directed path the low trophic level nodes would be the start of the path and the high level nodes would be near the end of the path. In a food-web the bottom nodes are plants and the top nodes are apex predators. This, however, is just a convention and the notion of top and bottom can be flipped by taking the transpose of the adjacency matrix (for example, when describing hierarchies of information flow from nodes to nodes).

Using directionality and hierarchy to analyse the structure of directed networks in this way is quite natural and as such alternative similar formulations exists which rank nodes and measure the global directionality. SpingRank [44] views the ranking problem as minimising the energy of a network of directed springs, leading to a similar minimisation problem as the one used in Trophic Incoherence. However, these authors focus on the node level ranks rather than the global directionality and add a regularisation term to remove the invariance of their rank equation to addition of a constant vector. There is also a methodology based on Helmholtz–Hodge decomposition for measuring “circularity” in directed networks [45, 181] which has been shown to be equivalent to Trophic Analysis [8].

4.2.2 Network Generation

In order to study how the properties of networks depend on their trophic structure it is necessary to be able to numerically generate networks which span the full range of trophic incoherence, while keeping the number of nodes and edges fixed. We adapt the Generalised Preferential Preying Model (GPPM) [34] in an identical way to [1] to the definition of trophic level which does not require basal nodes (vertices of zero in-degree) and use that to generate the networks we require. This works by generating an initial configuration of N nodes and a small number of random edges, calculating the initial trophic levels of this setup, adding edges up to the required amount using a probability determined by the trophic level and a temperature-like control parameter which can affect the spread of level differences. In order to generate a network with no basal nodes the initial configuration is that each node has in-degree one with the source vertex for that edge chosen uniformly at random from the other nodes in the network. Once the initial trophic levels $\tilde{h}$ are calculated via equation 4.2 then new edges, up to the required amount, can be added with probability defined as

$$P_{ij} = \exp\left[-\frac{(\tilde{h}_j - \tilde{h}_i - 1)^2}{2T_{\text{Gen}}}\right], \tag{4.5}$$

where P_{ij} is the probability of connecting nodes i to j. The parameter T_{Gen} controls this process. When this parameter is small it is likely that edges connect only between nodes where the level difference is 1 or near to it. When T_{Gen} is very large then the edge-addition probability goes towards 1 irrespective of the trophic level difference between the end and start nodes.

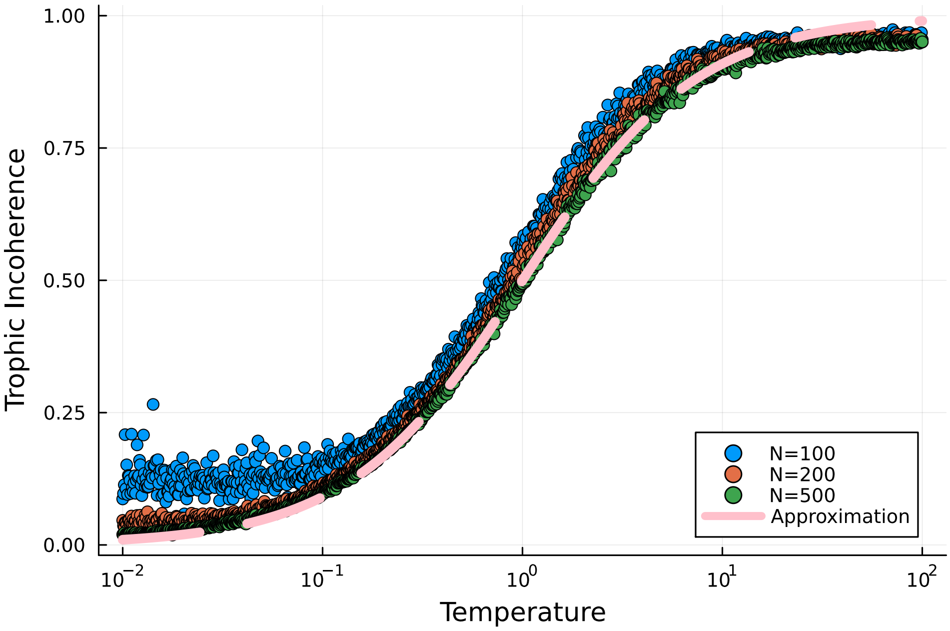


Figure 4.1: Relationship between Trophic Incoherence and generation temperature in the model used in this work, where each of the 1000 points per network size represents a distinct network generated by the model, with $N = 100$, $N = 200$ and $N = 500$, $\langle k \rangle = 20$ and no basal nodes. The generation temperature is logarithmically spaced between 10^{-2} and 10^{2}. We also plot with a dashed line an analytical approximation, given by equation (4.7), for the relationship between the Trophic Incoherence and Temperature.

The relationship between the generation temperature and the trophic incoherence is displayed in figure 4.1, which shows how the model can be used to create a sample of networks of varying incoherence. In order to efficiently sample the whole spectrum of the trophic incoherence we use logarithmic spacing of T_{Gen} throughout the paper, except for in the sections on the generalised rock-paper-scissors games and the out-component analysis. In these two sections we compare networks of low, intermediate and high trophic incoherence, for which we selected the generation temperatures to be $0.02, 1$ and 100, respectively. As shown in figure 4.1 this picks out each of the broad regimes of the generative model; the low temperature regime of very coherent networks, the intermediate regime where we see more variability with the temperature, and the high temperature regime of incoherent networks.

We also show in figure 4.1 how the behaviour of this model can be analytically approximated. In previous work on trophic analysis, where the ecological definition of trophic levels was used, the trophic incoherence, q, was defined as the standard deviation of the trophic level differences spanned by edges [5]. Under this definition the mean trophic level is always one, and a network is more incoherent the more heterogeneously trophic differences are distributed around this value. Given a set of trophic levels (by whichever definition), it is possible to convert between the two measures of incoherence via the formula defined in [8],

$$F = \frac{\eta^2}{1+\eta^2}, \tag{4.6}$$

where $\eta = \sigma/\mu$, σ is the standard deviation of the level differences and μ is the mean level difference. Hence, η is the appropriate replacement for the incoherence parameter q used in [5, 6] and subsequent papers, when using the MacKay level definition [8]. If we assume that the trophic level difference distribution across the edges in the generated networks is distributed as in the edge addition probability, we can replace η^2 with T_{Gen}, if we assume that iteration of the attachment probability given by equation (4.5) leads to an approximately Gaussian distribution of trophic differences. The differences in trophic level has been found roughly to follow a Gaussian distribution in real networks. Also, analytical results which hold for real networks have been based on the assumption that the level difference distribution is Gaussian [2]. The assumption that the trophic levels follow the same Gaussian as implied by the edge addition probability leads to the approximation that

$$F \approx \frac{T_{\text{Gen}}}{1+T_{\text{Gen}}}. \tag{4.7}$$

As shown by figure 4.1 this fits quite well for the larger networks sizes. We plot the data with a logarithmic scaling on the x-axis which allows the different regimes of low, intermediate and high incoherence to be visualised and leads to the sigmoid shape. As writing $= \log_{10} T_{\text{Gen}}$ leads to the alternative form

$$F \approx \frac{1}{1+10^{-a}} \tag{4.8}$$

which is equation of a sigmoid curve. This approximation fails at low temperatures for the small very dense networks, $N = 100$, as the generative model struggles to make networks which are very coherent at such a high edge density - it becomes difficult to place edges in locations where the coherence is maximised. We note that at high T_{Gen} we obtain $\eta^2 < T_{\text{Gen}}$, however the approximation works fairly well thanks to the sigmoid function, which is close to one for all large arguments. Hence, η^2 and T_{Gen} are not directly equivalent, but relatable when used to calculate F in this way. Nevertheless, this approximation provides an illustration of how the model works. Incoherence increases with temperature by augmenting the probability that edges are placed with edge difference further from one.

Additional detail of how to efficiently generate these networks by more efficiently sampling the space of edge addition probabilities so that each draw of a random number results in an edge being added is given in [1]. All graph manipulations in this work were carried out using Julia Package Graphs.jl [203].

4.3 Influence and Influenceability of Dynamics

In this section we present a wide range of dynamics and show how trophic level and incoherence can be used to provide insight into disparate and unrelated processes. The idea is to use simple dynamics to highlight the phenomena being picked out by trophic analysis. In this case we define 'Influence' to mean the ability of a targeted perturbation or modification of the nodes to affect the state of the system some time after it is applied. In each of the dynamics we show how the nodes which can be regarded as 'influential' are the ones with low trophic level – i.e. those at the bottom of the hierarchy. We also find that the 'influenceability' of the whole network by the low trophic level nodes depends on the network's trophic coherence. The goal of this section is to highlight the broad range of dynamics to which trophic analysis can be applied. In this section we use numerically generated networks only - as opposed to the structural section where we provide results on numerically generated networks and a data-set of real-world networks [185]. We generate networks numerically with the model described above, which allows us to set the numbers of nodes and edges and to vary the trophic coherence. We can also set the number of basal nodes (nodes with zero in-degree).

The dynamics of basal nodes are not affected by the states of other nodes, since they have no inputs. However, they are obvious candidates for nodes with a high influence on the whole network, and this has been demonstrated in previous work [193, 18]. While basal nodes will tend to have low trophic levels, trophic analysis is not needed in order to identify them. We therefore fix the number of basal nodes in our generated networks to be zero, so as to highlight the importance of trophic level even in networks where all nodes can be affected by the rest of the system.

Our hypothesis is that the nodes at the lowest trophic levels (regardless of whether they are basal nodes) are the most influential across a broad range of different dynamics. We test this in the following way. We set up initial conditions such that all the nodes begin in one state or frequency, except for a ‘perturbed fraction’ of nodes which start in a different state or frequency. We choose the nodes with lowest trophic level for this perturbation, and observe the subsequent dynamics of the system. Whenever the system evolves to the state or frequency initially given to, say, only 5% of the nodes, we can conclude that: the network is highly ‘influenceable’, and these are the most ‘influential’ nodes. We go on to find that influenceability depends on trophic coherence, and influence is indeed determined by trophic level, across several dynamics.

We present the results as scatter plots of individual networks, but also show the averages and standard deviations of the sets of networks we generate. This allows the variability of the dynamics for a small number of influential nodes to be visualised as well as showing the general trend. For each of the dynamics we influence 5%, 20% and 40% of the nodes with the lowest trophic level to show how varying the size of this set affects the influence and the spread of the results.

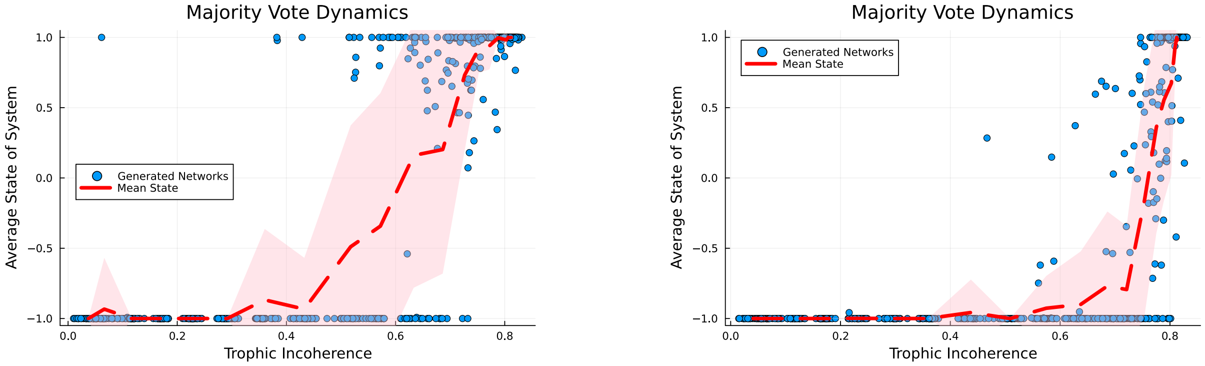
4.3.1 Majority Vote

Majority vote dynamics is the first dynamics to be studied as it is very simple to define as well as being widely used. This allows the primary focus to be on the network structure. Each agent (node) in the model is given an ‘opinion’ and then updates their opinion such that they select the opinion held by the majority of their neighbours. This model is very simplistic yet shares some properties with other common agent-based discrete dynamics widely used in complex networks, such as the SIS epidemic model [204], the Hopfield neural network model [1], the Ising model [205] and the Moran process from biology [206]. Each of these models has additional details which separate it from the basic majority vote, but the dynamics is governed by similar principles.

Majority Vote dynamics can be defined as a system where there are two opinions, denoted as +1 and -1. An agent holds either of the two options and updates their state using an update rule defined as

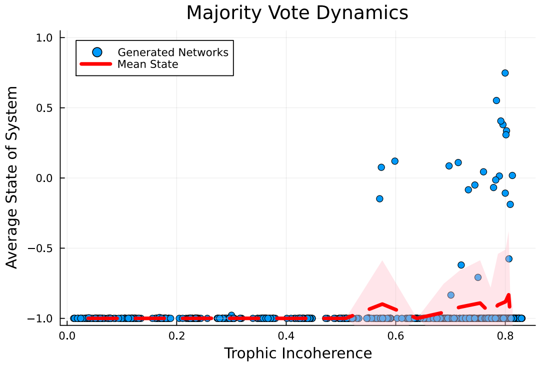
$$S_i(t + \Delta t) = \text{sgn}\left(\sum_{j=1}^{N} A_{ji} S_j(t)\right). \tag{4.9}$$

The updates can be done asynchronously or in parallel and in this work we chose parallel updates. This specific update rule is deterministic but it can be modified in a range of ways to add stochastic behaviour to the system. Additionally, more than two possible states could be added to model a larger number of opinions. An absorbing state is reached if all nodes have the same opinion. However, it is also possible for the system to remain in a fixed point or in a cycle involving nodes with different opinions. In practice, we allow the system to run for a specified number of updates before recording the proportion of nodes in the $+1$ opinion.



(a) Influence by 5% of nodes with lowest Trophic Level.

(b) Influence by 20% of nodes with lowest Trophic Level.



(c) Influence by 40% of nodes with lowest Trophic Level.

Figure 4.2: Majority Vote Dynamics after 1000 updates when a specified fraction of nodes are initially set to -1 with the rest of the nodes set to $+1$. This fraction is 5%, 20% and 40% in panels (a), (b) and (c), respectively. The nodes set to -1 are those with lowest trophic level. The average state of the system (the fraction in the +1 opinion) is shown against trophic incoherence,with each point a distinct network generated by the model in section 4.2.2 with $N = 500$ and $\langle k \rangle = 5$ and no basal nodes. Temperatures, T_{Gen}, are logarithmically spaced between 10^{-1} and 10^{2} with 20 distinct temperatures used. At each temperature we generate 30 networks and compute the mean and standard deviation of this set with the mean plotted with the red dashed line and the standard deviation shown with the shaded area.

The effectiveness of using trophic level to identify influential nodes is shown in figure 4.2. When a small number of nodes at the bottom of the hierarchy (nodes with low trophic level) are placed in the -1 opinion, most or all the rest of the nodes can evolve towards this state despite the majority of the nodes being initialised in the +1 opinion. This scenario holds except when the networks become too incoherent for the perturbed nodes to have a decisive influence. Viewed as a function of trophic incoherence, there is a transition from an influenceable regime (in which the low trophic level nodes dominate) to one which is less influenceable. Where this transition occurs varies with the fraction of perturbed nodes. Moreover, for a given trophic incoherence and perturbed fraction, some network realisations are highly influenceable and others are not, suggesting that there are other relevant network properties to be determined.

This is the expected behaviour in networks of lower incoherence as there is less feedback and cycles so the majority opinion at the bottom of the network moves up through the hierarchy, eventually changing the opinion of the whole system. In a network which is more incoherent this does not happen, for two reasons: there are fewer nodes connected only to the perturbed fraction; and there is more feedback (from directed cycles), which allows the unperturbed nodes to reinforce their initial opinion.

The standard deviation of the points is largest at the incoherence which is between the two regimes. When 40% of the nodes are perturbed, figure 4.2c, almost all nodes are influenced by the low level nodes apart from in the most incoherent networks, which may remain in an intermediate state. Similar behaviour is seen when 20% of nodes are perturbed, figure 4.2b, although there is now a clearer regime of networks which are too incoherent to be influenced by this fraction of nodes. When only 5% of nodes are perturbed, fig 4.2a, despite the number of nodes being small, they are able to influence the state of many of the networks of low coherence and the average state only increases as the incoherence becomes intermediate and there are more cycles and feedback in the system. There are a few outlier points at low incoherence. This is to be expected as we perturb such a small fraction of the nodes that there may be features of the network which make it difficult for them to influence the system. For example the number of edges which leave the set which is perturbed may be small or the trophic levels may be organised in such a way that the small set does not fill the lowest level of the network [1]. However, these simulations still demonstrate the usefulness of this method. Indeed, in very coherent networks specific targeted influence can overcome an opinion held by 95% of the network. This example provides perhaps the simplest demonstration of the insight trophic analysis can give into network dynamics. This may have potential applications in social networks and organisations, particularly in the promoting of cooperation in prisoner dilemma-like games on networks [207].

4.3.2 Synchronisation Phenomena and Kuramoto Oscillators

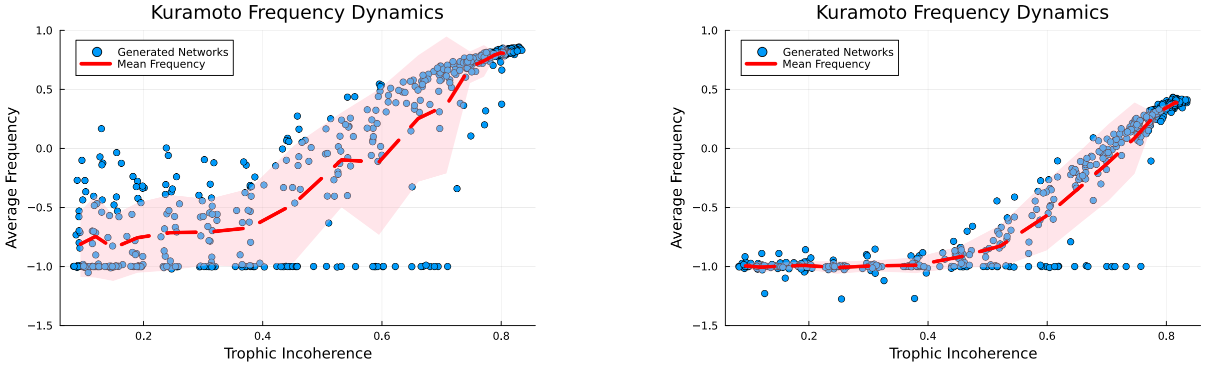
A very similar result to that observed in the discrete majority vote dynamics can be observed in the frequency synchronisation of continuous Kuramoto oscillators, where the low level nodes can influence the frequency of the whole system. The Kuramoto model is a well-known model of synchronisation with a wide range of applications, from neuroscience to power grids [208, 209, 210, 211, 212]. We use NetworkDyanmics.jl [213] to solve the system of differential equations used in our variant of the model. Each oscillator (node) i has a phase, θ_i, which evolves according to the equation

$$\frac{d\theta_i}{dt} = \omega_i + \frac{K}{k_i^{\text{in}}} \sum_{j=1}^{N} A_{ji} \sin\left(\theta_j - \theta_i\right), \tag{4.10}$$

where K is the coupling constant, k_i^{in} is the in-degree of the node and ω_i is the natural frequency of the node. We use the form normalised by in-degree so that the oscillators update at similar rates regardless of the number of input nodes. For the system used we set the coupling constant to $K = 20\langle k \rangle$, which is well above the critical threshold for maintaining frequency and phase synchronisation when the system is initialised at a single phase. This equation could be modified by adding noise or delays to the updates to make the system more realistic. However, we focus here on the simplest case. Phase Synchronisation can be measured by the order parameter

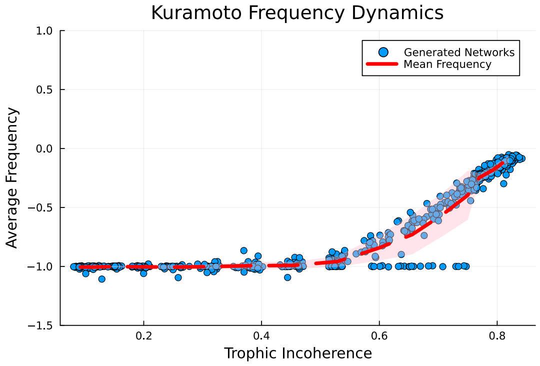
$$r = \frac{1}{N} \left| \sum_{i=1}^{N} e^{i\theta_i} \right|, \tag{4.11}$$

which reaches one when all the oscillators share the same phase but is zero when the phases are uniformly randomly distributed from 0 to 2π. How the low trophic level nodes influence the frequency in networks with varying trophic coherence is shown in figure 4.3, where a fraction of the low trophic level nodes have natural frequency $\omega = -1$ and the remainder have $\omega = +1$. Average frequency is measured by sampling differences in node phase during the latter half of the simulation and dividing by the time differences, averaging over samples and nodes. Since we are interested in which frequency the nodes synchronise to, we set the initial condition so that the nodes begin with the same phase and the dynamics are driven by the topology and natural frequencies only, and not the varying initial conditions. The networks maintain phase synchronisation, r close to 1, and adequate frequency synchronisation, standard deviation of node frequencies is generally very small and always less than 1 (equivalent to standard error less than 0.045), as the simulation evolves due to the initial conditions and strong coupling. Networks with low incoherence propagate the frequency of the low-level nodes through the whole system and the network synchronises at that frequency. In networks of high trophic incoherence the feedback from the higher level nodes back to the lower level nodes dilutes this effect, so the final average frequency of the system is further from that at the low level nodes and closer to that of the higher level nodes.



(a) Influence by 5% of nodes with lowest Trophic Level.

(b) Influence by 20% of nodes with lowest Trophic Level.



(c) Influence by 40% of nodes with lowest Trophic Level.

Figure 4.3: Kuramoto Model Dynamics after simulating for 20 time units when different fractions of nodes, chosen by lowest Trophic Level, are given intrinsic frequency -1 while the rest of the nodes are given intrinsic frequency $+1$; for varying Trophic Incoherence, where each point is a distinct network generated by the model in section 4.2.2 with $N = 500$, $\langle k \rangle = 5$ and no basal nodes. Temperatures, T_{Gen}, are logarithmically spaced between 10^{-1} and 10^{2} with 20 distinct temperatures used. At each temperature we generate 30 networks and compute the mean and standard deviation of this set, with the mean plotted with the red dashed line and the standard deviation shown with the shaded area. The coupling constant, $K = 100$, is twenty times the average degree to ensure synchronisation. Nodes are initially synchronised with phase 0.

This transition is different from the majority vote transition since both phase and frequency are continuous, rather than the discrete states available to the majority vote dynamics. Additionally, in this case we are permanently changing an intrinsic property of the nodes which is maintained throughout the process, whereas previously the perturbation was to the initial conditions. However, the fact that applying the same principle to two very different systems results in qualitatively similar behaviour highlights the usefulness of Trophic Analysis as a tool. When only 5% of the low level nodes are selected in the Kuramoto case, figure 4.3a, the trend is noisy and the standard deviation is large. However, even in this regime we see the trend of the more coherent networks being more easily influenced by the low level nodes and only the most incoherent networks resistant to this. When 20% of the low level nodes are set, figure 4.3b, the trend is much clearer. The most coherent networks are all very strongly influenced by the low level nodes, and there is a clear transition as the network becomes more incoherent, with a lower standard deviation. When 40% of the nodes are perturbed, figure 4.3c, the system is more strongly influenced by the low level nodes and the frequency is reduced away from one, even in the most incoherent networks. In all cases, even at high incoherence there are some networks which synchronise with the 'influenced' (low level) nodes.

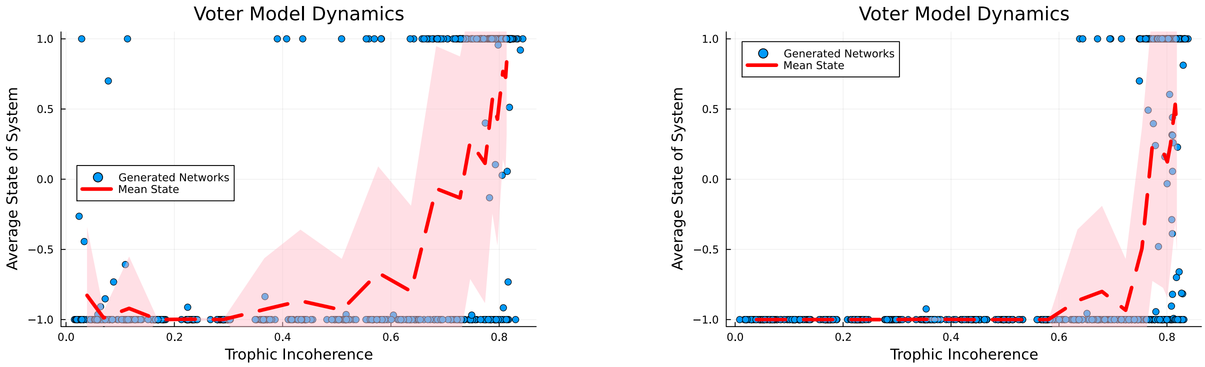
The oscillators begin in a synchronised state, so we find similar results when the end time of the simulation is varied. If a different oscillator function were used it may be possible to exploit the network hierarchy to create more complex states. It has recently been shown that oscillators on non-normal networks can lead to chimera states [214], and it is known that non-normality is related to trophic coherence [18, 8].

4.3.3 Voter Model

A Voter model is another way to model opinion formation for which similar results around influence and influenceability can be demonstrated. Similar to the majority vote dynamics the agents can be given states of either +1 or -1 and updated according to an update rule. However, instead of taking the majority opinion of the neighbours the agent can update its state by choosing at random one of its incoming neighbours and adopting the selected state. This model can be adapted, increased in complexity and then applied to study real voting processes [215], economics [216] and chemistry [217, 218]. The model has two absorbing states where all nodes share the same opinion (consensus). However, after a finite time the system can find itself in an intermediate state which includes both opinions (and on a directed network the absorbing states can be inaccessible).

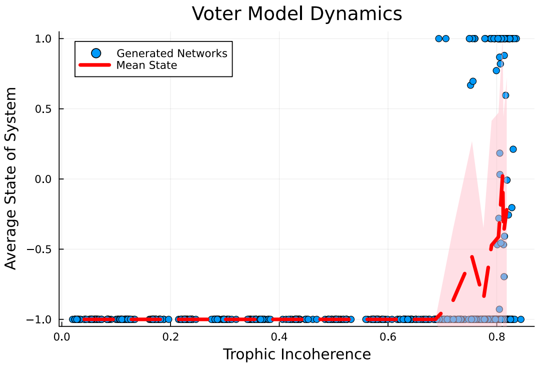
Similar results to the previously obtained ones can be seen, where a new opinion introduced at the lowest trophic level nodes spreads well in coherent networks but is less likely to establish itself in more incoherent networks. This is demonstrated in figure 4.4. In the low incoherence networks the standard deviation is quite small and the ability of the low level nodes to influence the system is clear. As we increase incoherence this is no longer always the case and we pass through a region of higher variability as we transition to the incoherent regime, where the dynamics cannot be as easily shaped by the low level nodes. When 40% of the nodes are set to -1, figure 4.4c, almost all the networks flip to the minority state and only a small number of very incoherent networks maintain the majority state. Very similar behaviour is found when 20% of the nodes are set to -1, figure 4.4b, with most of the networks being easily influenced and only some of the high incoherence networks being resilient to the perturbation. When only 5% are set to -1, figure 4.4a, we see the same trend but a smaller fraction of the networks are influenced, with more networks being outliers from the trend. In a similar way to the majority rule case, targeting a very small number of nodes makes it more likely that an insufficient number of edges leave the perturbed set to influence the whole network [1].

This section has shown how in different dynamical processes the nodes which can be regarded as influential can be determined by using trophic levels, and the ability of the network to be influenced is heavily shaped by the trophic coherence.



(a) Influence by 5% of nodes with lowest Trophic Level.

(b) Influence by 20% of nodes with lowest Trophic Level.



(c) Influence by 40% of nodes with lowest Trophic Level.

Figure 4.4: Voter Model Dynamics after 1000 updates when different fractions nodes, chosen by lowest Trophic Level, are set to the initial condition -1 while the rest of the nodes are initially $+1$; for varying Trophic Incoherence, where each point is a distinct network generated by the model in section 4.2.2 with $N = 500$, $\langle k \rangle = 5$ and no basal nodes. Temperatures, T_{Gen}, are logarithmically spaced between 10^{-1} and 10^{2} with 20 distinct temperatures used. At each temperature we generate 30 networks and compute the mean and standard deviation of this set, with the mean plotted with the red dashed line and the standard deviation shown with the shaded area.

4.3.4 Generalised Rock-Paper-Scissors Dynamics

We show that Trophic level can also be used as an analysis tool for the states of generalised Rock-Paper-Scissors games where the interactions between strategies are defined by a complex network. A standard Rock-Paper-Scissors game can be described with a directed cycle, in which each strategy has an edge to the strategy it defeats. In this case, there is no overall best choice of strategy thanks to the symmetry of the situation. This, however, may not be the case when the strategies interact through a more complex “strategy network” which does not feature this cyclic structure (e.g. interactions between strategies and characters in video-games or ecological interactions such as competition between bacteria [219], as shown in figure 4.5). In such cases there may be strategies which perform better than others.

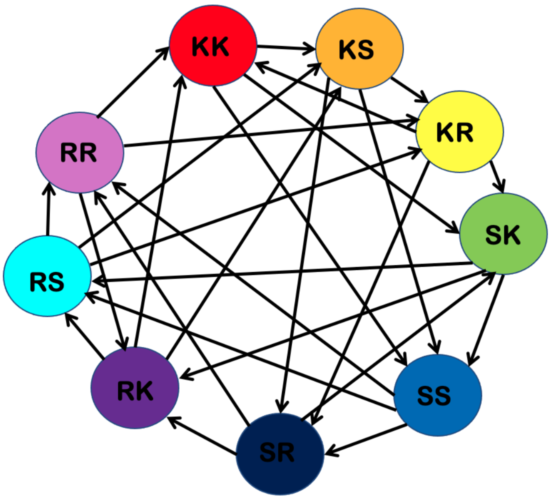


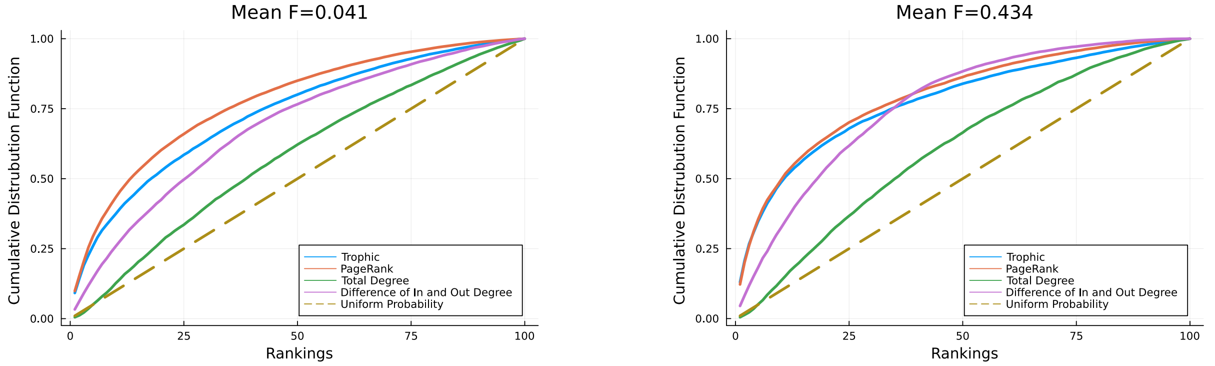
Figure 4.5: Example of a network of agents competing with each other through a complex interaction topology where an edge represents that an agent type is dominant over another. This is a network of bacteria competing through toxin warfare [219]. Each node represents a type of bacteria (a strategy), which dominates over those types it has directed edges to, and is dominated by those it receives edges from. Hence, the network represents the relationship between bacteria rather than a spatial structure.

The interaction between individual agents can be defined on a spatial structure like a lattice or by allowing every agent to interact with every other as in a complete graph. For simplicity we allow all the agents to interact with each other and ignore spatial structure. This setup shares many similarities with mean-field analysis of Lotka-Volterra systems, which have been studied with respect to trophic levels and coherence in [5]. It has also been much more widely studied in the regime of large random systems [220, 221]. Most studies on non-random systems have looked at smaller systems, quite often with spatial aspects to them [222]. There has been some work looking at networks of generalised Rock-Paper-Scissors games but it mostly focuses on varying the strength of parameters rather than looking at large varied structures. This work has mostly been numerical [223, 224, 225, 226, 227], with some looking at the behaviour of smaller systems with weighted interactions and weaker species. There has been some analytical work on Rock-Paper-Scissors-Lizard-Spock networks which have a more complex topology than the basic Rock-Paper-Scissors game [228].

The setup used here is a graph of 100 nodes representing the possible strategies. Then 1000 players per graph play each other at random with the interactions determined by the strategy graph. The initial strategy of each node is randomly assigned from the set of 100 possible strategies. If an edge points from strategy i to strategy j then if a player playing strategy j meets a player playing strategy i they will be beaten and switch from strategy i to strategy j. This definition could easily be flipped and then successful strategies would be those of high trophic level. However, we use this convention to match the earlier results. These dynamics can be quite complicated to analyse for several reasons. ‘Weaker’ strategies may survive better than expected if the strategies that they are weak to are made extinct before them. The presence of cycles and neutral interactions means that one strategy taking over everywhere is not the norm and instead the system moves to a dynamic equilibrium where many of the strategies coexist and “defensive alliances” are possible [219]. What makes a strategy successful is a complex problem - it depends on the balance of how many strategies it beats or is beaten by, as well as where those strategies fit into the global meta-game. For example, it is better to be weak to a strategy which is overall not widely used and then strong against a strategy which is widely played. In this setup a strategy which is influential is one which becomes widely played. As a test for the ability of trophic level to predict influence we compare the probability of a strategy being played with the trophic level ranking of a node and then compare this to ranking by traditional centrality metrics such as PageRank [184, 229].

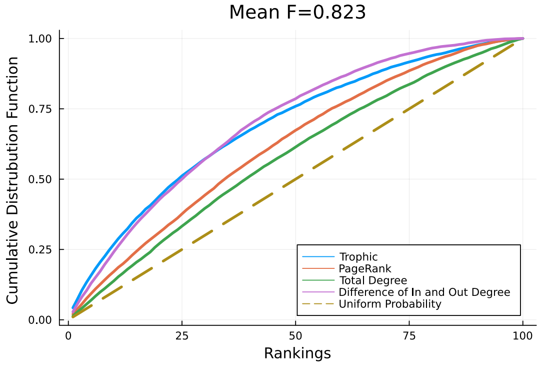
The results are shown in figure 4.6 for networks with low, intermediate and high trophic incoherence. We consider the following centralities: trophic level, PageRank, out-degree, and imbalance (the difference between in-degree and out-degree). In the case of PageRank and imbalance, we apply the centrality to the adjacency matrix such that influence should correlate with a high out-degree, which may require transposing the matrix depending on convention used. The higher the area under the curve for a given centrality, the better it performs at identifying the most successful strategies.

For the most coherent networks, the best predictor of influence is PageRank, closely followed by trophic level, figure 4.6a. In these networks PageRank correlates with trophic level but also reveals information about a node's reach, and we hypothesise that both these features contribute to a strategy's success. For networks of intermediate incoherence both trophic level and PageRank again are the best predictors of a strategy being successful, figure 4.6b, although imbalance is also now a good measure. However, this changes for networks with high incoherence, where the imbalance between in- and out-degrees starts to matter more than PageRank. Trophic level and the degree imbalance are now the best predictors, with PageRank performing similarly to out-degree, figure 4.6c. This demonstrates how trophic level is a good measure of influence as it compares well to the best centrality measure in each case. It also highlights the utility of trophic coherence as a measure to understand network structure, since it helps to explain why the best centrality measure depends on the network. Similar results can be found for many standard network types like random graphs or scale-free networks, where again trophic level is competitive with the best other centrality metrics. It is noteworthy that trophic level is a good predictor of strategy success even in highly incoherent networks. However, if the network were maximally incoherent ($F = 1$), all the nodes would have the same trophic level and hence, according to this predictor, an equal probability of success. This is the case, for instance, in the standard Rock-Paper-Scissors game.



(a) Networks of low trophic incoherence

(b) Networks of intermediate trophic incoherence



(c) Networks of high trophic incoherence

Figure 4.6: Cumulative Distributions of probability of playing a strategy per player per game per network by different centrality rankings and different mean incoherence over 1000 network samples generated by the model in section 4.2.2 at fixed temperatures corresponding to low, medium and high incoherence: $T_{\text{GEN}} = 0.02, 1$ and 100, respectively. Each network has with $N = 100$, $\langle k \rangle = 5$ and 1000 players playing a generalised Rock-Paper-Scissors game.

4.4 Influence and Influenceability of Structure

In this section we demonstrate how several topological notions of ‘influence’ and ‘influenceability’ based on the eigenvectors of the adjacency matrix can be understood and interpreted by looking at the trophic structure of directed networks. This section provides an explanation for the effect of trophic coherence on dynamics seen in the last section, and how networks can be better understood through trophic analysis. In particular, we show why the importance of low trophic level nodes depends on the network’s trophic coherence. We provide results for numerically generated networks to control for variations in size, as well as results on a diverse data-set of real-world networks [185]. In real-world networks, such as the ones contained within our sample, there are a variety of network sizes, mean degrees and degree distributions. However, we show in this section that the general trends hold in both the numerically generated and real-world networks.

4.4.1 Localisation of Eigenvectors

One simple way to quantify influence in a network is eigenvector centrality, a widely used centrality metric [10]. The eigenvector centrality score of a node is determined by the centrality scores of its neighbours [10]. This makes sense as we assume that important nodes also connect to other nodes of high importance. This can be shown to be equivalent to the principal eigenvector of the adjacency matrix and provides one measure of the importance of nodes in a network [10]. As we shall see, in trophically coherent networks the eigenvectors are localised. This has many implications for the dynamics and affects the sensitivity of the network to perturbation and being disrupted by a small subset of nodes. The localisation of eigenvectors was first discovered in physics [230] where the phenomenon of electron localisation known as Anderson localisation was put forward. It has more recently been widely studied in random matrices [231]. It has wide implications for the dynamics of both physical systems and biological neural networks [232, 233, 234].

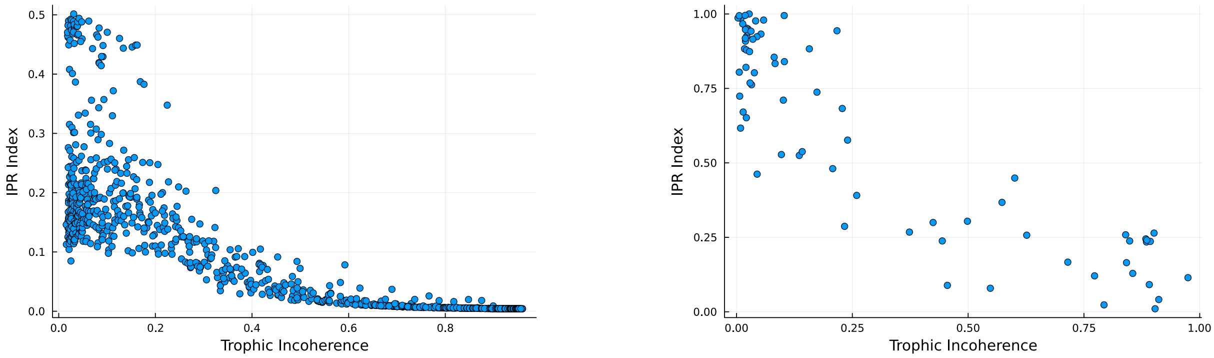
The localisation of the eigenvectors can be measured in a variety of ways and it is also important to consider which nodes the eigenvectors localise around. As the ability to influence a network depends on the distribution of the centrality and where the high centrality nodes are in the network.

Inverse Participation Ratio

The inverse participation ratio measures the localisation of an eigenvector. It is defined for the nth eigenvector as

$$\mathrm{IPR}_n = \frac{\sum_{i=1}^{N} |\Psi_i^n|^4}{(\sum_{i=1}^{N} |\Psi_i^n|^2)^2}. \tag{4.12}$$

Where $|\Psi_i^n|$ is the absolute value of each component of the nth eigenvector. This sum is maximised when all non-zero components are concentrated at one value and takes its minimum value when the non-zero components are exactly equally distributed. In figure 4.7 we show, for each network, the average IPR_n over eigenvectors, $IPR = N^{-1}\sum_n IPR_n$. The localisation varies with Trophic Incoherence: it is large when the network is more coherent and the eigenvalues are localised; it decreases when the network is more incoherent and the eigenvectors delocalise. Moreover, at low incoherence there is a higher variability in IPR between different networks.



(a) 1000 data points each representing a network generated by the model in section 4.2.2 of $N = 500$ nodes, $\langle k \rangle = 20$. Generation temperatures are logarithmically spaced between 10^{-2} and 10^{2}.

(b) Real Networks- Taken from [185]. Each point representing a single network.

Figure 4.7: Average Inverse Participation Ratio (IPR) of L^2 normalised eigenvectors of the adjacency matrix of real and generated networks for varying trophic incoherence

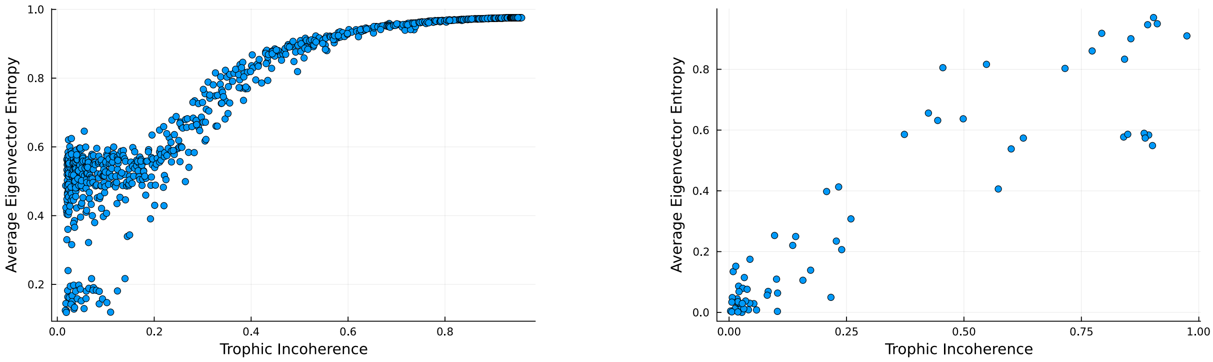
For numerically generated networks, 4.7a, the effect is very clear. The inverse participation also follows the same trend in a data-set of real world networks, figure 4.7b, which includes food-webs, trade networks, neural and social networks [185]. However, the real networks vary in size, density and degree heterogeneity, and thus present a noisier picture. The maximum localisation is also larger than in the numerically generated case. This helps to explain why in the previous section we found that a small number of low trophic level nodes can influence the dynamics when the network is more coherent, as this is the regime where the eigenvectors localise and ‘influence’ is concentrated.

Entropy of Eigenvectors

The entropy of an eigenvector is another way to measure localisation based on the information about the system carried by the vector. It is defined for the nth eigenvector Φ^n (normalised so that the absolute values of the elements sum to 1) as

$$S(\Phi^n) = \frac{-1}{\ln N} \sum_{i=1}^{N} |\Phi_i^n| \ln |\Phi_i^n|. \tag{4.13}$$

This is minimised when all the weight of the eigenvector is concentrated in one node, and hence we know the most information about the system as all the importance is concentrated in that node. The entropy is maximised when the weight of all nodes is equal and all nodes are equivalent, so we have the least knowledge about the structure of the system. We normalise by the maximum value, $\ln N$, so that that $0 \leq S \leq 1$ and we can compare networks of different size. A network can be characterised by the average, $\bar{S} = N^{-1} \sum_n S(\Phi^n)$ In figure 4.8 we show $\bar{S}$ for networks of varying trophic incoherence.



(a) 1000 data points each representing a network generated by the model in section 4.2.2 of $N = 500$ nodes, $\langle k \rangle = 20$. Generation temperatures are logarithmically spaced between 10^{-2} and 10^{2}.

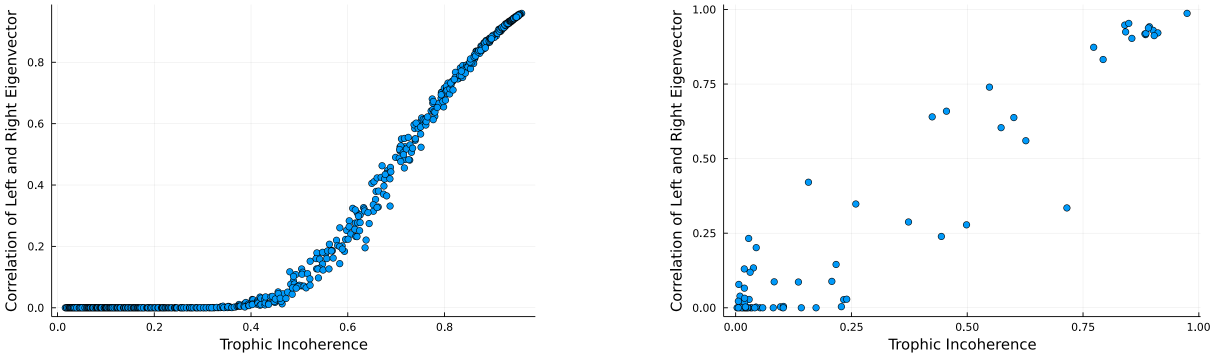
(b) Real networks from [185]. Each point represents a single network.

Figure 4.8: Average entropy of L^1 normalised eigenvectors of the adjacency matrix of real and generated networks for varying trophic incoherence

The trend in the numerically generated networks, figure 4.8a, is very clear, with the entropy of the very coherent networks being low and then increasing with incoherence. The real networks, figure 4.8b, produce a similar trend to the numerically generated networks, but again the data is noisier because of the more varied structure of real systems. This again is consistent with networks being sensitive to perturbations or attacks targeting the nodes of low trophic level, but the degree of sensitivity depending on the trophic coherence of the network.

4.4.2 Correlation Between Left and Right Eigenvectors

A node can be considered important if it is able to receive information from and input information into the rest of the network. In directed networks the underlying hierarchy of trophic levels may mean that the nodes which are able to reach the most nodes in the network and the nodes which are reached by the most in the network are distinct groups. This is different from the undirected case where a hub node can effectively do both. This can be understood by looking at the correlation between the left and right principal eigenvectors. The left eigenvector can be thought of as a measure of the centrality of a node based on in-degree and its ability to receive information, and the right eigenvector can be thought of as the ability to emit information. This is just convention and transposing the adjacency matrix swaps these roles. One way to understand this is to look at the scalar product between the eigenvector centrality, given by the principal eigenvector of the adjacency matrix, and that of its transpose. Due to the Perron–Frobenius theorem both of these eigenvectors are real and non-negative so the multiplication of each element of the vector is real and non-negative. This is shown in figures 4.9a and 4.9b. We see that the correlation is small when the networks are coherent, as nodes of high centrality do not overlap; while when the network does not have such a well-defined hierarchical structure (i.e. it is more incoherent) there is a larger overlap, tending towards 1 as the eigenvectors are both normalised. This highlights the effects of hierarchy on the notion of node importance and that hierarchy can induce an asymmetry in node behaviour.



(a) 1000 data points each representing a network generated by the model in section 4.2.2 of $N = 500$ nodes, $\langle k \rangle = 20$. Generation temperatures are logarithmically spaced between 10^{-2} and 10^{2}.

(b) Real networks from [185]. Each point represents a single network.

Figure 4.9: Correlation between left and right principal eigenvectors of the adjacency matrix of generated (a) and real (b) networks for varying trophic incoherence. Eigenvectors are L^2 normalised.

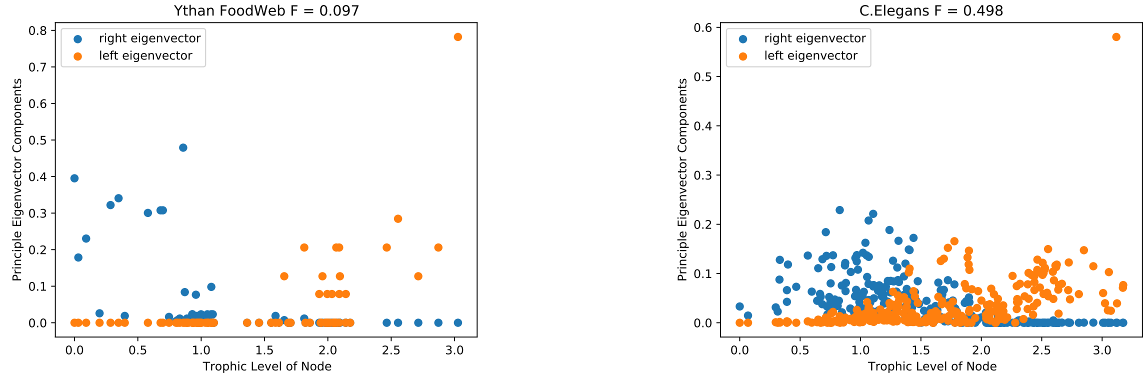
In the generated networks the correlation between the eigenvectors follows a smooth trend whilst again in the case of real networks the overall correlation is reproduced but the results are much more noisy. These results can also be viewed in terms of matrix normality, which measures how well the adjacency matrix commutes with its transpose. This has previously been shown to be linked to trophic incoherence [18, 8]. However, the correlation between right and left principal eigenvectors provides a more direct measure of whether the influential nodes are also those that are influenceable.

Example Networks

The previous results on the localisation of the eigenvectors and the correlation between the left and right eigenvectors, on both numerically generated and real-world networks, can be better understood by looking at some specific network examples. In coherent networks with a clear hierarchy of trophic levels, such as the Ythan estuary food web, figure 4.10a, the left and right eigenvectors localise to different parts of the network hierarchy. The nodes of large left eigenvector centrality are towards the top of the hierarchy while the nodes of large right eigenvector centrality centre on the nodes of lower trophic level. This reflects the intuition around the localisation of eigenvectors and the difference between the left and right eigenvectors, as well as what we know about food webs where energy flows from the bottom to the top of the system. This phenomenon can also be observed in real networks of intermediate coherence such as the connectome of the nematode *C.Elegans*, figure 4.10b. In this network the localisation is less pronounced than in the food web due to the network being more incoherent and having more feedback. There is, however, still clearly visible localisation with the non-zero elements not being evenly distributed with respect to trophic level, and the distribution of the non-zero elements of the left and right eigenvectors being centred at different places in the hierarchy.

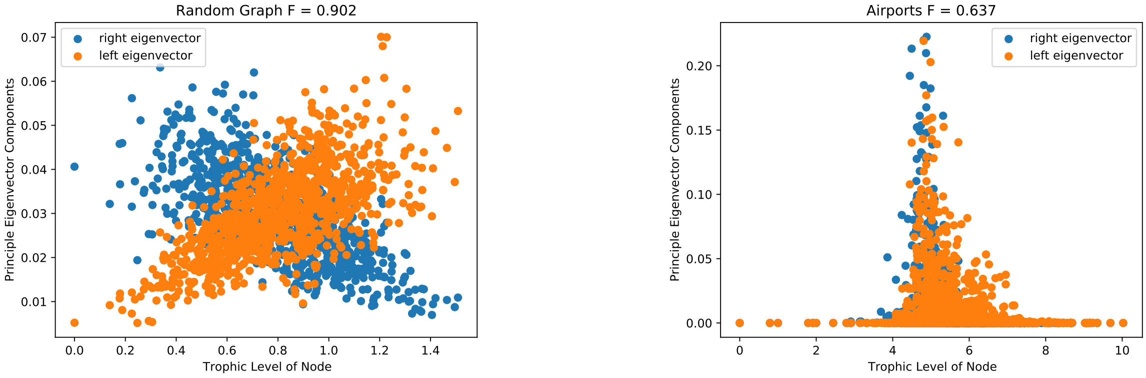
A non-trivial relationship between trophic level and the distribution of eigenvectors can also be observed in some random graphs, figure 4.10c, where one would not expect there to be much useful hierarchical structure to observe. In a random graph the left and right eigenvectors are not as strongly localised and there are many non-zero elements shared by both the left and right eigenvectors. However, there is a positive correlation between the left eigenvector and trophic level, and a negative correlation between the right eigenvector and trophic level. This implies that nodes which are the best at emitting information and reaching the whole network are at the bottom of the hierarchy, nodes which receive information are at the top and nodes which do both equally are in the middle. This agrees with the well-known bow tie structure observed in directed networks [124].

There do, however, exist networks which break this trend. Figure 4.10d shows the Federal Aviation Administration (FFA) preferred routes between airports. This network is directed, but since it is an airport network it features hubs which are hubs of both in and out degree. Due to the fact that certain airports are very important hubs in both senses, the left and right eigenvector peaks overlap more than in previous real-world examples, as we can see in 4.10d. Thus, this kind of network is quite different from, say, a food web, which has an overall directionality. The airport network is more coherent than a random graph (in part because the degree imbalance is larger). However, the level distribution does stretch out beyond the central peak to span a number of levels. This shows how trophic analysis can be used to identify structural features related to network function. In particular, it distinguishes clearly between networks with a directional flow, like a food-web or neural network, and those lacking this property, like the airport network.



(a) Ythan Estuary Food Web with low incoherence, $F = 0.097$, [185]. Scalar product between left and right eigenvectors 0.003.

(b) *C.Elegans* Connectome of intermediate incoherence, $F = 0.498$, [185]. Scalar product between left and right eigenvectors 0.278.



(c) Random graph with $N = 1000$, $\langle k \rangle = 10$ and high incoherence with $F = 0.902$. Scalar product between left and right eigenvectors 0.904.

(d) FAA preferred routes between airports, $F = 0.637$. Taken from [235]. Originally sourced from [236]. Scalar product between left and right eigenvectors 0.831.

Figure 4.10: Principal left and right eigenvectors (L^2 normalised) for four example networks, with the trophic level of the nodes on the horizontal axis.

4.4.3 Pseudospectra and Pseudospectral Radius

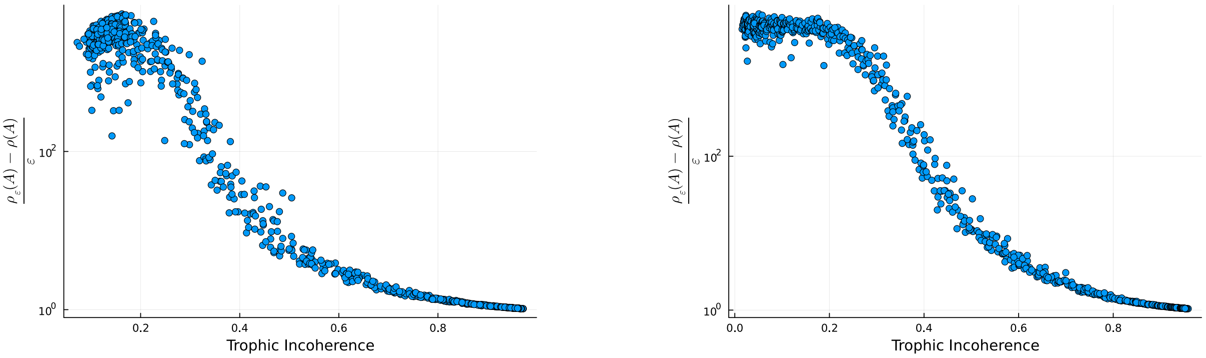
A network can be influenced if it is sensitive to perturbations; in particular, if a disruption to a small number of nodes leads to a large change in the behaviour of the system. This kind of phenomenon can be linked to the non-normality of the adjacency matrix [160], i.e. how far it is from commuting with its transpose. Networks which are highly non-normal (a feature that has been shown analytically to be related to low trophic incoherence [18, 8]) have the property that their eigenvalues are extremely sensitive to perturbations [160]. This can be impactful in many fields, such as fluid mechanics, acoustics, condensed matter physics and construction of numerical methods [160, 237, 162, 163, 164].

The pseudospectrum of a matrix A with eigenspectrum $\sigma(A)$ is defined as

$$\sigma_{\epsilon}(A) = \{\sigma(A + E) : ||E|| \leq \epsilon\} \tag{4.14}$$

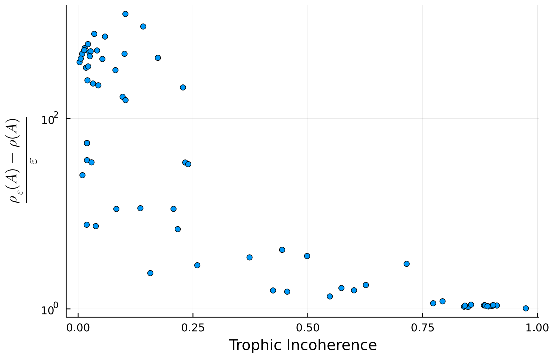
for some $\epsilon > 0$ and E a matrix of norm less than ϵ. It measures how the spectrum changes subject to perturbations, and can be computed using the Julia package [238] based on EigTool [239]. The pseudospectra has recently been shown to be important in complex networks and the stability of ecosystems [19].

One way to measure the sensitivity to perturbation is to compute the pseudospectral radius, the spectral radius of the perturbed matrix minus the original spectral radius, and divide by the size of the perturbation. If this quantity is if of order 10^0 then the system is stable to perturbations of that scale. The size of perturbation used can be very small. In the following figures the perturbation is of order 10^{-3}. The pseudospetral radius exhibits a transition as trophic incoherence is varied for generated networks, figure 4.11a and 4.11b, being large for networks of low incoherence and then decreasing as incoherence increases, as we would expect.. A similar result can be found for real-world networks, figure 4.11c.



(a) 1000 data points each representing a network generated by the model in section 4.2.2 of $N = 100$ nodes, $\langle k \rangle = 20$. Spectral perturbation size 10^{-3}. Generation temperatures are logarithmically spaced between 10^{-2} and 10^2.

(b) 1000 data points each representing a network generated by the model in section 4.2.2 of $N = 500$ nodes, $\langle k \rangle = 20$. Spectral perturbation size 10^{-3}. Generation temperatures are logarithmically spaced between 10^{-2} and 10^2.



(c) Real Networks- Taken from [185] and excluding genetic networks for run time. Each point representing a single network. Spectral perturbation size 10^{-3}.

Figure 4.11: Pseudospectral Radii scaled by perturbation size with Trophic Incoherence for numerically generated networks and real-world networks [185]

We again produce a similar trend for both the real and generated networks, with the real network data appearing more noisy, as expected. As with the various dynamics described above, the pseudospectral radius demonstrates an increased sensitivity to perturbations – in this case structural – as networks become more coherent.

4.4.4 Out-Components

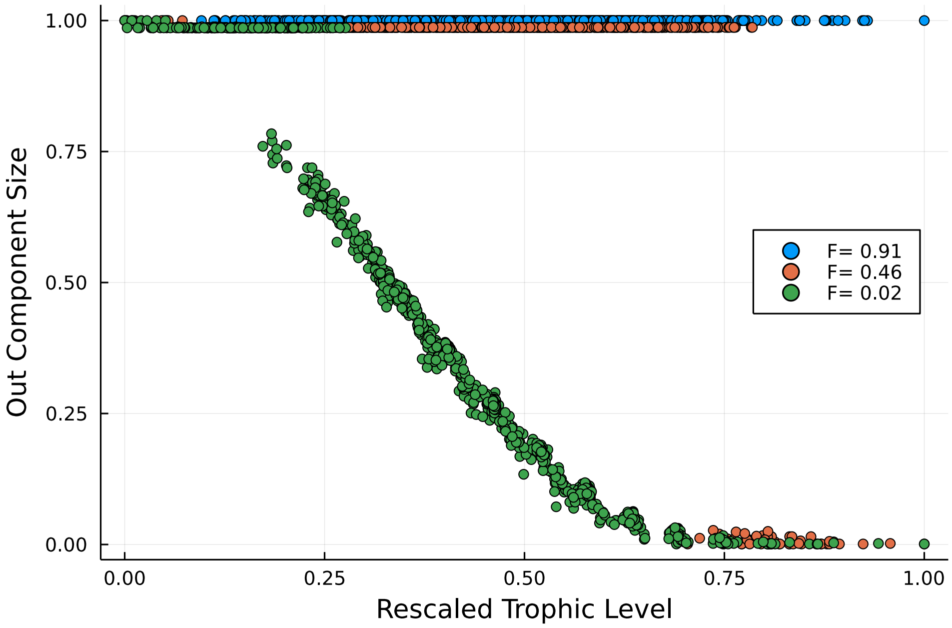


Figure 4.12: Size of the Out-Components of nodes with their trophic level rescaled by the maximum trophic level. Networks, generated by the model in section 4.2.2 at a single temperature, of low, intermediate and high incoherence with $N = 1000$ and $\langle k \rangle = 10$. And $T_{\text{GEN}} = 0.02, 1, 100$ for the low, intermediate and high incoherence networks, respectively.

One way to understand the transition in influence of nodes with hierarchical ordering is to look at the number of nodes which are reachable from a a given node – its ‘out component’ – and how that changes with the trophic level of the node, and with the trophic coherence of the network. This is shown in figure 4.12.

When the network is very incoherent it is strongly connected and there is no heterogeneity in the ability of one node to influence other nodes. When the incoherence is intermediate there is still a large strongly connected component, however the nodes at the top of the network are unable to influence the network as they lie outside this component. When the network is very coherent and F is close to zero, the strongly connected component is small and the size of the node’s out-component is strongly linked to its trophic level. This leads to an asymmetry in the network due to the hierarchy of trophic levels, where some nodes can reach the whole network whereas others have a very small out-component. These results are a simple representation since the precise size of the out-component can vary widely depending on the type of network and how cycles are distributed throughout it. However the general principle that networks of low incoherence lead to an asymmetry in component size is generally true due to the lack of feedback, and agrees with results from the literature [199]. This is also in agreement with other work on Trophic Analysis and the intuition behind it, which has analytically linked the emergence of a giant strongly connected component in a network to its trophic properties [2].

4.5 Discussion and Conclusion

These results provide a different perspective on influence and influenceability in directed complex networks by using the fact that directed networks have an underlying hierarchical structure, unlike the undirected case. Thus, Trophic Analysis can give some insight into the function of a complex system. It reveals the links between many network properties, and how a node's trophic level can determine its ability to influence the rest of network.

Trophic Analysis is based on a simple calculation, a linear equation dependent only on the degrees and the adjacency matrix, and is straightforward to interpret. We hope that highlighting the diverse ways it can shed light on network function and structure might prompt its use in future work. In particular, when applied to real-world networks for analysis of structural features or understanding of dynamics, as we expect the phenomena we describe here to be quite general and applicable to many real-world systems. Since the equation is linear it can be solved for large real-world networks. Additionally, the results can be related to network properties such as the spectral radius, non-normality or strong connectivity [8, 2]. In particular, networks of low trophic incoherence are highly non-normal. It has been shown recently that non-normal networks are very common [19], that non-normality of the adjacency matrix can have a large effect on the stability of a system [165], and it has been related to economic bubbles [38].

The general principle that the influence of a node is a function of its position in a hierarchy does not necessarily require the use of trophic levels to measure this and another metric such as PageRank could provide a similar result. However, trophic analysis allows a local measure of node importance to be related to trophic coherence, which gives a measure of how important the hierarchy is expected to be to the system. This is useful when Trophic Analysis is applied to real-world systems, such as when it has been used to investigate the hierarchy in a network of Sustainable Development Goals [47, 48]. This paper highlights how the importance of node-level measures of centrality (such as trophic level or PageRank) depends strongly on how these measures are distributed amongst the nodes, as well as on global network properties (trophic coherence) which may hinder or accentuate their effects. Trophic Analysis can be a useful way to understand directed networks as it does not simply rely on either the in or out degree. In a directed network the ability to influence or be influenced may be of different relative importance depending on the dynamics, and it is possible that no correlation (nor more complex statistical relationship) exists between in and out degree. So nodes of importance in one measure may not be important in another. Trophic level simplifies this as the low level nodes are good at emitting and have many nodes downstream of them while nodes at the top of the network receive many paths from below. The interplay between trophic levels and degree distributions is something that could have a large impact on influence and will be the subject of future work. For example, a network could have a scale free distribution in either in or out degrees or both, which may or not be correlated, or bear some relationship to the trophic structure.

In conclusion, we have highlighted how there are many disparate ways to view influence and influenceability in real-world and generated networks, such as the ability to shape various discrete and continuous dynamics, the localisation of eigenvectors, the sensitivity of the spectra to structural perturbations, or the distribution of out-components within networks. We have shown that all these phenomena can be thought of in terms of the local placement of nodes within the hierarchical structure of trophic levels, which is mediated by the global directionality given by trophic coherence. And we have described how this insight can be used to understand many structural and dynamical processes in directed complex networks, which we hope prompts the use of Trophic Analysis in the study of specific real-world systems.

CHAPTER

5

NETWORK HIERARCHY AND PATTERN RECOVERY IN DIRECTED SPARSE HOPFIELD NETWORKS

This chapter is based on

- Niall Rodgers, Peter Tiňo, and Samuel Johnson. “Network hierarchy and pattern recovery in directed sparse Hopfield networks”. In: *Physical Review E* 105.6 (June 2022), p. 064304. ISSN: 2470-0045. DOI: 10.1103/PhysRevE.105.064304. URL: https://link.aps.org/doi/10.1103/PhysRevE.105.064304

Relationship of Work to Thesis

This chapter comprises the first paper on my PhD [1]. This work applied Trophic Analysis to study a specific type of system motivated by beliefs about the structure of biologically inspired neural networks. This work gave me experience in understanding the behaviour of hierarchical networks and how this could be understood via Trophic Analysis. This knowledge gained allowed the results of the rest of my PhD to be achieved. The features and phenomena observed here around the ability of a small number of nodes to control the state in a network with a strong hierarchical structure would also form the basis of our work on network influence, chapter 4. This work also highlighted the issues with using `Python` during my PhD as the training, dynamics and generation of the networks were all time consuming. Promoting the move to `Julia` for the rest of the computational work and motivating the study of new generative process such as based on network fitness presented in chapter 6. We also observed when working on this project the impact that the size of the strongly connected components could have on the dynamics which motivated thinking about how this could be linked to the hierarchy, chapter 3. It additionally links to the work on fitness-based generative models, chapter 6, as in a biologically system there may be different types of nodes which have different connection rules and different underlying connection parameters which an extension of the work in chapter 6 could capture.

Abstract

Many real-world networks are directed, sparse and hierarchical, with a mixture of feed-forward and feedback connections with respect to the hierarchy. Moreover, a small number of ‘master’ nodes are often able to drive the whole system. We study the dynamics of pattern presentation and recovery on sparse, directed, Hopfield-like neural networks using Trophic Analysis to characterise their hierarchical structure. This is a recent method which quantifies the local position of each node in a hierarchy (trophic level) as well as the global directionality of the network (trophic coherence). We show that even in a recurrent network, the state of the system can be controlled by a small subset of neurons which can be identified by their low trophic levels. We also find that performance at the pattern recovery task can be significantly improved by tuning the trophic coherence and other topological properties of the network. This may explain the relatively sparse and coherent structures observed in the animal brain, and provide insights for improving the architectures of artificial neural networks. Moreover, we expect that the principles we demonstrate here, through numerical analysis, will be relevant for a broad class of system whose underlying network structure is directed and sparse, such as biological, social or financial networks.

5.1 Introduction

Models of the brain provided the original inspiration for the invention of artificial neural networks. However, biological neural networks have a much richer structure than their artificial counterparts. In particular, they are not exclusively feed-forward like conventional deep network architectures, yet there is a direction to information processing, unlike in recurrent network models. For example, the neural network of the nematode *C. Elegans* [240, 11] – the only animal nervous system to have been fully mapped at the level of neurons and synapses – is quite sparse and displays a non-trivial mix of feed-forward and feedback connections, as revealed by a recent technique from the field of complex networks called Trophic Analysis [8]. What might explain this particular neural-network architecture? We address this question by studying the relationship between trophic structure and the dynamics of a simple model which we refer to as a Hopfield-like neural network.

Trophic Analysis, inspired by ecological networks, assigns to each node a 'trophic level', which can be regarded as a position in a hierarchy; and measures the 'trophic coherence' of the whole network, a property which indicates to what extent this hierarchy is well defined, conferring to the network an overall directionality. In this work we take the convention that the bottom of the hierarchy is where information enters the system, just as energy flows up from plants in a food web. This may be different in other fields, for example in the study of 'hierarchical trees', but all definitions are equivalent up to relabelling 'top' and 'bottom' or by reversing the edge directions. When the *C.Elegans* neural network is visualised so as to show the trophic level of each neuron, as in figure 5.15 in the appendix, it is observed that while most of the synapses are consistent with an overall direction, there are some which feed back as in a recurrent architecture. In fact, when the trophic coherence is calculated, it lies exactly half way between a maximally coherent (i.e. entirely feed-forward) network, and one which is entirely incoherent (fully recurrent). Moreover, it has been shown previously that this level of coherence amounts to a significant deviation from the kind of networks which arise from random graph models such as Erdős–Rényi model. [180, 6].

How dynamics and hierarchy interact is demonstrated in this paper by performing a pattern recognition task (described in detail in the next section) on network architectures which span a range of hierarchical structures. We find that trophic coherence is very strongly linked to the ability to correctly recognise and display the pattern shown. Maximally coherent networks lack the feedback to store patterns, while maximally incoherent networks are unable to change state when presented with fractions of new patterns. The optimal configuration is intermediate coherence, a mixture of feed-forward and feed-back structure which is shared with many biological systems. A similar result was reported in Ref. [18] for a system in which elements followed majority rule dynamics where the stability of the *C. Elegans* neural network was analysed using Trophic Analysis. We concentrate our study on synthetic networks inspired by this network which can be made dense enough to store multiple pattern states and lack basal nodes (nodes with no in-degree) which would act as input to the system without being influenced by it.

There are clear differences between the structures of biological neural networks and artificial, recurrent neural networks, such as standard implementations of the Hopfield model. Biological networks are sparse, whereas the artificial versions are often based on complete or very dense graphs. They are also directed, since chemical synapses have a pre- and a post-synaptic neuron [241], while some models such as that of Hopfield tend to assume symmetric synapses in order to avoid the possible periodic or chaotic behaviour associated with asymmetric interactions [242] or to align with experimental data limited to the undirected case [241].

And in nature there are a limited number of sensory neurons which receive information directly from the outside world, a fact not usually replicated in Hopfield models. However, it is possible to implement a Hopfield-like model on sparse, directed networks, and to present stimuli only to a subset of neurons, as we go on to do here in order to investigate how dynamics is affected by modifying the trophic structure.

Feed-forward artificial neural networks, such as those used in deep learning, in these respects resemble more closely the architectures of biological neural networks, at least in the case of nature's only fully mapped connectome, that of *C. Elegans*. The main difference is that deep neural networks tend to be maximally coherent, with each layer corresponding to a distinct (integer) trophic level.

We show, through numerical analysis, that network hierarchy can be exploited in order to use a small subset of neurons to drive the system, with how well a pattern is recovered being strongly influenced by where in the hierarchy it is received. Hierarchical structure creates heterogeneous dynamics with different parts of the network recovering patterns differently. Additionally, we show that by preferentially adding edges to lower level nodes, pattern recovery can be made more consistent. This has potential applications for how artificial neural networks are designed [243, 244], as well as for controllability of dynamics on general directed complex networks [245, 168, 246], which could range from biological neural networks [247, 248], to ecosystems, economies [34] or the Internet [249]. In particular, Hopfield networks have recently been used to model Gene Regulatory Networks [250, 251]. We will therefore use this model to highlight principles which may be of general application to any system wired according to a directed network. This is the first work in which Trophic Analysis has been applied to Hopfield-like networks which have been trained to store patterns.

5.2 Using Trophic Analysis to Quantify Network Hierarchy

Trophic Analysis is a method of quantifying the hierarchy of nodes and the global directionality of a directed complex network, first introduced in 2014 [5], which is based on the ecological concept of trophic level [252]. A directed network, or graph, can be represented via an adjacency matrix, defined as:

$$A_{ij} = \begin{cases} 1 & \text{if there exists an edge } i \to j \\ 0 & \text{otherwise} \end{cases} . \tag{5.1}$$

Unlike in undirected networks, this matrix is not necessarily symmetric, $A_{ij} \neq A_{ji}$. Directed networks have the additional complexity of the notion of in- and out-degrees, where the in-degree is the number of incoming edges a vertex receives and the out-degree is the number of edges leaving a vertex. In undirected networks the in- and out-degrees coincide. Directed networks can also be weakly or strongly connected. Weakly connected means that there is a path between all pairs of vertices if you ignore the edge directions, while strongly connected means there is such a path respecting the edge directions. The networks studied in this work are all weakly connected but may not be strongly connected.

Trophic Analysis was recently extended and redefined to cover more general networks [8], removing the requirement that networks must have basal nodes (nodes with in-degree 0). This is the definition that will be used in this work. Trophic structure has been used to study spreading processes in neural and epidemiological settings [34], infrastructure [36, 37] and the structure of organisations [7]. Trophic Analysis is composed of two parts: the node level information, trophic level, which describes where each node sits in the overall hierarchy of a network; and the global information of how directed, or coherent, the overall network is. The idea of trophic level arises from ecology where the lowest trophic level nodes represent plants which sit at the bottom of the network hierarchy, and the highest trophic level nodes are carnivores at the top of the food chain. Trophic level can be calculated for a network of N nodes by solving the $N \times N$ matrix equation

$$\Lambda h = v, \tag{5.2}$$

where h is the vector of trophic levels, v is the imbalance of in-degree and out-degree of a node, $v_i = k_i^{in} - k_i^{out}$, and Λ is the Laplacian matrix:

$$\Lambda = diag(u) - A - A^T. \tag{5.3}$$

This depends on the sum of the in- and out- degrees of each node, $u_i = k_i^{in} + k_i^{out}$, the adjacency matrix, A, of the graph and its transpose, A^T. This definition can also be extended to cover weighted adjacency matrices [8]. The solutions to equation 5.2 can be modified by adding a constant vector since Λ acting on a constant vector is zero. This allows the minimum level to be set at zero by convention and fully coherent networks to have integer levels.

Trophic coherence is based upon the distribution of trophic levels of the nodes in a network. How coherent or incoherent a network is can be described by the parameter

$$F = \frac{\sum_{ij} A_{ij}(h_j - h_i - 1)^2}{\sum_{ij} A_{ij}}. \tag{5.4}$$

We call F the *trophic incoherence*, such that when $F = 0$ the network is completely coherent and when $F = 1$ it is completely incoherent. This depends on the levels of each node h_i and the entries of the adjacency matrix A_{ij}. Loosely speaking, F quantifies, per connection in the graph, to what degree the connections $i \rightarrow j$ are not “one-step” connections in the order of trophic levels, i.e. by how much $(h_j - h_i)$ differs (in the mean square sense) from 1. In principle these could have positive weights but throughout this work we will take the entries of the adjacency matrix to always be 0 or 1 to avoid confusion with the trained weights associated with the neural network. A network for which $F = 0$ is acyclic and completely free from any feedback, with the amount of feedback and cycles growing as this parameter increases to 1 [8]. This is reflected in results showing an increase in spectral radius and a reduction in the deviation from normality of the adjacency matrix, how far the matrix is from commuting with its transpose, as incoherence increases [6, 8].

Note that the levels h, defined by Eq. (5.2), can be regarded as the argument which minimises F, as given by Eq. (5.4) [8]. One can therefore think of the trophic levels of a network as those which maximise its trophic coherence which relates to how it was derived in [8].

5.3 Hopfield-Like Networks

The Hopfield Model is a recurrent neural network model which is very similar to the Ising model studied in statistical physics [242]. The neurons can take binary states $+1$ or -1. Due to similarity to the Ising model these neuron states are sometimes referred to as spins and the order parameter measuring the state of the system can be referred to as a magnetisation. A Hopfield network can store binary memories, or patterns, by setting the weights of connections between neurons such that when an update rule is applied the system moves across an energy landscape to its attractors, which correspond to the stored patterns. This system can, in some cases, be studied via mean-field theory or other theoretical methods [253]. In our case, however, due to the asymmetric connections and complex network topology, we will use numerical simulations.

We want the system to update in such a way that it moves towards the minima in the energy landscape defined by

$$E = -\sum_{ij} w_{ij} A_{ij} s_i s_j, \tag{5.5}$$

where w_{ij} is the coupling between neurons i and j, which may be positive or negative depending on patterns stored. The states of the neurons take values $s_i = \pm 1$ and A_{ij} are the elements of the adjacency matrix, as defined by Eq. (5.1). There are many possible update rules which can achieve the desired behaviour, such as the Metropolis–Hastings algorithm [254]. We use a sigmoid probability function such that

$$s_i(t + \Delta t) = -s_i(t) \tag{5.6}$$

with

$$\text{probability} = \frac{1}{1 + \exp \frac{\Delta E}{T}}, \tag{5.7}$$

where ΔE is the energy change associated with flipping the neuron state and T is a temperature parameter which makes the system stochastic. To reduce complexity and uncertainty, the results we present here are for a temperature very close to zero, $T = 10^{-5}$, so the dynamics is essentially deterministic and equivalent to using the sign of the incoming field, the sum of the states of the in-neighbours, as the update rule. The system can therefore be referred to as Hopfield-like, or simply as a Hopfield network, which is generally taken to be deterministic, as opposed to Boltzmann machines, which are stochastic [255]. However, even in this regime the asymmetry in A leads to a range of surprising behaviours not observed in undirected networks [256].

Updates to the system can be made in parallel or asynchronously. We use a parallel update rule, which allows for complex behaviour such as limit cycles [245].

5.3.1 Training the Network

Setting the weights so that the attractors of the system correspond to the random binary patterns we wish to store in the network is a key part of the process. The traditional method of setting weights in a Hopfield network so that the network recalls the desired patterns is Hebb's rule [257]. This is often summarised as "neurons that fire together wire together". That is, if two neurons have the same state in a particular pattern the connection between them is strengthened, and if they are in opposite states it is decreased. For learning P patterns, where for each pattern each neuron has a fixed state $\xi_i^p = \pm 1$, the rule sets the weights as

$$w_{ij} = \frac{1}{P} \sum_{p=1}^{P} \xi_i^p \xi_j^p. \tag{5.8}$$

This very simple rule works and can be used on any network topology. It has the benefit of being a "one shot" rule in that it only requires one loop over the set of patterns to train the network. However, it suffers from the fact that on a graph which is not complete the information about the correlations between disconnected neurons is not used. We found during initial tests that on very sparse directed networks the memory capacity of the network was substantially reduced. This is very similar to the finding of Tanaka et al. [258] for undirected networks. They remedy this issue by adopting an iterative version of Hebb's rule based on earlier work [259, 260] which was found to increase capacity substantially, with other similar results noted in the literature [261]. For the remainder of this work we implement this rule [258]. Both the original Hebb rule and the adapted version are local, in that synaptic weights are updated using only information from the pre- and post-synaptic neurons – as also happens, we believe, in the brain [262].

The iterative Hebb rule works to set the weights so that every pattern corresponds to a local minima of the energy landscape where updates of the system stop. This condition can be expressed as

$$\xi_i^p \left(\sum_j A_{ji} w_{ji} \xi_j^p \right) \geq \delta \tag{5.9}$$

for all P patterns and N nodes, and δ a positive constant. This means that at each node, for every pattern the polarities of the state and the incoming field are the same. As a result it is always energetically unfavourable to flip the state at zero temperature so the system is stable.

The iterative Hebb rule is laid out in detail in Algorithm 1.

Algorithm 1: Iterative Hebb Rule [258]

```
Set the initial weights $w_{ij} = 0$ for all nodes $i, j$.
Set the stop condition flag, flag = $0$.
Set the step counter, steps = $0$.
while flag = $0$ and steps < steps_max do
    flag=1 ;
    for p in range P do
        for i in range N do
            field = 0 ;
            for j in range N do
                field ← field + $A_{ji} w_{ji} \xi_j^p$
            end
            if field × $(\xi_j^p) < \delta$ then
                for q in range N do
                    $w_{qi} \leftarrow w_{qi} + \frac{A_{qi} \xi_q^p \xi_i^p}{N}$ ;
                    flag = 0
                end
            end
        end
    end
    steps ← steps + $1$
end
```

At each iteration the weights are updated by

$$w_{ji} \leftarrow w_{ji} + \frac{A_{ji} \xi_j^p \xi_i^p}{N}, \tag{5.10}$$

until the required condition is met. For this study δ was always set at 1, but other values can be used to change the stability of the patterns. If a stable solution of this set of inequalities exists it should always converge in a finite amount of time [259]. However, a solution does not always exist for sparse, directed networks, so the algorithm needs to be terminated after a chosen maximum number of iterations. Here we use 400 iterations. The patterns can still be quite successfully stored and recovered if full convergence has not been achieved, as the number of weights continually updated is small after only a few iterations.

Pattern recovery is measured with an order parameter, which we call magnetisation, and is defined for each pattern p as the scalar product of the state of the system and the pattern:

$$m_p = \frac{1}{N}\sum_{i=1}^{N} s_i \xi_i^p . \tag{5.11}$$

This is equivalent to the cosine of the angle between the state and the pattern. In this work we study patterns which are random, independent and identically distributed. Correlation between patterns and between patterns and the network topology may affect the performance of the network in a wide variety of ways depending on the topology, sparsity and nature of the correlation [258, 263], so this may be a potential avenue for future work.

5.4 Network Generation

To generate networks with a specified trophic coherence and fixed numbers of nodes and edges, we use a variant of the Generalised Preferential Preying Model (GPPM) from Refs. [33, 34], although the original work used a different definition of trophic level.

We generate networks such that each node has in-degree at least 1. One reason for this is that if the network contains basal nodes (nodes with in-degree 0), one must choose whether their states s should remain constant, take random values at each time step, or act as external inputs to the system. Moreover, it is known that basal (or source) nodes can drive dynamics on directed networks in certain contexts [18, 193]; but, to the best of our knowledge, we investigate here for the first time the importance of trophic level for dynamics on networks without basal nodes.

The detailed steps of the generative process are laid out in appendix 5.7.2. In short, we randomly generate an initial configuration of N nodes where each node has in-degree 1 and then calculate the initial trophic level, $\tilde{h}$, of this configuration. Then edges are added until the specific number is reached where the probability of connecting node i to j is

$$P_{ij} = \exp\left[-\frac{(\tilde{h}_j - \tilde{h}_i - 1)^2}{2T_{\text{Gen}}}\right]. \tag{5.12}$$

Afterwards, the updated trophic levels, h, are recalculated. With this method networks of any incoherence can be generated by varying the control parameter T_{Gen}, as demonstrated in Fig. 5.14 in the appendix.

The networks generated via this method can act as an approximation to the hierarchical structures seen in real-world systems. In Ref. [8] it was shown that many real-world networks conform approximately to an analytical prediction for their scaled spectral radius, ρ_s, as a function of the incoherence parameter, F. This relationship is

$$\rho_s = \exp\left[\frac{(1-\frac{1}{F})}{2}\right], \tag{5.13}$$

and can be derived from the 'coherence ensemble' of random graphs [6]. Here, ρ_s is defined such that it is scaled between 0 and 1 to compare networks of different sizes:

$$\rho_s = \frac{\rho}{||A||_2}, \tag{5.14}$$

where ρ is the standard spectral radius of the adjacency matrix, and $||A||_2$ is the 2-norm of A – that is, $||A||_2^2$ is the largest eigenvalue of AA^T. As we show in Fig. 5.1, the generated networks we use in this work also have ρ_s close to the value given by Eq. (5.13). This justifies the assumption that the numerically generated networks reflect some of the characteristics exhibited by real world networks.

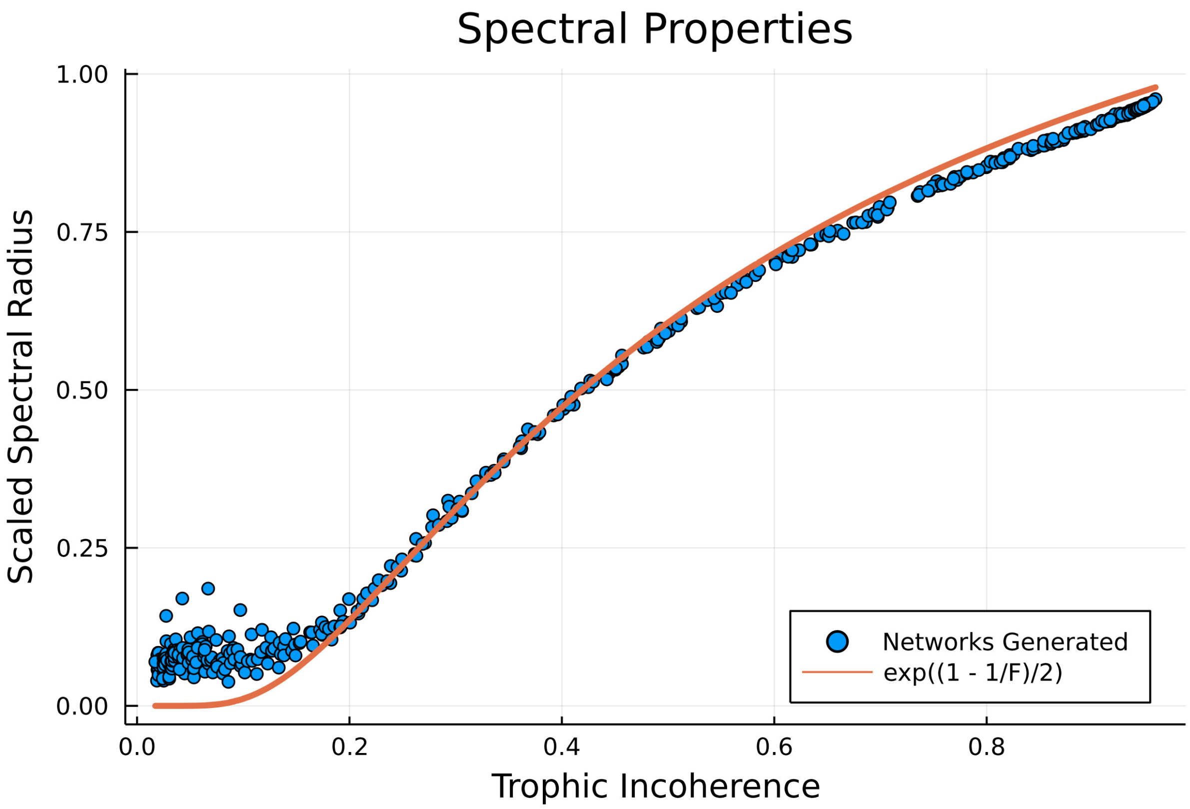


Figure 5.1: Scaled Spectral Radius of Generated Networks against trophic incoherence following the same analytic prediction as real networks as shown in Ref. [8]. The number of nodes is always $N = 500$, and the mean degree $\langle k \rangle = 20$.

5.5 Results

Firstly, as we impose the constraint that only a subset of neurons are presented the pattern to make the setup more like real-world systems, we must decide which set of neurons are to be shown the pattern and assess the effects of this choice. It was chosen that for this model 20% of the neurons would be set into a pattern state and then it would be measured how well the system recovered the remainder of the pattern from this setup. The location of pattern presentation is analogous to the initial conditions of a dynamical system where the question would be which initial condition sends the system into the desired state given the constraint of only controlling a small number of elements. To assess the effect of hierarchy on pattern recovery, patterns were shown to the 20% of nodes with the lowest trophic level (at the bottom of the hierarchy), highest trophic level (at the top of the hierarchy), and a random 20% of nodes. The results are shown in figure 5.2 for networks spanning a range of trophic coherence. We plot the results for each individual network, rather than just the averages with error bars, in order to highlight the breadth and distribution of network behaviour, which becomes more apparent as we study sparser networks in section 5.5.1. These results demonstrate the difference in dynamics depending on the part of the network shown the pattern. When the pattern is shown to 20% of the nodes randomly this is not enough to move the system into a new state, so the shown pattern is not recovered well across the whole range of trophic coherence. It is only possible to extend down to networks of intermediate coherence at this edge density with the generative method used. When the perturbation is made to the state of the top 20% of nodes by trophic level, it has little effect on the state of the system. This is because the perturbation cannot filter back down the system, so the top nodes do not drive the dynamics. For sparse enough networks and high coherence, it is unlikely there will be any paths from the highest trophic levels to other nodes further down. If the network is denser, such paths may exist, but they will still be few compared with the number of paths form lower levels to higher. Hence, information flow will always be predominantly form lower to higher trophic levels in coherent networks.

The dynamics are more complex when patterns are presented to the lowest level nodes, since we observe different behaviours when trophic incoherence is varied. For the most incoherent networks, which are most similar to random graphs, the performance is on average poorer as the system is more stable due to the amount of feedback in the system. By stability we mean here the system's resistance to changing state when a new pattern is presented. At intermediate coherence, the network has an overall direction, so the perturbation at low level nodes is transmitted through the hierarchical network structure and pattern recovery is quite good even though only 20% of nodes are stimulated. This is behaviour that would not be seen in a Hopfield model on a complete graph, nor on a random graph, since more than half the nodes would need to be changed to a new pattern in order to change the state of the system. These results demonstrate the variety of dynamics that can be induced by the more complex, hierarchical networks as compared to a complete or random graph [264, 242, 265].

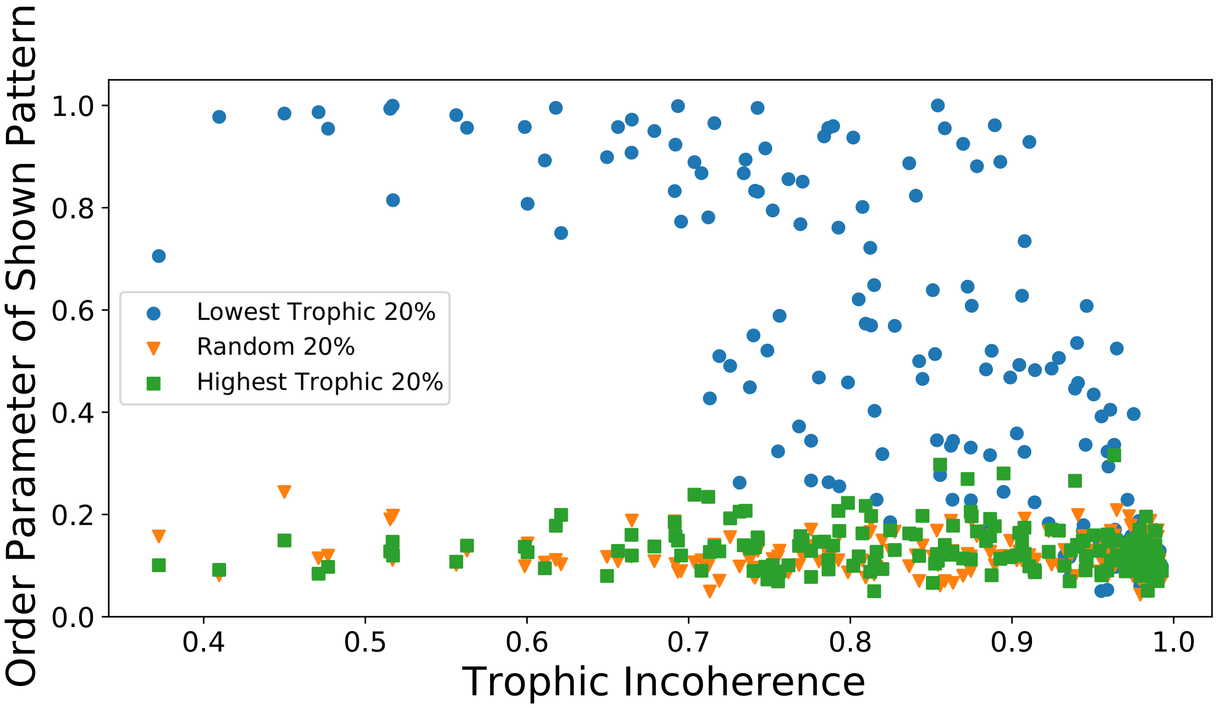


Figure 5.2: Performance of 200 Networks with $N = 500$, $\langle k \rangle = 100$ recovering 10 patterns plotted against trophic incoherence. Showing patterns to different 20% sets of nodes.

When the constraint of a small number of input neurons is removed, the effect of hierarchy on the dynamics is less obvious. Figure 5.3 illustrates the case when the patterns are shown to 60% of neurons. When this many neurons receive an input the distinction between outcome of showing a pattern to a random 60% and the lowest level 60% is blurred, with both being able to recover the pattern across a range of trophic coherence. This highlights the impact of removing the constraint of a small number of inputs. When the inputs are large the effect of trophic level is hidden as randomly chosen inputs can control the system. However, for the highest level nodes this is still not the case. Even at 60%, the higher level nodes fail to influence the coherent networks, as the lowest level nodes still have more control over the system and prevent the pattern from being modified. When the network is hierarchical, perturbations can be both amplified or damped by the structure, something we don't see in either a complete or a random graph Hopfield network. This is again different behaviour than what would be observed on a dense network with no internal structure, as 60% of neurons being flipped would be enough to change the state to that of the new pattern in all cases. This highlights the connection between the trophic level of a node and its ability to control the network: the high level nodes have much less ability to influence the system than those at a low level. This difference remains at all levels of trophic coherence, but is most pronounced for more coherent structures. In all examples the trophic incoherence does not actually reach 1, where all the nodes would have the same level. This is because this only happens in balanced networks, such as a directed cycle, and the limit of our model is Erdős–Rényi random graphs, which have incoherence around 0.95. It is interesting to note the graphs which are random still have a slight hierarchical structure which can be revealed by the trophic levels.

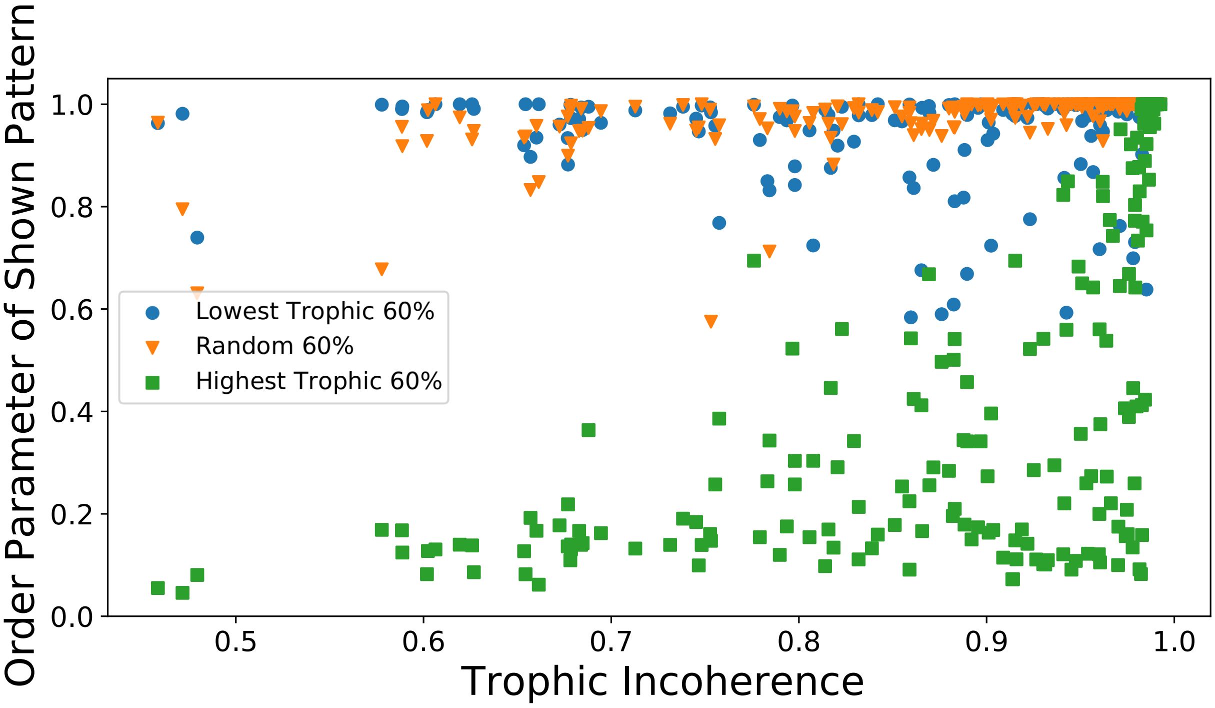


Figure 5.3: Performance of 200 Networks with $N = 500$, $\langle k \rangle = 100$ recovering 10 patterns plotted against trophic incoherence. Showing patterns to different 60% sets of nodes.

5.5.1 Sparser Networks

When the networks are made sparser – that is, the average degree $\langle k \rangle$ is reduced from 100 to 20 – the results are broadly the same as on denser networks, but there is more variation in the performance of different networks, even for similar trophic coherence. For networks of this sparsity the whole range of coherence can be investigated, as there are no difficulties associated with generating the more coherent networks. For inputs to both randomly selected and highest level nodes, the recovery is very poor, just as it was before. When it is the lowest level nodes which receive the input, behaviour depends on the trophic incoherence of the network. For the networks with lowest incoherence, the performance is generally very poor. This is due to the fact that these networks have very little feedback and small strongly connected components, so the patterns are not well recovered. For the intermediate coherence networks, performance is inconsistent. Some networks perform very well, with their structure being suited to controlling the system with only the low level nodes, while other networks perform very badly. Finally, higher incoherence networks are again more likely to get stuck in a pattern rather than to respond to the stimulus at the lowest level nodes, due to the high amount of feedback in the system, and the maximum performance begins to decrease again. Therefore, for sparser networks we find that the best performance is found at intermediate coherence – although not all networks in this range are necessarily high performing.

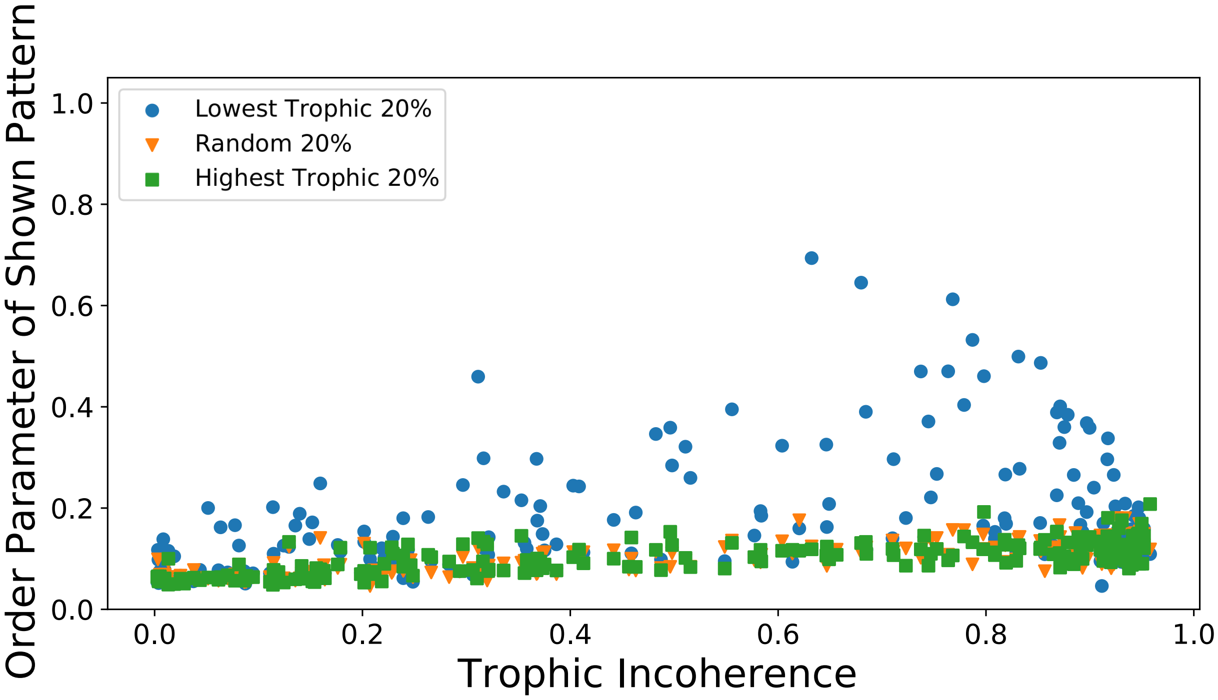


Figure 5.4: Performance of 200 Networks with trophic incoherence showing patterns to the 20% lowest (blue), highest (green) and random (orange) nodes by trophic level. $N = 500$, $\langle k \rangle = 20$

The relationship between average degree and recovery of patterns is shown in figure 5.5, where all networks have 500 nodes and are generated using $T_{GEN} = 1$. The task cannot be performed by the most sparse networks, as they all fail to store any patterns. At an average degree of around 20, we reach the regime where some recovery is possible. For higher density, recovery reaches an inconsistent regime, where performance varies greatly for networks of similar degree and trophic properties. This kind of regime is most interesting to study since the dynamics have a lot of variability, and successful pattern recovery is possible but not sure. Above an average degree of about 200, the structural features of the network are lost as the network is too dense and it simply gets stuck in one state for the whole dynamics and there is no ability to update when presented with a small number of inputs. Hence, figure 5.5 demonstrates that increasing the network density can make performance at a pattern recovery task worse, which is counter to the general expectation for Hopfield networks where higher connectivity improves performance [266, 265].

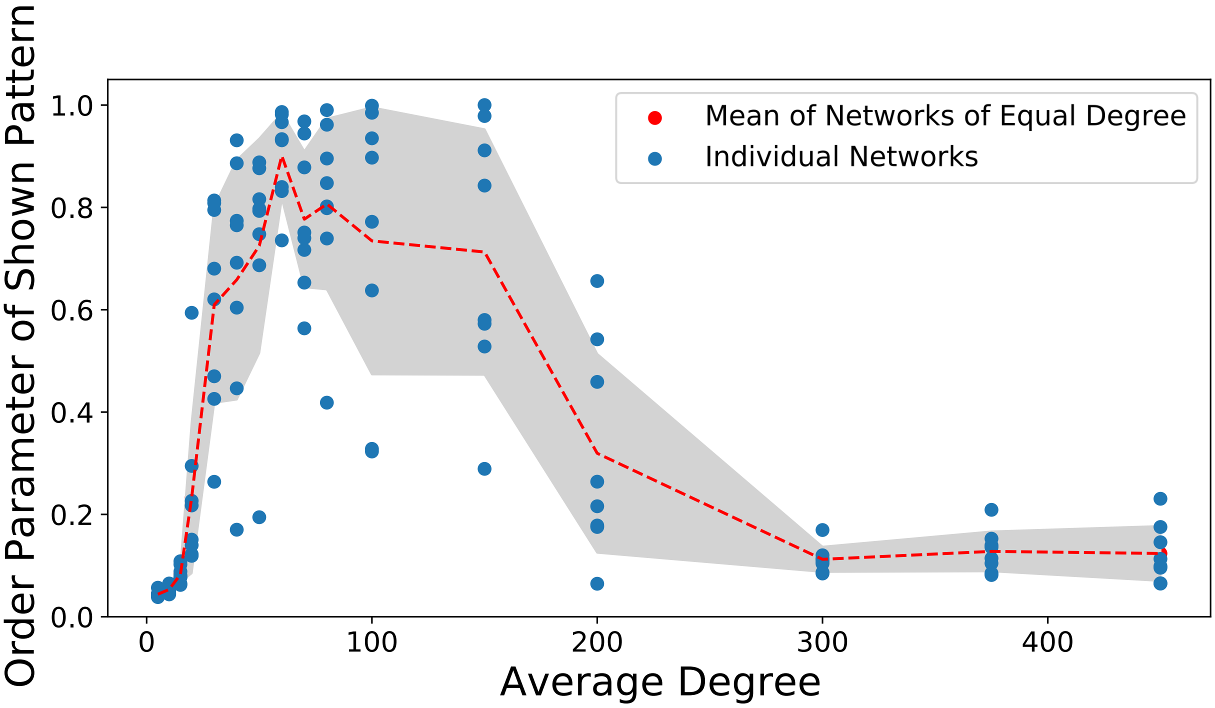


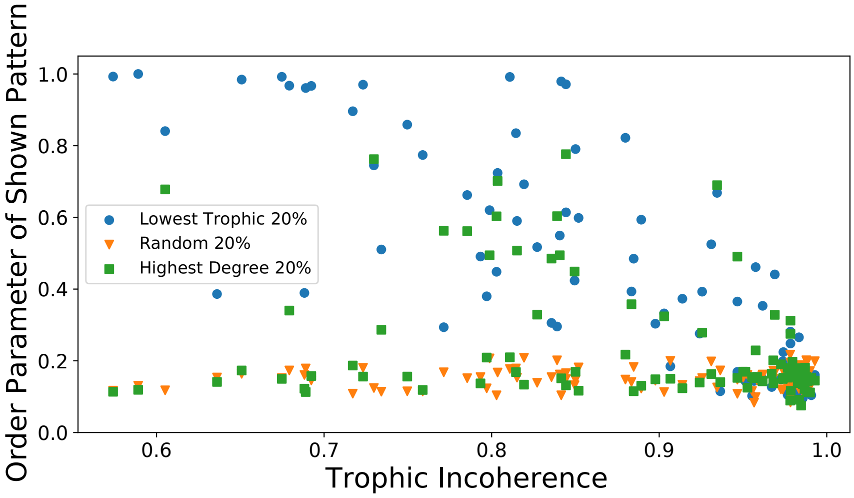
Figure 5.5: Performance of Networks of varying degree for fixed generation temperature, $T_{\text{GEN}} = 1$, showing patterns to the 20% lowest nodes by trophic level. $N = 500$. With the average trend shown by the dashed red line and the standard deviation shown in the shaded area.

5.5.2 Comparison of Targeting Highest Degree Nodes

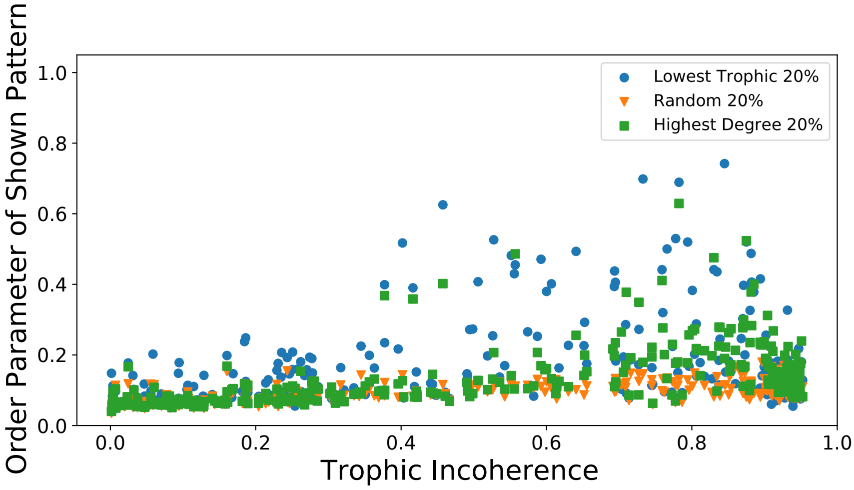
To validate our choice of nodes we compare our results to a targeted presentation of the pattern to the 20% of nodes of highest out-degree, which one might assume form the subset of nodes with greatest local influence on the system. This comparison is shown in figure 5.6, which compares the influence of the nodes of high degree to the selection of nodes by their local trophic properties. The set of nodes with highest degree do not influence the network to the extent that the lowest level nodes do. However, they do perform better than a random set of nodes, as expected, in both networks of average degree 20 and 100. In the networks of average degree 100 (figure 5.6a), the lowest trophic level nodes are better than the highest degree nodes when the network is more coherent and hierarchical, as in this case the system is more strongly controlled by the low level nodes. When the networks are less hierarchical, the influence of the high out-degree nodes becomes comparable to the influence of the low level nodes. This highlights a crucial point: in a complex network, the “importance" of nodes can be determined both by their degree-based centrality and by their relative position in the hierarchy, depending on how trophically coherent the overall system is. In a very hierarchical (i.e. coherent) network, even if a node has a high out-degree, the state of the system can still be more controlled by lower out-degree nodes below it in the hierarchy. Our results, due to the generative model, focus on networks where the degree distributions are not extremely heterogeneous. The fact the in very hierarchical networks low level nodes control the state of the nodes above them would still hold in a very heterogeneous network. However, degree may be a more important factor if the out-degree of a few nodes were so large that they directly affected much of the network. These network properties can interplay in a variety of ways and may be the subject of future work.

5.5.3 Structural Properties of Networks Affecting Performance

We hypothesised that some network properties outwith trophic coherence could explain the range and inconsistency of behaviour for sparse networks. One possible measure was the



(a)



(b)

Figure 5.6: Distribution of Performance for Networks showing 10 patterns to lowest trophic level, highest degree and random 20% of nodes. N = 500 (a) $\langle k \rangle = 100$, (b) $\langle k \rangle = 20$.

number of edges leaving the node set shown the pattern compared to the total number of edges. When very few edges connect the nodes shown the pattern to the rest of the network, it is unlikely for the pattern to be successfully recovered, as when the pattern is updated it cannot be properly transmitted outside of the set shown the pattern. The results of this are displayed in figure 5.7. This shows that there is a strong correlation (correlation coefficients in the legend) between the edge ratio and performance, but it does not exactly determine the behaviour of the system. However, it is very clear the worse performing networks have very small values of this parameter, and it can be used to identify the failing networks, if not precisely to select the very best networks.

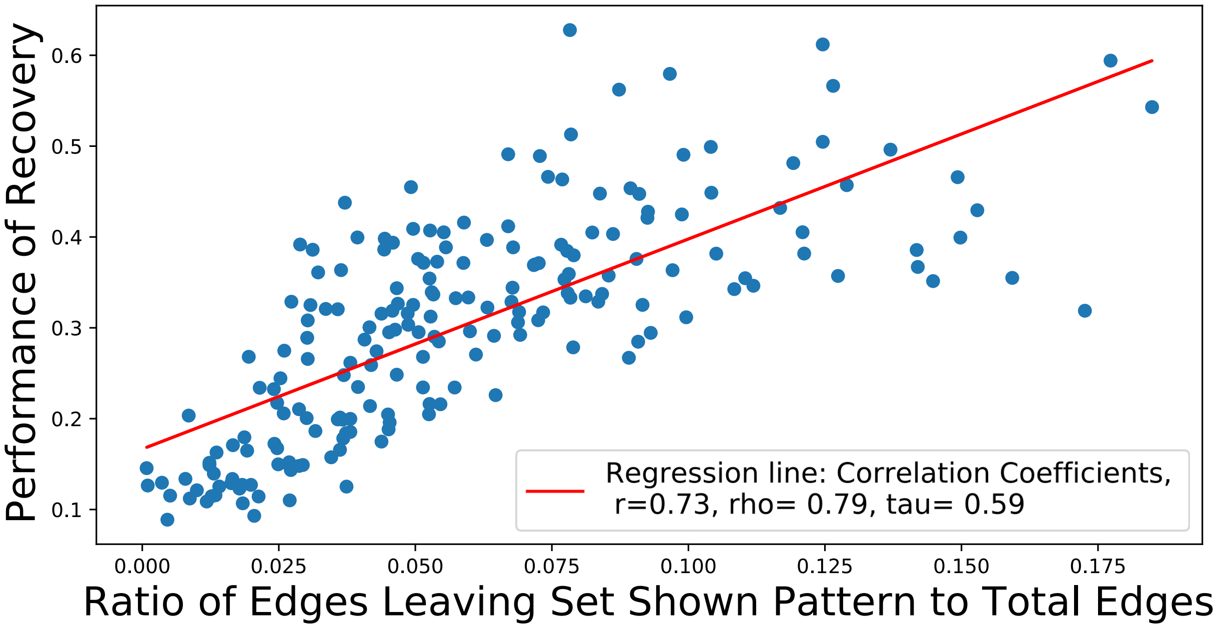


Figure 5.7: Relationship between network performance and the ratio between number of edges leaving the set shown the pattern and total edges in the network. $N = 500$, $\langle k \rangle = 20$. Networks of Intermediate Incoherence.

Another factor which we thought may influence the performance was the distribution of trophic levels amongst the nodes. In networks generated with the model used here (see section 5.4), edges tend only to span a small difference in trophic level. We would therefore like the level distribution to be peaked towards lower levels, so that more nodes have a lower level and are more likely to be densely interconnected with the set of nodes shown the pattern. This is shown in figure 5.8, where we sum the cumulative distribution of the number of nodes of trophic level less than αh_{max}, for α in the range 0 to 1. This function is maximised when the level distribution peaks towards lower level nodes, and so provides a good measure of where the peak in trophic level lies, while being normalised so different networks can be compared. It shows a similar profile to the result of figure 5.7, where the correlation is again strong but does not precisely predict the performance of the network.

We therefore surmise that the performance of a network at this task depends on several topological features, including but not limited to: trophic coherence, mean degree, mean degree of the lowest level nodes, and trophic level distribution.

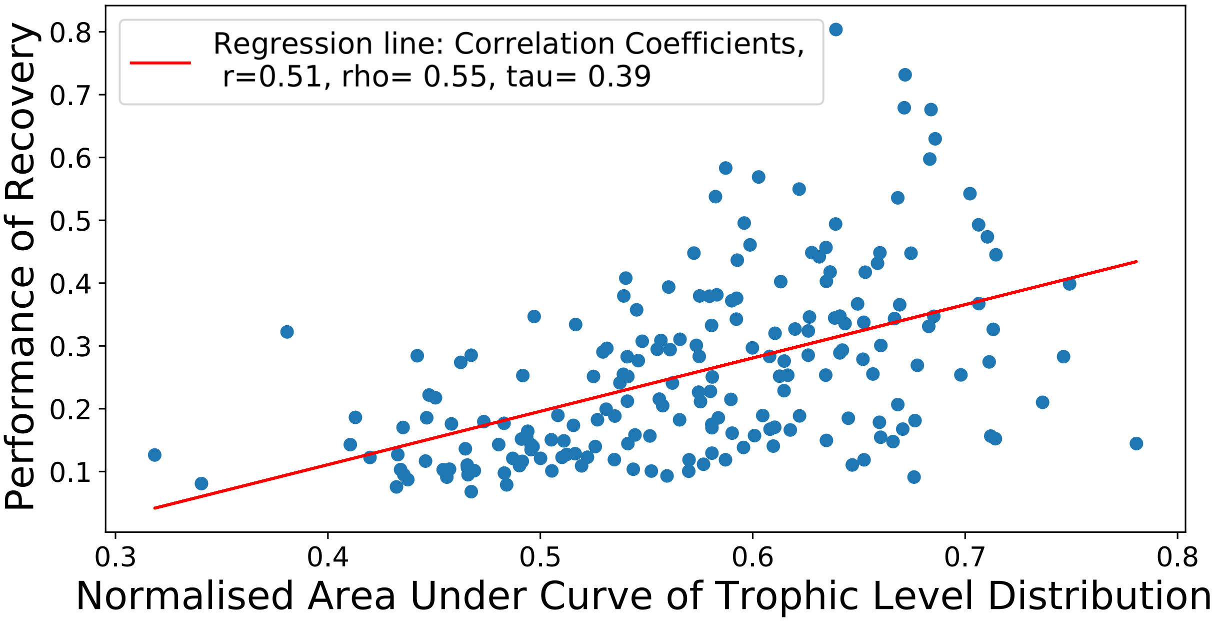


Figure 5.8: Distribution of Performance of 200 Intermediate Incoherence Networks against the integral from 0 to 1 over a parameter α of the curve of number of nodes of trophic level less than αh_{max}. $N = 500$, $\langle k \rangle = 20$. Networks of Intermediate Incoherence.

5.5.4 Time Series of Pattern Recovery in Sparse Network Components

In this section we review the time series of the dynamics of pattern recovery in a network with average degree 20, and highlight some of the reasons for the inconsistency in performance between similar networks. In all of the following example time series the pattern is presented to the 20% of nodes with the lowest trophic level.

We find that the network structure can induce quite heterogeneous dynamics. This is something that is not noticeable when the recovery is working well. Let us consider first the case of a dense network, with mean degree 100, as shown in figure 5.9. In this time series each colour represents the pattern which has been most recently presented to the network, while the y-axis represents the order parameter corresponding to that pattern. For a well performing network, the order parameter quickly returns near to 1 whenever a new pattern is presented. This is the case for the network shown in figure 5.9. Due to the recovery being this good, and the edge density being high, heterogeneous dynamics is not observed. Patterns are recovered to the same extent in all parts of the network hierarchy, and additionally the whole network is strongly connected, so there is no difference in dynamics inside or outside that component.

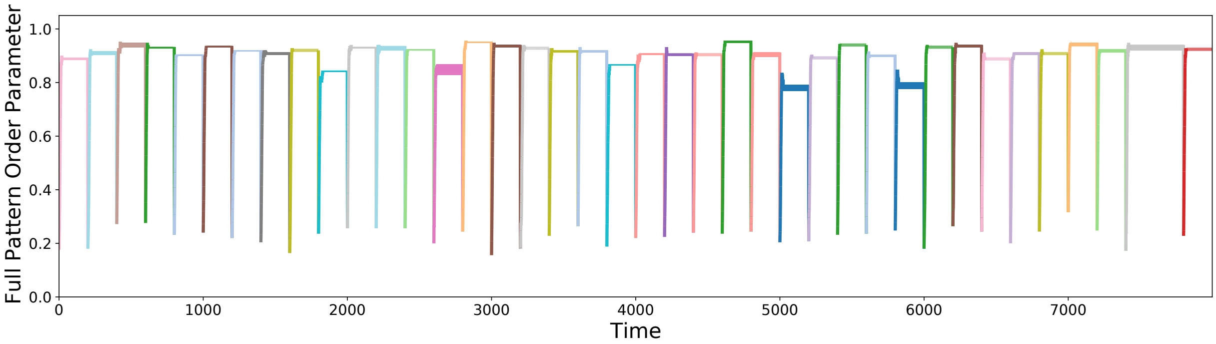
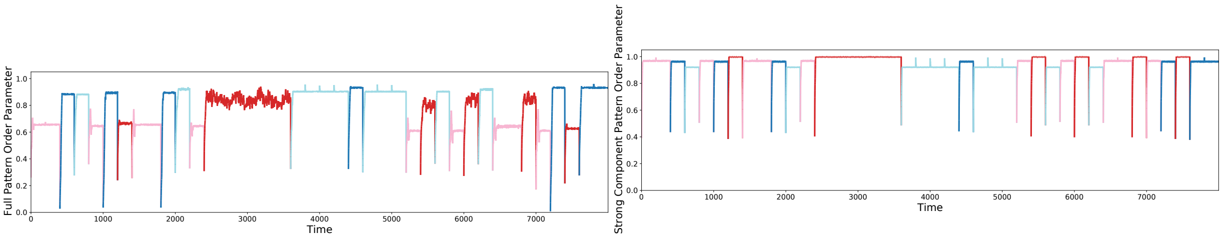


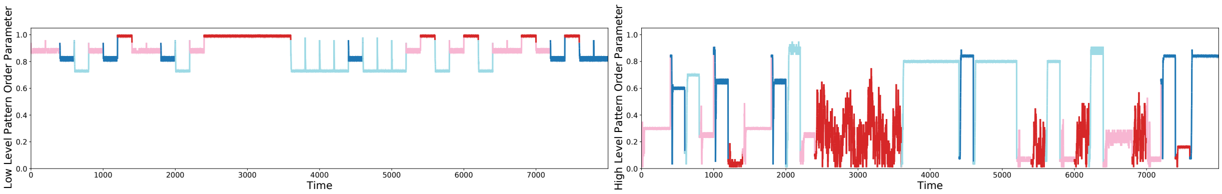
Figure 5.9: Time Series of Pattern Order Parameter for average degree 100 network with 500 nodes storing 20 patterns. Where each colour represents the pattern most recently having been shown to the network. At this edge density recovery is very consistent.

This is very different from the dynamics exhibited by the sparse network used in figure 5.10, which stores four patterns. This network is a specific example of a network which performs reasonably well, but it should be borne in mind that many sparse networks fail very badly. The dynamics are analysed by considering four different network components (subgraphs): the whole system; the largest strongly connected component; the bottom 20% of the nodes by trophic level; and the top 20% of nodes by level. Noting that these components are simply where the data was collected and the presentation location was unchanged. In the full system, figure 5.10a, recovery is good for some patterns but fails badly for others. The behaviour of each pattern is roughly consistent, and if a pattern fails or succeeds at one presentation it will repeat the same behaviour at subsequent presentations. The order parameter dips when a new pattern is presented, then moves to its new stable value. Additionally, there are fluctuations around the stationary states and updates to the system do not stop (i.e. some neurons continue to change state in subsequent time steps). This is different to the dynamics inside the largest strongly connected component, 5.10b, where for the fully recovered stable patterns updates stop and there are no fluctuations. This highlights the stabilising effects of feedback associated with being strongly connected. Among the low level nodes, figure 5.10c, for those patterns which are correctly recalled, the order parameter goes to 1 when the new pattern is presented. However, if a pattern is not recovered by the low level nodes then this precludes the possibility of that pattern being successfully transmitted



(a) Full Pattern Order Parameter.

(b) Strongly Connected Component.



(c) Bottom 20% of nodes by trophic Level.

(d) Top 20% of nodes by trophic level.

Figure 5.10: Time Series for different network components for average degree 20 network with 500 nodes storing 4 patterns. Where each colour represents the pattern most recently having been shown to the network.

through the network. This means that if a pattern is not recovered by the low level nodes, figure 5.10c, then it will also fail to be recovered by the high level nodes 5.10d. Recovery by the high level nodes is the least consistent, and fluctuates the most, since these nodes are furthest from where the patterns are presented. In addition, the order parameter initially drops to zero whenever a new pattern is presented as it is not shown to any of the nodes contained in this set.

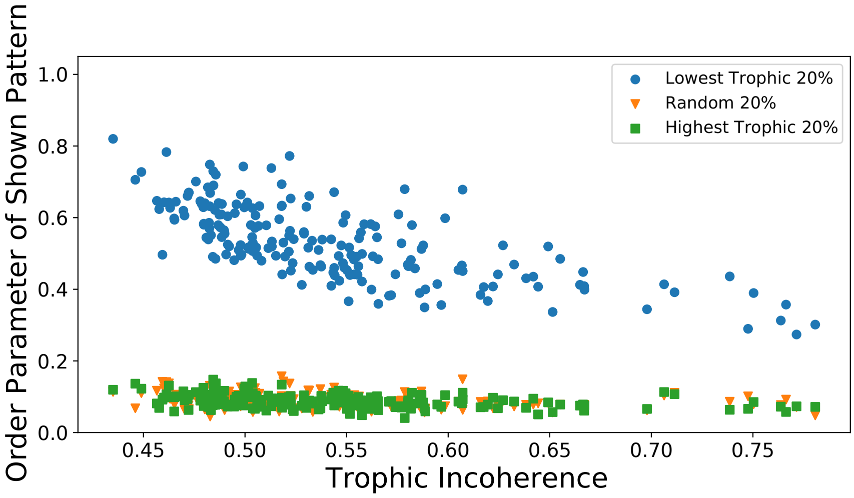
These results might be different if the network included basal nodes (those with no in-neighbours), and would depend on what update rule we chose for these – e.g. maintain their state indefinitely, update randomly, etc.

5.5.5 Search for Improvements to Network Structure

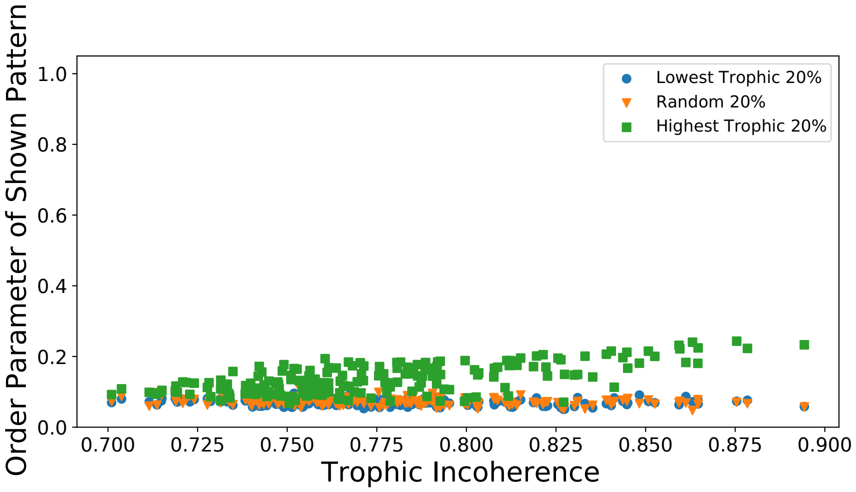
The results relating the distribution of trophic levels to neural-network performance open the possibility of biasing the network generation process so that it preferentially leads to networks with topology better suited to the task. A simple way to accomplish this is to generate the networks in the same way as previously, but modify the probability of adding edges so that it is biased towards adding edges to lower level nodes. This can be accomplished by modifying the probability of placing and edge so that

$$P_{ij} = \exp\left[-\frac{(\tilde{h}_j - \tilde{h}_i - 1)^2}{2T_{\text{Gen}}} + \gamma \tilde{h}_i\right], \tag{5.15}$$

where the $\gamma \tilde{h}_i$ modification in the exponential acts to bias the distribution towards high or low levels, depending on the sign of γ. In what follows we choose $\gamma = -0.5$ in order to add more edges to nodes with lower trophic level. One downside of this method is that it is harder to control precisely the trophic incoherence of a network and to span the full range of incoherence.



(a) Bias Towards Low Level Nodes. $\gamma = -0.5$



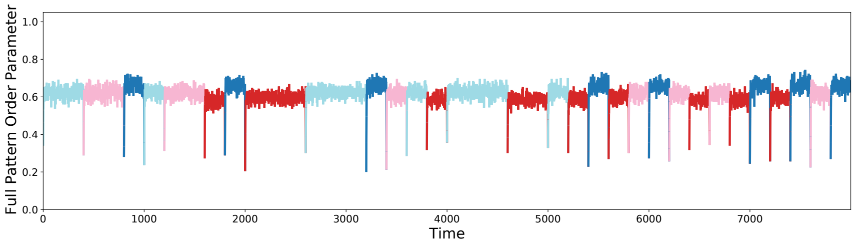
(b) Bias towards High Level Nodes. $\gamma = 0.5$

Figure 5.11: Distribution of Performance for Biased Networks biased. N = 500 $\langle k \rangle = 20$.

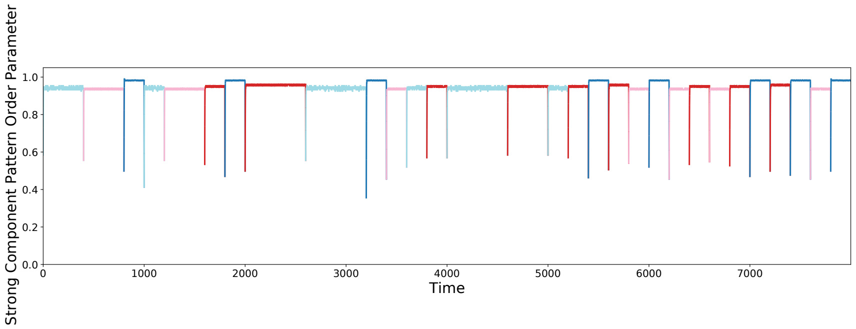
The broad effects of biasing the network generation and performance are demonstrated in figure 5.11. This shows that when edges are more likely to connect to low level nodes, figure 5.11a, the very worse performing networks are essentially eliminated, and all the sparse networks recall at least a fraction of the pattern. This biasing has no effect on performance when presenting the pattern to the random or higher level nodes, as they still fail to force the system to change state when the perturbation is applied to these nodes.

To demonstrate the importance of where feedback is placed in the hierarchy we change the sign of the biasing factor and make it more likely that edges are added to the higher level nodes, figure 5.11b. This creates networks which are not suited to the recovery task and perform badly in all cases. This is due to the fact that the edges connecting to high level nodes do not allow both for the pattern to be stable and for the information to be transmitted across the system. One issue with biasing the network generative process is that it becomes more difficult to control precisely the trophic coherence of the network, which is why the range of trophic incoherence is restricted in figure 5.11.

The time series of pattern recovery for sparse biased networks clearly demonstrate how this biasing procedure modifies the dynamics of the system. Pattern recovery across the whole system, figure 5.12a, is very consistent compared to the unbiased networks (figure 5.4), which fully recover some patterns and fail to recover others. This time series is a representative example of the behaviour seen in biased networks and comes from a single network. The consistent level which they reach however is below 1 so the patterns are not fully recovered and the recovery is not as high as the maximum seen in some specific unbiased networks (figure 5.10). Whether this is better may depend on the context: remembering part of every pattern so it can be identified may be preferable to recalling some patterns perfectly but not recovering others at all. Additionally, for biased networks there are large fluctuations and updates continue when the system has reached the new state. This can be explained by looking at the dynamics inside the largest strongly connected component only, figure 5.12b. In this component recovery is very consistent and all patterns are fully recovered, so the network does much better when this component is larger. It also explains why, in the time series for the dynamics of the full network, fluctuations around a stable point are observed, since updates to neuron states stop in the strongly connected component but continue outside of it. The fact that the recovery is very good inside the largest strongly connected component opens up the possibility of selectively generating networks which are both biased towards lower level nodes, and have large strongly connected components.



(a) Order Parameter of Whole Network



(b) Largest Strongly Connected Component Only

Figure 5.12: Time Series of Pattern Order Parameter calculated inside the different components for average degree 20 network with 500 nodes storing 4 patterns. Generated with a bias towards adding edges to lower level nodes. Where each colour represents the pattern most recently having been shown to the network.

This is demonstrated in figure 5.13, which shows the performance of biased networks where the largest strongly connected component comprises more than 60% of the nodes. These networks are simply generated by repeating the generative process and discarding networks which do not meet this requirement. The higher this threshold, the more inefficient the process but the more likely we are to keep only highly performing networks. At at threshold of 60% all very poorly performing networks are eliminated, and the recovery performance is consistently around 0.6.

These results demonstrate that despite the variability in the dynamics of directed sparse Hopfield networks, it is possible to generate structures which perform well consistently by tuning a few parameters: T_{GEN} to set the trophic coherence, γ to place edges preferentially at lower level nodes, and the threshold for the minimum size of the strongly connected component.

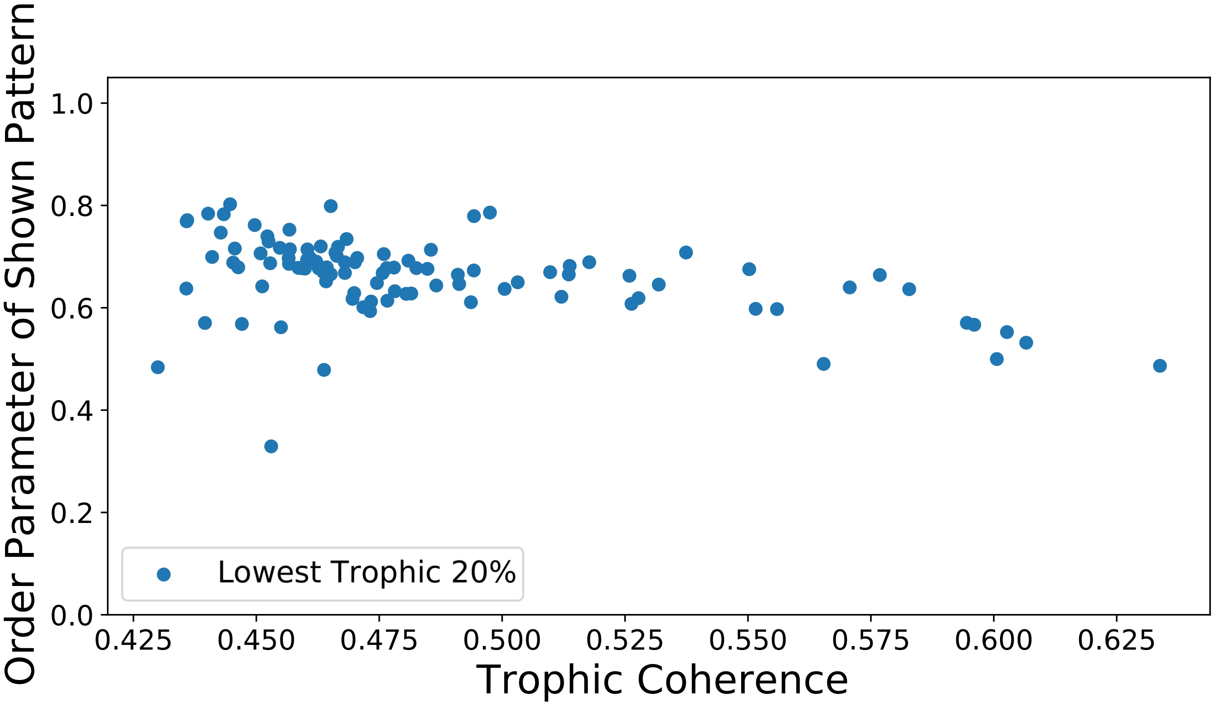


Figure 5.13: Performance of Low Level Biased Networks with average degree 20 and 500 nodes where the largest Strongly Connected Component contains at least 60% of the neurons.

There are many possible ways to modify network structure to maintain performance and we just give a small sample here. Biasing is limited by the fact it reduces the control of the trophic structure and that strongly biasing may decrease the size of the strongly connect component which is needed for recovery. The best way to improve network structure depends on the constraints, on whether edges can be added or removed, and on how success is defined. Biasing makes the recovery more consistent, but the performance of unbiased networks may peak higher for certain networks and patterns, which may be preferred in some situations.

5.6 Discussion and Conclusion

We have shown that neural networks based on sparse, trophically coherent graphs have a much wider range of possible behaviour than ones based on either fully random or complete graphs [264, 242, 265], where all nodes necessarily have very similar dynamical roles. This symmetry is broken in a coherent network, as different nodes can have very different abilities to affect the dynamics of the system. The interplay between trophic structure and dynamics has already been observed across a range of systems in the literature [5, 34, 7]. It has also been shown that the coherence of a network is linked to the non-normality of the adjacency matrix [18, 8]. Non-normality in networks has in turn been linked to sensitivity to perturbations and to the stability of the system across a wide range of dynamics [19, 267, 268, 154, 269], which is consistent with our results that more coherent networks are more sensitive to targeted perturbations and less stable.

The behaviour observed in the system studied here relies on two key facts: that the networks are sparse and that the sets of input nodes are small. If the networks are too dense then hierarchical structure is destroyed and the asymmetry between nodes does not exist (there is a limit to how coherent a dense network can be). Moreover, it is thanks to the network's trophic coherence that a small subset of nodes is able to drive the dynamics of the whole system. Many real-world systems display both of these properties. Additionally, they are often neither highly coherent nor incoherent, but have trophic coherence in the intermediate range which allows for a balance between stability and sensitivity to stimuli [8, 18, 6]. Therefore, we believe the principles studied here for the case of Hopfield-like neural networks may be broadly applicably to a range of real-world systems. The limitations of these methods are that since trophic incoherence is an average global network property it lacks the precise detail to characterise fully the behaviour of the system in all cases. It is challenging to control precisely both the trophic incoherence and another aspect of network structure, since one may restrict the other, as with the biasing method. In future this work could be extended by looking at a time series of patterns which are correlated with each other [263], patterns correlated with the structure, or networks with heterogeneous degree distributions and varying in- and out-degree correlations.

In conclusion, we have demonstrated, through numerical analysis, that trophic structure strongly shapes pattern recovery in directed Hopfield-like networks. In particular, on a sparse, directed network a small number of input neurons – which can be identified by their trophic levels even in the absence of basal nodes – are able to drive the system in such a way that it recovers patterns. This would not be possible on either a complete or fully random network, which require at least about 50% of the nodes to receive the input in order to change state. In order for such networks to recover patterns successfully, they must have the correct balance between feedback and directionality – a feature which is determined by the trophic coherence. However, we observed that setting the appropriate trophic coherence was not enough to guarantee good performance. We found that by biasing the network generation process so as to add edges preferentially to lower-level nodes, and then discarding networks with strongly connected components below a minimum size, we could reliably produce architectures that performed the task well.

5.7 Appendix

5.7.1 Software Tools Used

Various software packages were used manipulate the networks and perform the simulations. The Python package Graph Tool [129] was used for some of the network manipulation. Networkx [270] was used for Network drawing and some network manipulation and analysis. The Julia package LightGraphs.jl was used for the spectral radius results [271]. All the updating and training of the Hopfield-like networks was done with the aid of the Cython package [272] to convert Python Code to C as pure Python was found to be too slow to allow efficient study.

5.7.2 Network Generation

The detailed steps to the network generative process are as follows:

1. Create the N nodes of the network and assign to each node one in-coming edge, in each case from a randomly chosen other node. After this, each node has in-degree 1.

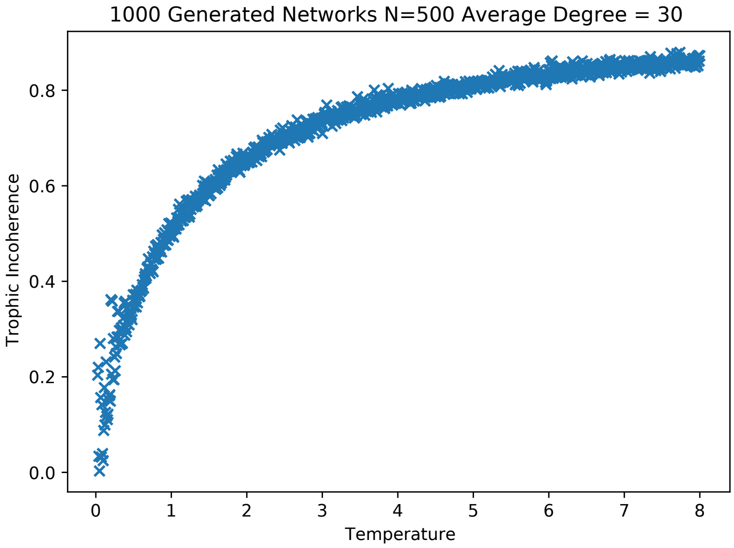


Figure 5.14: An example of the distribution of trophic incoherence with temperature like parameter, T_{GEN} in this generative model.

2. Compute the initial trophic levels, $\tilde{h}$, using equation 5.2. This is best solved iteratively, since this method is fast and works even is there are small disconnected components.

3. Add edges up to the desired edge number with probability dependent on the trophic level difference between the nodes minus 1. The edge probability used was Gaussian and defined as
$$P_{ij} = \exp\left[-\frac{(\tilde{h}_j - \tilde{h}_i - 1)^2}{2T_{\text{GEN}}}\right], \tag{5.16}$$
where T_{GEN} is a temperature-like parameter used to control how coherent the network is: small T_{GEN} generates networks which are highly coherent.

4. Recompute the trophic Levels, h, including the newly added edges. Then compute the incoherence parameter, F, of the generated network.

This method works best for reasonably sparse networks, since when the edge density is too large it becomes difficult to find configurations of high trophic coherence, if they exist at all. On the other hand, if the edge density is very low the resulting network may not be even weakly connected. However, for a large range of densities it will encounter no issues. Due to the stochastic nature of the method it is is not possible to predict precisely the incoherence of a generated graph . For example 1000 networks generated with 500 nodes and 30×500

edges, and temperature $T_{GEN} = 1.3$, cluster around $F \approx 0.59$, with most networks in the interval $F \in (0.56, 0.65)$. However this level of precision is sufficient for analysing general regions of behaviour with no issues.

The third step can be quite computationally inefficient for large networks with many possible edges as the probabilities for adding an edge at most locations are very close to zero. This can be improved by more efficiently sampling the probability distribution using the method outlined below.

The goal of this sampling method is to set up the sampling so that each time a random number is drawn it results in an edge. This avoids repeatedly drawing numbers for the majority of edges which are unlikely to be added. The steps are:

1. Label all the possible edges and probabilities with an integer l and P_l respectively.

2. Compute the sum of all these probabilities,

$$S = \sum_l P_l.$$

3. Draw a random number, r, between 0 and S.

4. Sum the probabilities one at a time until you reach the random number, r.

5. Add an edge at the space, l, corresponding to the probability P_l which made the same greater than r.

6. Set $P_l = 0$ and repeat sets 2-6 until the required edge number is reached.

This method is much more efficient: the sums can be computed quickly as it avoids the many repeated random number draws for every single missed edge that would otherwise be necessary. It is possible to also create variants of this method by modifying the initial structure to which subsequent edges are added; or to recast the model so as to start from a dense network and prune edges with a similarly defined probability to generate networks of the desired trophic incoherence.

5.7.3 Connectome of *C.Elegans* plotted by trophic level

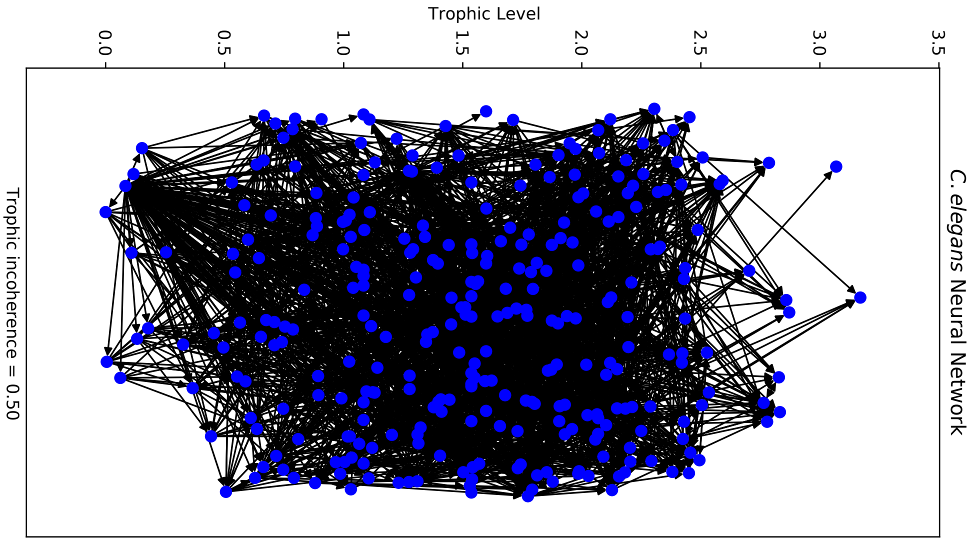


Figure 5.15: Illustration of the the real world connectome of *C.Elegans* shown which has intermediate incoherence with node height drawn using Trophic Level. Data from[185]. Drawn with Networkx Graph Package [270].

CHAPTER

6

FITNESS-BASED GROWTH OF DIRECTED NETWORKS WITH HIERARCHY

This chapter is based on

- Niall Rodgers, Peter Tiňo, and Samuel Johnson. “Fitness-Based Growth of Directed Networks with Hierarchy”. In: *Journal of Physics: Complexity* (Aug. 2024). ISSN: 2632-072X. DOI: 10.1088/2632-072X/ad744e

Relationship of Work to Thesis

In this chapter we present the paper “Fitness-Based Growth of Directed Networks with Hierarchy" [4] which attempts to explain the ubiquity of hierarchy in real directed networks by highlighting how it can arise through fitness-based interactions. The work was motivated by several factors that had arisen throughout my PhD. The other methods used for generating networks in this thesis allow only limited control of the type of hierarchical structure which emerges as well as being computationally inefficient. This prompted the idea to use fitness-based methods to generate networks as this could allow control of the number of levels and number of nodes per level using the fitness distribution. Fitness-based models could also allow more control over the probability that edges break the hierarchy which was shown to be important to the strongly connectivity in chapter 3 as well as providing a more realistic way to generate networks as agents in a system may observe the properties of nodes but not be aware of the entire network structure.

Additionally, it allowed us to understand the relationship between heterogeneous degree distributions and the hierarchy measured with Trophic Analysis. The observation that hierarchy is common in many real-world systems justifies the importance of studying this property in the other parts of the thesis so it made sense to study why it arises. This chapter also rounds off the thesis by studying the generation of hierarchical network which complements the study of structure and dynamics. The work of this chapter could form the basis of future studies of how hierarchy affects various types of dynamics in the style of chapters 4 and 5 however with an improved generative method.

Abstract

Growing attention has been brought to the fact that many real directed networks exhibit hierarchy and directionality as measured through techniques like Trophic Analysis and non-normality. We propose a simple growing network model where the probability of connecting to a node is defined by a preferential attachment mechanism based on degree and the difference in fitness between nodes. In particular, we show how mechanisms such as degree-based preferential attachment and node fitness interactions can lead to the emergence of the spectrum of hierarchy and directionality observed in real networks. In this work, we study various features of this model relating to network hierarchy, as measured by Trophic Analysis. This includes (I) how preferential attachment can lead to network hierarchy, (II) how scale-free degree distributions and network hierarchy can coexist, (III) the correlation between node fitness and trophic level, (IV) how the fitness parameters can predict trophic incoherence and how the trophic level difference distribution compares to the fitness difference distribution, (V) the relationship between trophic level and degree imbalance and the unique role of nodes at the ends of the fitness hierarchy and (VI) how fitness interactions and degree-based preferential attachment can interplay to generate networks of varying coherence and degree distribution. We also provide an example of the intuition this work enables in the analysis of a real historical network. This work provides insight into simple mechanisms which can give rise to hierarchy in directed networks and quantifies the usefulness and limitations of using Trophic Analysis as an analysis tool for real networks.

6.1 Introduction

Complex networks are evolving systems and much of the research in network science has been dedicated to finding models which explain how networks can be formed in such a way which reproduces a certain property observed in real-world systems. Real directed networks have properties which are unique to the directed case such as non-normality, global directionality and hierarchical organisation of the nodes. It has been shown that networks which are non-normal [165, 19, 20] or have a global directionality as measured by trophic incoherence [8, 2, 3, 18, 20] are very common in real-world settings. We propose a generative model based on the interactions between node fitness and degree-based preferential attachment which explains this behaviour in real-world systems. We also show how the properties of the fitness model can be linked to the structural features related to hierarchy and directionality as measured by the technique of Trophic Analysis [8] which justifies its usefulness as an analytical tool. Trophic Analysis is a method for studying directed networks which allows the local position in the hierarchy, Trophic Level, and the global directionality, Trophic Incoherence, to be measured. It has been related to the spectral properties [6, 41, 8] and strong connectivity in real directed networks [2]. As well as notions of network influence [3], directed Hopfield networks [1], historical networks [52] as well as trade, social systems, and economic networks [38, 48, 47] with additional equivalent formulations [8] also used [75].

We study a growing network model where the probability of connecting to a node is a function of the fitness difference in combination with preferential attachment based on degree. This idea builds on many models present in the literature which use node fitness as a way to build networks.

The earliest models of complex network evolution based on fitness and preferential attachment, which used connection probabilities based on the fitness of a node without interaction, allowed the previously observed scale-free network property to be better understood [273]. For example, the Bianconi–Barabási model which combined node fitness with degree-based attachment [273], where nodes with higher fitness are more likely to accrue more connections. This provided a fitness-based extension to the earlier models highlighting the ubiquity of scale-free networks [12]. With later models also studying how the fitness distribution can translate into properties of the the degree distribution [274]. In this work we take a similar approach but tackle the problem of network hierarchy and show how fitness models allow the emergence of network hierarchy to be understood.

In previous work, networks of varying non-normality and trophic coherence have either been created artificially using degree imbalances [165], using node arrival time and a reciprocity parameter to create hierarchical structure [19, 20] or using static models [44], like the variants of the generalised preferential preying model [1, 2, 3, 34] which is based on the initial trophic level of the nodes of a seed network. However, these methods are not realistic in that in a real systems networks grow over time, the possible structures are limited [19] or individuals may not have access to the network properties and choose nodes to connect to based only on fitness of the nodes they observe. Hence we demonstrate how the emergence of wide range of hierarchical structures can be found in fitness-based growth models.

The range of possible phenomena that can be explained by fitness models increases when one allows for interactions between the fitness of the connecting nodes. In order to induce a hierarchy within the network we study models where the probability to attach depends on the fitness differences between nodes with an offset. Fitness-based models without an offset, which can be seen as a specific case of our model when this parameter is set to zero, have been widely used to study a variety of phenomena. This includes models which create scale-free networks with homophilly [275, 276, 277], used to study inequality [278, 279] and spreading processes in social settings [280]. Fitness interactions have also been used to study the interactions between countries in trade networks [281]. Models to study citation networks can also be viewed as models based on fitness difference interactions as the time of publication of a paper can be used as fitness and the decay in the citation probability with time viewed as the interaction between fitness parameters as well as any other metrics based on the success of the paper [282, 283, 284]. In some systems however, it makes sense to try to connect to another node who has a different fitness to the parent node. For example, in ecology an animal may as a first approximation be able to eat a smaller animal rather than connecting to a prey of the same size [285]. This leads to models describing ecosystem formation based on the niche widths of species [285], which is closely related to one of the cases our model captures.

A model of network formation based on fitness differences with an offset makes sense in many settings in which hierarchy has been observed. The most obvious case is ecology, where a species consumes a species which is just below it in the trophic hierarchy however this may also make sense in other areas. In a network of trades between sports teams you may want to buy players from a team which is below in the hierarchy and sell to teams above. In trade networks there is a fitness hierarchy, known in economics as upstreamness, depending on how far along the chain of the processing a good is. For example, a company which makes batteries may want to buy raw materials directly but a company making consumer electronics wants to buy the batteries and does not buy the raw materials directly imposing a hierarchy of transactions. Similar affects could also be seen in neural or communications networks where connections want to be made into the next layer of the system and to respect this ordering. Related phenomena may also arise in certain social settings, where the reciprocity of interactions depends on the social status of the individuals [130].

6.2 Background

6.2.1 Hierarchy in Directed Networks

Hierarchy in directed networks can be quantified in many ways [25, 21] in terms of either flow hierarchy or a nested hierarchy. In this work, we speak of hierarchy in terms of flow hierarchy. That is the nodes can be ordered on a one dimensional axis via a method like trophic analysis [8], SpringRank [44], an ordered stochastic block-model [128] or another method so that edges point in the direction of the flow hierarchy as much as possible given the constraints of the topology and ranking algorithm. This flow hierarchy can have many effects on network structure and dynamics [18, 3, 2, 6, 5, 109] and understanding how it is arises it vital for understanding complex systems. The hierarchy and directionality we use specifically describes a layered flow hierarchy, where edges point upwards a specified distance on the one dimensional axis, which differs from some ideas of flow hierarchy where it is not important how far up the direction the edges point.

Trophic Analysis

Trophic Analysis is a method which allows the study of linear hierarchy and global directionality in directed networks [8]. It was originally conceived as a tool for networks science in [5] where it was proposed as a solution to "May's paradox" [31] in ecosystems. However this original definition was constrained so that a network required nodes of zero in-degree and that these nodes were always at the bottom of the hierarchy. An improved version of Trophic Analysis which removed this constraint was proposed by MacKay et al. [8], which is the definition we use in this work. Trophic Analysis is composed of two parts, the local measure of where individual nodes sit in the hierarchy known as *trophic level*, and the global quantity, *trophic incoherence*, which measures the global directionality of the network and how much the edges point in the same direction with respect to the hierarchy.

In this work we studied unweighted directed complex networks represented by the an $N \times N$ adjacency matrix with the following convention,

$$A_{ij} = \begin{cases} 1 & \text{if there exists an edge } i \to j \\ 0 & \text{otherwise} \end{cases}. \tag{6.1}$$

Trophic Analysis can simply extend to the weighted case [8] but here we present the unweighted case for simplicity. Trophic Analysis can be formulated as an optimisation problem where we want to select the optimal set of trophic levels for the nodes which minimises the trophic incoherence. The trophic incoherence, F, is defined as

$$F = \frac{\sum_{ij} A_{ij}(h_j - h_i - 1)^2}{\sum_{ij} A_{ij}}. \tag{6.2}$$

Equations 6.2 states that we wish to select trophic levels, h_i such that if there is an edge from node i to j then node j has trophic level, h_j, which is exactly one more than the trophic level of node i, with any deviations from this incurring penalties in the square of the deviation. Due to the structure of F it can be minimised by simply taking the derivative with respect to the trophic levels. This leads to the following linear equation for the vector of trophic levels

$$\Lambda h = v, \tag{6.3}$$

where v is the degree imbalance vector defined as $v_i = k_i^{\text{in}} - k_i^{\text{out}}$ and Λ is defined as

$$\Lambda = diag(u) - A - A^T, \tag{6.4}$$

with u being the vector of the sum of the in and out degrees of each node, $u_i = k_i^{\text{in}} + k_i^{\text{out}}$. As equation 6.3 is linear it can be solved relatively easily with a few caveats. The matrix Λ cannot be inverted as it always has a zero eigenvalue. This issue can be resolved by fixing the level for one of the nodes, [8], which can be done as equation 6.3 is invariant up to the addition of a constant vector to h, so the minimum value of h can be rescaled to any value. This relates to the fact F only depends on the difference between the levels of nodes. Where we refer to trophic incoherence, F, throughout this work we refer to equation 6.2 evaluated using the value of h which minimises it. We choose to work in the convention where the minimum trophic level is set to zero. Another approach which can be taken is to solve for h iteratively using techniques of sparse linear algebra.

When the trophic level vector h which minimises F is substituted into 6.2 it acts of a measure of how hierarchical the network is and it quantifies the global directionality of the edges. This minimum value of F is what we refer to as the incoherence of a network for the remainder of this work. This value is bound between 0 and 1 [8]. With $F = 0$ being attained when the network has a perfect hierarchy like a directed path where the levels are integers with steps of exactly $+1$ between nodes. While $F = 1$ when the network is balanced (i.e. the in-degree matches the out-degree for each node), so every node takes level $h_i = 0$ and there is no hierarchy. Real networks exhibit a wide spectrum of trophic incoherence. Some, like food-webs which have a clear ordering of the edges, have low values of F; while networks which have many reciprocal connections or cycles, like social networks or those with little structure like Erdős-Rényi random graphs, have a higher F. Trophic Incoherence is linked to other network structure features such as the spectral radius [6, 8], non-normality [18] or the emergence of a strongly connected component [2].

The method of Trophic Analysis is closely related to several other ranking methods, SpringRank [44] and a method for analysing 'circularity' [45] based on Helmholtz-Hodge decomposition. The method of [45] has been shown to be equivalent to Trophic Analysis [8] however with a different set of terminology. SpringRank [44] views the ranking problem as minimising the energy of network of directed springs and devises a very similar function to minimise as F, just with a different normalisation. However, some versions of SpringRank introduce a regularisation term to remove the invariance of the ranks to the addition of a constant vector and give the ranking equation a unique solution.

In [18, 8] it was proposed that there is a relationship between the non-normality of the adjacency matrix and trophic incoherence. This was shown by measuring the normality in [8, 20] and the pseudospectral radius, a property related to non-normality, in [3]. A matrix is normal if

$$AA^T = A^T A \tag{6.5}$$

and a non-normal matrix is one where the adjacency matrix does not commute with its transpose [160]. It can be quantified the extent to which a matrix does not commute with it's transpose. For a example, a network with very few reciprocal edges is much more non-normal than a network with many reciprocal connections with the extreme case being an undirected graph where every edge is both bidirectional and A is symmetric. This also shows why trophic incoherence and normality can be related, as the fraction of reciprocal edges and cycles also impacts the coherence and hierarchical structure of the network [20] (with some work on non-normal networks referring to these networks as flow hierarchical [166]).

The fact that a matrix is non-normal can play a role in the stability of the dynamics and the sensitivity of the spectra to perturbations [19, 160]. Matrix non-normality impacts many fields

[160] including condensed matter physics, acoustics, the behaviour of numerical methods and fluid mechanics [160, 237, 162, 163, 164]. Its importance as a framework to understand directed networks has also been highlighted in network science [165, 19, 38, 166, 167, 3, 168, 20] where it has been linked to the behaviour of dynamics and the stability of complex systems. In addition, non-normality has been shown to be a very common phenomenon [19, 18, 8, 165, 20] present in many systems. In this work we propose a fitness-based model which, by explaining the wide spectrum of trophic incoherence found in nature, also gives an explanation as to the ubiquity of non-normal networks. However, we also note that the relationship between non-normality and trophic incoherence proposed in [18, 8] is for a particular graph ensemble, although it fits well with real network data. As such there are examples of specific adjacency matrices where the relationship between trophic incoherence and matrix normality does not hold in the same way [20], particularly in the case of weighted networks. In [20] small example network structures (some weighted) where this is the case are demonstrated, however, a correlation between trophic and non-normality based measured of directionality is still observed in the real-data used in [20].

6.2.2 Preferential Attachment and Fitness Models

Preferential attachment is one of the main paradigms of network science and the scale-free property of networks has been of great interest to science since it was discovered, and it has been analysed and interpreted in various ways [286]. The discovery that preferential attachment based on degree can lead to scale-free networks was one of the great achievements of early network science [12], and much of the field has been built on this work. Soon afterwards, however, it was noted that nodes may not attach based on only the degree a node but also based on the fitness of a node [273]. We base our study of degree-based preferential attachment on the Directed Scale-Free Model (DSF) [287] which provides analytical expression for the power-law exponent in certain regimes in the directed case and highlights the impact of varying the ratio of incoming and outgoing edges to the newly added nodes.

Preferential attachment models can however have some caveats associated with them.

The initial conditions of the network can play a role and affect the equilibration time of the model [288] or the scale-free effect may also be hidden by finite size affects in real systems [289]. Additionally, node age can play a role in the dynamics of networks grown with degree-based preferential attachment as the oldest nodes are most likely to gain the highest degree as the system evolves [290]. This a natural place where fitness models can play a role as in many systems, such as citations networks. This is not realistic as the number of citations should decrease with the age of the work and the growth of the average number of citations should not depend on the time frame sampled [290]. As such there are various methods to modify preferential attachment to account for this such as adding a time varying fitness, an ageing fitness parameter or a factor based on the age difference of the nodes [290, 291, 292, 283]. Additionally, given a real network the parameters that generated it may not be known and there has been work on how the fitness and preferential attachment parameters can be inferred from network growth data [293, 294].

It has been shown [295] that fitness interaction based preferential attachment and fitness distributions can lead to scale-free networks in the case of symmetric interactions and undirected networks, which helps to explain the ubiquity of the scale-free phenomenon [296]. Network models using fitness interactions have been further studied in [297] with work on relating model properties to the degree distributions [298] and percolation in network models based on fitness interactions [299]. However, this work differs from the model we propose as we use a fitness offset to study the hierarchical nature of directed networks. Our model, in the case on only interactions based on degree, is most closely related to [287]. Fitness based preferential attachment models can also be used to model specific phenomena by coupling the evolution of the network to dynamics taking place in the network [300].

Fitness based models without degree-based preferential attachment are also commonly used in ecology, motivated by the concept of a niche axis [285]. However, it is also possible to make an attachment model which attaches based on the ratio of in and out degree [301] designed to model food webs where you want to attach to nodes with high prey and low predator numbers. Niche models have limitations and it has been proposed that a one dimensional niche axis does not capture ecosystem complexity [302]. Moreover, existing niche models fail to reproduce the trophic coherence of real food webs [5]. In this work, we use a one-dimensional fitness as we wish to study linear hierarchy, but fitness distributed in a different topological space could be an avenue of future work. In the study of social networks there is also a class of model called latent space models where nodes connect based on the distance between nodes in this space [303], which may be higher dimensional [304]. Our fitness space could be interpreted as latent space model with several modifications, such as the fact we use a growing network model with fixed edge number.

There has also been work on using degree-based preferential attachment based models and edge reciprocity to create networks of varying non-normality [19]. In [19] a model is introduced which uses Price's model [305] as a base, to which they add an extra step to control the non-normality. In this model of directed network formation, when new nodes are introduced they connect into the existing network using degree-based preferential attachment in such a way which would create a directed acyclic graph as nodes are ordered by arrival time. However, there is an additional parameter which tunes the probability for the edge added to be reciprocal. This can then tune the amount of hierarchy in the system by adding edges which break the ordering. In [20], Trophic Incoherence and non-normality were used to study the entropy production rate of various dynamics on networks and it was shown that this parameter could be linked to Trophic Incoherence found in the generated networks [20]. An extension of this model, with a modification to the placement probability of reciprocal edges based on the the inverse of the out-degree, was used to study the emergence of "leader" nodes (source/sink nodes depending on convention) [166] and their importance to dynamics in networks which are non-normal and hierarchical, where the position in the hierarchy is measured by steps from the "leader nodes".

Non-normality is also created in networks with preferential attachment in [38] where the impact on of non-normality and hierarchy on the behaviour of financial bubbles and meme stocks was studied. In this model, they start with several top nodes and then introduce nodes via preferential attachment in a similar way to [19, 166], but with the condition that probability for an edge to be reciprocal is a function of the trophic level of a node. This is explained by the observation that in a Reddit discussion forum users with more popular comments are less likely to reciprocally comment with a user replying to them [38]. However, this is not the case in all work on non-normal networks, since these can also be created by starting from a ring-like structure similar to that found in small-world network models and using edge weights to induce non-normality which does not involve preferential attachment, as in [267]. Other work growing network models with varying reciprocity includes [306], where a network growth model was studied where the likelihood to reciprocate edges varies with different groups of users in social networks, something which is observed in real-network data [306].

6.3 Fitness Difference Model

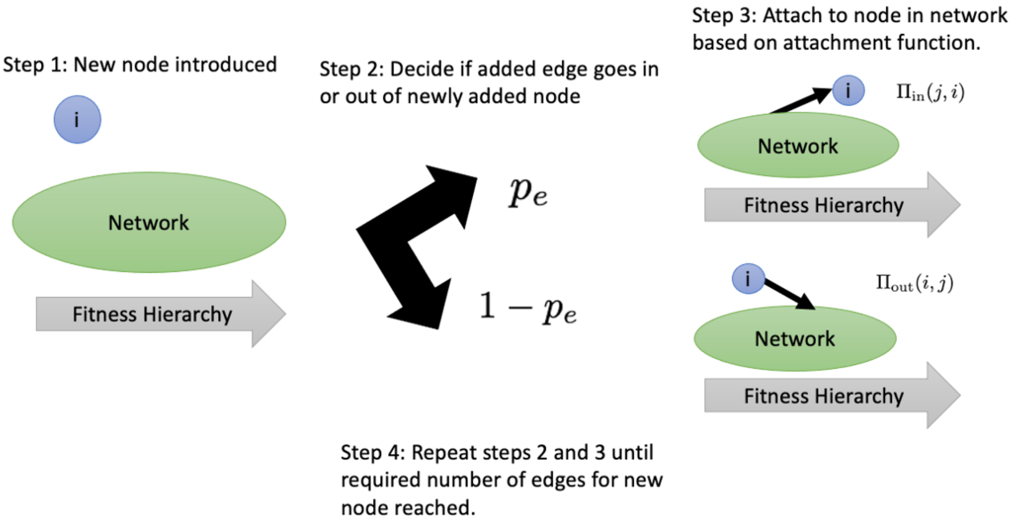


Figure 6.1: Schematic Diagram of the Generative model used.

In this work, we define a model of network formation where at each time step a new node is introduced and m edges are added to it, which connect to the other nodes dependant on the fitness interaction and degree of the nodes. We define a probability, p_e, which is the probability that the edge currently being added points to the new node (incoming edge). The edge points out of the new node (outgoing edge) with probability $1 - p_e$. We use the value

$p_e = 0.5$ unless otherwise stated so that the fraction of in and out edges are roughly similar most of the time and the distributions of in- and out- degrees are the same. This model is similar to the Directed Scale Free (DSF) model introduced in [287] apart from the fact that we allow in the number of in- and out- edges to randomly fluctuate and that we add the fitness interaction, as well as degree-based preferential attachment. Our model and the DSF model [287] differ from previous work on models which lead to directed scale free networks [307] in that the number of edges is known and fixed beforehand. We do not consider weighted networks in this work, but our model could be extended to the case of weighted networks by adding a mechanism to update the edge weights [308], which could be made a function of fitness interactions.

A general way to formulate connection probability based on fitness is that edges connect out of the new node i with probability

$$\Pi_{\text{out}}(i, j) = \frac{m(k_j^{\text{in}}) f(\beta_j, \beta_i) g_{\text{in}}(\beta_j)}{\sum_q m(k_q^{\text{in}}) f(\beta_q, \beta_i) g_{\text{in}}(\beta_q)}, \tag{6.6}$$

where β_j is the fitness parameter of node j which could be drawn from a fitness distribution or calculated from a property of the network; $m(\cdot)$ is a function which represents how degree is taken into account when selecting a node to attach; and $f(\beta_j, \beta_i)$ is a function which represents the interaction of the fitness of the two nodes which may attach and $g_{\text{in}}(\beta_j)$ is function representing the contribution of the fitness of node j to the probability of attachment. With a similar equation and set of generic functions for edges incoming to the new node,

$$\Pi_{\text{in}}(j, i) = \frac{m(k_j^{\text{out}}) f(\beta_i, \beta_j) g_{\text{out}}(\beta_j)}{\sum_q m(k_q^{\text{out}}) f(\beta_i, \beta_q) g_{\text{out}}(\beta_q)}. \tag{6.7}$$

The probabilities could also be defined as the probability of connections into/out of the network so in/out labels could be swapped [287]. Care must be taken with the convention choice here.

We simplify to focus on the combination of degree-based preferential attachment, parameterised by α, and functions $S(\cdot)$ of fitness differences (which may be offset to create hierarchy):

$$\Pi_{\text{out}}(i,j) = \frac{(k_j^{\text{in}})^{\alpha} S(\beta_j - \beta_i)}{\sum_q (k_q^{\text{in}})^{\alpha} S(\beta_q - \beta_i)}, \tag{6.8}$$

$$\Pi_{\text{in}}(j,i) = \frac{(k_j^{\text{out}})^{\alpha} S(\beta_i - \beta_j)}{\sum_q (k_q^{\text{out}})^{\alpha} S(\beta_i - \beta_q)}. \tag{6.9}$$

The function $S(\beta_i - \beta_j)$ can always be multiplied by a constant as this will not change the behaviour of the model, as it will cancel in equations 6.8 and 6.9. This allows $S(\beta_i - \beta_j)$ to be associated to a probability distribution if the normalisation constant is appropriately chosen. This is not necessary but this is something we will do later in this work in order to characterise the functions using standard features of probability distributions and to relate to the fitness differences observed in the generated networks.

Many fitness based ideas can be expressed as specific cases of this general model if the functions are selected to reproduce the desired behaviour. By setting the fitness function to one for all inputs we create a variant of the generalised BA preferential attachment to directed networks found in [287]. Directed variants of homophilly models, inspired by the scale-free homophillic model [275, 276], can be created by setting the offset parameter to zero and having the function S representing the preferences of interaction between discrete groups labelled by fitness,

$$S(\beta_i - \beta_j) = 1 - B_{ij}, \tag{6.10}$$

where B_{ij} takes a value between 0 and 1 depending on the interactions between groups. Models of this type have been used in the study of network inequality looking at the differing experiences of groups within the network [278, 279]. It is also possible to produce variants of homophilly models based on an exponentially decaying function to connect with fitness difference [280], which have been used to study the spread of opinion on network constructed with homophilly. This can be done be choosing

$$S(\beta_j - \beta_i) = \exp\left(-c|\beta_j - \beta_i|\right), \tag{6.11}$$

where β_j is node fitness and then c is a non-negative control parameter. Our model can also link to the concepts used in the study of citation networks. By choosing the fitness of a node to represent time of publication we can create a model very similar in concept to those used in citation network analysis [284] by choosing a function which decays with the time between the publication of the papers

$$S(\beta_j - \beta_i) = (t_j - t_i)^{-d}. \tag{6.12}$$

Here we need to place extra restrictions on the model so that t_j is always greater than t_i for two connected nodes and we preserve causality.

An offset could quite naturally be included in this fitness function as it can be difficult to cite a paper which is published very close to that date when your own is published. However, most of the models used in the literature based on the interaction between the fitness of nodes do not use an offset parameter, with exception being ecology. In ecology, it has been assumed that organisms have a niche profile [309]. This mean that they consume species at a certain fitness (approximated by body size) below their own level. For example, this could be when $S(\beta_j - \beta_i)$ is a Gaussian in the fitness differences. This is

$$S(\beta_j - \beta_i) \propto \exp\left[-\frac{1}{2}\left(\frac{\beta_j - \beta_i - \mu_f}{\sigma_f}\right)^2\right], \tag{6.13}$$

which is very similar to the one used to model the niche width in ecology in the influential paper where it was introduced [285].

In this work, we assume the fitness of each node is uniformly distributed between 0 and 10 but there is no reason why this restriction has to be in place and any range will work if the parameters are modified accordingly. Node fitness could be distributed according to an exponential, Gaussian or any other physically relevant distribution if that better reflects the system being represented. A non-uniform distribution could be used to modify the degree distribution, to modify the size of the community structures, to create variations in the edge density across the fitness scale or to represent the time distribution of events. It has been shown that using log-normally distributed fitness and a simpler attachment function based only on fitness can lead to power-law degree distributions [274], which is an example of the range of possibility that could be induced by varied fitness distributions. As such we expect a variety of complex effects could be observed by mixing various attachment functions with non-trivial fitness distributions.

6.3.1 Fitness Functions Used

Many possible functions could be chosen to represent the interaction between the fitness parameters of the nodes. In general, we need functions which are defined for positive and negative fitness differences. However, in order to induce hierarchy and for simplicity we choose functions that can be normalised to standard unimodal distributions and for mathematical convenience have a well defined mean and standard deviation, apart from in some specific cases which we use as examples. Any normalisation will cancel in the computation of the edge addition probabilities, equations 6.8 and 6.9. However, we give the form normalised to a probability density function associated with the functions where it is useful to show that the input fitness function can reflect the empirically measured distribution of fitness differences; and so that we can use the standard analytical expressions for mean, μ, and standard deviation, σ, of the distributions.

The simplest function we use is a function which represents a Gaussian distribution

$$S(\beta_j - \beta_i) = \frac{1}{\sqrt{2\pi\sigma_f^2}} \exp\left[-\frac{1}{2}\left(\frac{\beta_j - \beta_i - \mu_f}{\sigma_f}\right)^2\right], \tag{6.14}$$

where the mean $\mu = \mu_f$ and standard deviation $\sigma = \sigma_f$.

We also introduce the Laplace distribution, which has a more pronounced peak than a Gaussian but decays more slowly (wider, longer tails)

$$S(\beta_j - \beta_i) = \frac{1}{2b} \exp\left[-\left|\frac{\beta_j - \beta_i - \mu_f}{b}\right|\right], \tag{6.15}$$

where the mean $\mu = \mu_f$ and standard deviation $\sigma = \sqrt{2}b$.

The Laplace and Gaussian distributions can also be encompassed by the generalised normal distribution, which allows the exponent to be varied and distributions of different shapes to be created. When the exponent ν is very large the distribution tends to a top-hat shape,

$$S(\beta_j - \beta_i) = \frac{\nu}{2b\Gamma(\frac{1}{\nu})} \exp\left[-\left|\frac{\beta_j - \beta_i - \mu_f}{b}\right|^{\nu}\right], \tag{6.16}$$

where the mean $\mu = \mu_f$ and standard deviation $\sigma = b\sqrt{\frac{\Gamma(\frac{3}{\nu})}{\Gamma(\frac{1}{\nu})}}$. With $\Gamma(x)$ being the standard gamma function of x.

We also include distributions which can be skewed such as the Gumbel distribution that can used to model extreme values such as the maximum of a sample (the form used here),

$$S(\beta_j - \beta_i) = \frac{1}{b} \exp\left[-\left(\frac{\beta_j - \beta_i - \mu_f}{b} + \exp\left(-\frac{\beta_j - \beta_i - \mu_f}{b}\right)\right)\right], \tag{6.17}$$

where the mean $\mu = \mu_f + b\gamma_{\mathrm{E}}$ with γ_{E} being the Euler–Mascheroni constant and the standard deviation $\sigma = \frac{\pi b}{\sqrt{6}}$.

We further include the exponentially modified Gaussian distribution which reflects the distribution of the sum of normally and exponentially distributed random variables and can be skewed. This distribution is given by

$$S(\beta_j - \beta_i) = \frac{\lambda}{2} \exp\left[-\frac{\lambda}{2}\left(-2(\beta_j - \beta_i) + \lambda\sigma_e^2 + 2\mu_f\right)\right] \operatorname{erfc}\left[\frac{-(\beta_j - \beta_i) + \lambda\sigma_e^2 + \mu_f}{\sqrt{2}\sigma_e}\right], \tag{6.18}$$

where the mean $\mu = \mu_f + \frac{1}{\lambda}$ and standard deviation $\sigma = \sqrt{\sigma_e^2 + \frac{1}{\lambda^2}}$.

We also introduce several fitness functions, equations 6.19, 6.20 and 6.21, which do not have a single peak and do not lead to the same kind of hierarchical structure which we use when studying the distribution of trophic levels with fitness, section 6.4.5. Firstly, we introduce the hyperbolic tangent function of the fitness differences which plateaus to a constant value for large positive fitness differences,

$$S(\beta_j - \beta_i) = C_1 \left(\tanh \left(\frac{\beta_j - \beta_i - a}{T_1} \right) + 1 \right), \tag{6.19}$$

where C_1 is an appropriate normalisation constant found by integrating over the fitness range and T_1 is a parameter which sets how sharp the transition in the hyperbolic tangent function is with fitness difference.

We additionally include a fitness function where edges try to maximise the absolute value of the fitness difference

$$S(\beta_j - \beta_i) = C_2 \left| \frac{\beta_j - \beta_i}{T_2} \right|, \tag{6.20}$$

where C_2 is an appropriate normalisation constant found by integrating over the fitness range and T_2 is a scaling parameter to set the growth of the penalty.

Finally, we have a fitness interaction which is uniform which does not create any structure based on fitness.

$$S(\beta_j - \beta_i) = \text{constant}, \tag{6.21}$$

where $constant$ can be chosen as the inverse of the span of the fitness range if fitness normalisation is required.

6.4 Results

6.4.1 Degree Distributions

Firstly, we study how the addition of the hierarchy affects the degree distribution of the networks compared to the preferential attachment without the imposition of hierarchy. This is shown in figure 6.2. We plot the probability and cumulative degree distribution for networks with $\alpha = 1$ and a Gaussian fitness function of various standard deviations and compare to degree-based preferential attachment alone where the fitness function is constant. We choose $\alpha = 1$ so we can plot our results against the analytical power law for the Directed

Scale-Free (DSF) model [287] which our model is very similar to. This model generalises the BA model to generate directed scale-free networks with fixed number of nodes and edges as well as control of the number of in and out edges added with each new node. The degree exponents for this model are a function of the ratio of in and out edges added. The mean-field degree distribution in this model can be calculated by taking the continuous approximation so that the evolution of the node degree [287] can be written as a set of differential equations, given by

$$\frac{dk_j^{\text{in}}}{dt} = m_{\text{in}} \frac{k_j^{\text{in}}}{\sum_q k_q^{\text{in}}}, \tag{6.22}$$

$$\frac{dk_j^{\text{out}}}{dt} = m_{\text{out}} \frac{k_j^{\text{out}}}{\sum_q k_q^{\text{out}}}. \tag{6.23}$$

Which leads to degree probability distributions which can be approximated as [287]

$$\begin{aligned} p(k^{\text{in}}) &\sim (1 + \frac{m_{\text{in}}}{m_{\text{out}}}) m_{\text{in}}^{(1+\frac{m_{\text{in}}}{m_{\text{out}}})} (k^{\text{in}})^{-(2+\frac{m_{\text{in}}}{m_{\text{out}}})}, \\ p(k^{\text{in}}) &\sim (k^{\text{in}})^{-\gamma^{\text{in}}}, \end{aligned} \tag{6.24}$$

where the in-degree exponent $\gamma^{\text{in}} = 2 + \frac{m_{\text{in}}}{m_{\text{out}}}$ and

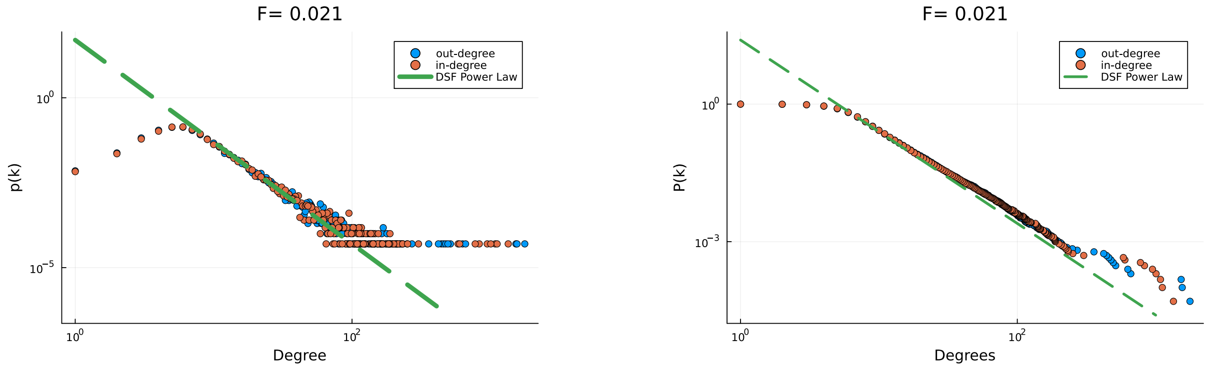
$$\begin{aligned} p(k^{\text{out}}) &\sim (1 + \frac{m_{\text{out}}}{m_{\text{in}}}) m_{\text{out}}^{(1+\frac{m_{\text{out}}}{m_{\text{in}}})} (k^{\text{out}})^{-(2+\frac{m_{\text{out}}}{m_{\text{in}}})} \\ p(k^{\text{out}}) &\sim (k^{\text{out}})^{-\gamma^{\text{out}}} \end{aligned} \tag{6.25}$$

where the out-degree exponent $\gamma^{\text{out}} = 2 + \frac{m_{\text{out}}}{m_{\text{in}}}$, following the notation convention of [287].

In the case where the in and out degree of the added nodes are the same the exponent reduces to the same value as in an undirected BA network, $\gamma^{\text{out}} = \gamma^{\text{in}} = 3$, and the power law is the same for both in and out degree. This is the regime that we work in and the power-law that we plot as we set the probability of an incoming or outgoing edge to be equal.

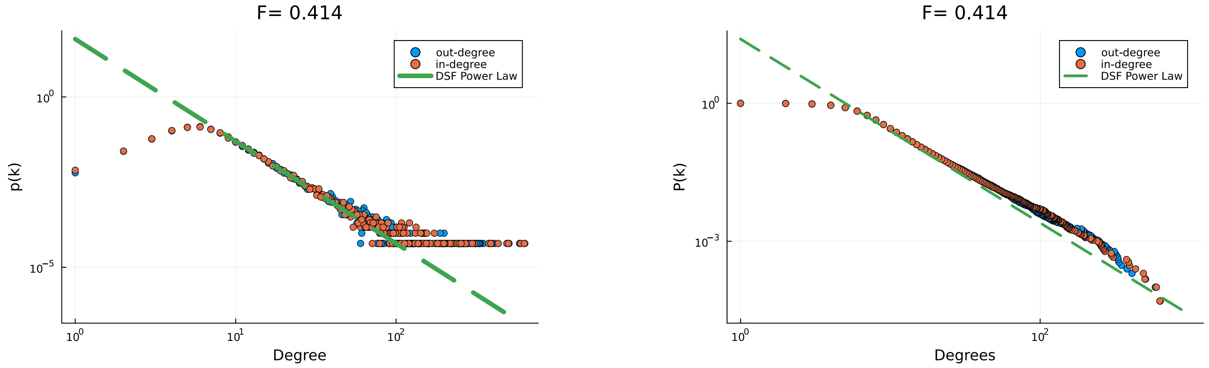
The main difference between our model and the DSF model, apart from the imposition of a fitness function, [287] is that we do not fix the number of in and out edges added to the new nodes and instead add incoming or outgoing with a prescribed probability. So in the equation for the power-law we replace the number of in and out edges added with the expected value of their ratio. This is simply an approximation which works well enough when we add $m = 10$ edges to each node but may fail when the number of edges added is lower or the edge type probability is imbalanced, so there are relatively larger fluctuations about this ratio.

Despite the addition of the hierarchy, at standard deviations small enough to induce hierarchy of the fitness functions, the power-law from the DSF model is quite well reproduced, figure 6.2, in a similar way to when we only have degree-based preferential attachment and no fitness, figures 6.2e and 6.2f. This makes sense as imposing the fitness hierarchy does not change which nodes grow in popularity due to the preferential attachment, it merely restricts the range of nodes which can be connected to it by splitting the network into different fitness regions. This may lead to finite size affects being more pronounced, particularly in the case of very strict fitness functions as the effective network seen by a node is reduced in size even if the same power-law behaviour happens in that subset. An analytical argument of why the hierarchical fitness functions have little impact of the power-law behaviour is given in the next section, section 6.4.1. There is some difference in the behaviour of the tails of the power-laws between the networks of stronger hierarchy. This may be due to fitness edge affects which we explore further in section 6.4.1. When the hierarchy is very strict nodes at the very top of the hierarchy have no other nodes above them to which a connection is preferred, so will have very low out-degree and while connections from below are not penalised by the fitness function leading to high degree imbalance. A very similar effect occurs at the bottom of the fitness hierarchy with the sharp edge of the fitness distribution limiting the range of connections available.



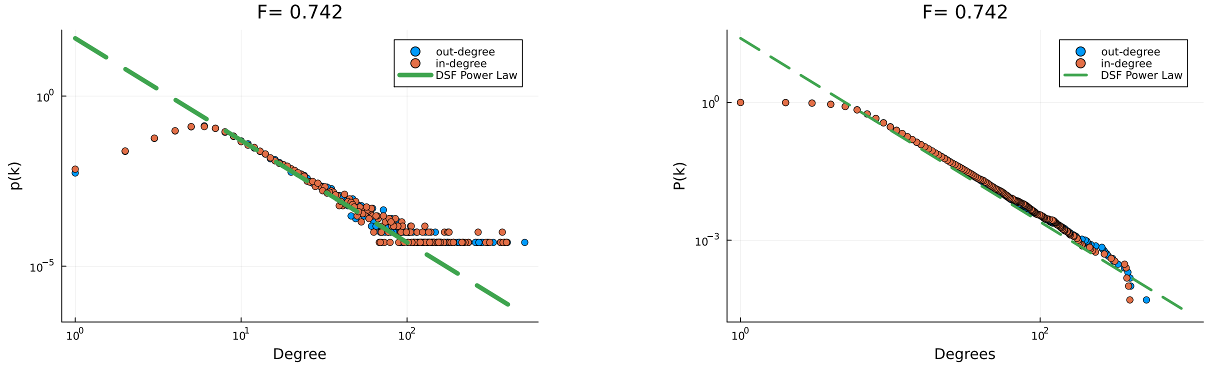
(a) Degree Probability Distribution Functions. Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 0.1$.

(b) Degree Cumulative Distributions. Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 0.1$.



(c) Degree Probability Distributions. Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 1$.

(d) Degree Cumulative Distributions. Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 1$.



(e) Degree Probability Distributions. Preferential Attachment only. $S(\beta_j - \beta_i) = 1$

(f) Degree Cumulative Distributions. Preferential Attachment Only. $S(\beta_j - \beta_i) = 1$.

Figure 6.2: Degree distributions of networks with Fitness Functions and Preferential Attachment. $N = 20000$, $m = 10$, $\alpha = 1$. Seed graph is a path of length $m = 10$. Power-law for derived from DSF model [287] in the case of equal probability of an edge being incoming or outgoing to a new node, equations 6.24 and 6.25.

The numerical tests in figure 6.2 demonstrates that fitness hierarchy can coexist with a scale-free degree distribution, which makes sense as these phenomena are both known to be features of real networks.

Mean-Field Analysis of Degree Distribution

We now conduct mean-field analysis to justify why the impact of the fitness function on the formation of the power-law degree distribution is small by showing the mean-field calculation approximately reduces to the same equations as found in the DSF model [287]. In the numerical case, we used finite sized networks and a finite span of fitness values where it worked well, however in order to conduct the mean-field analysis we need to make several assumptions regarding large networks sizes and range of fitness values which we detail below. This difference means that the effects highlighted by the mean-field may exist outside the regime of parameters where it can be conveniently calculated.

By taking a continuous approximation for the degree evolution of our model, as network size tends to infinity, we can write a mean-field expression for evolution of the in-degree of a node with fitness β_j as

$$\frac{dk^{\text{in}}_{j,\beta_j}}{dt} = m_{\text{in}} \frac{k^{\text{in}}_j \int_{\beta_{\text{min}}}^{\beta_{\text{max}}} d\beta' \; S(\beta_j - \beta' - a)\rho(\beta')}{\sum_q k^{\text{in}}_q \int_{\beta_{\text{min}}}^{\beta_{\text{max}}} d\beta'' \; S(\beta_q - \beta'' - a)\rho(\beta'')}, \tag{6.26}$$

where $\rho(\beta)$ is the fitness density distribution. In this case, we write the fitness interaction function as $S(\beta_j - \beta' - a)$ to explicitly highlight the fact that we are using a non-zero fitness offset, given by the parameter a, which can be accounted for in the change of variable required. We also select a fitness function which can be normalised to a probability distribution so that it can be quantified via the standard deviation. A similar expression and for which the following arguments hold identically can be constructed for the out-degree.

The expression given, equation 6.26, is very similar to the expression which arises in the DSF model [287] apart form the addition of the integral involving the fitness. This may explain why in some cases the DSF power-law exponent approximately holds when a hierarchical ordering function is imposed. In the case of uniform fitness, $\rho(\beta)$ is a constant for all β. So this cancels leading to the expression,

$$\frac{dk^{\text{in}}_{j,\beta_j}}{dt} = m_{\text{in}} \frac{k^{\text{in}}_j \int_{\beta_{\text{min}}}^{\beta_{\text{max}}} d\beta' \; S(\beta_j - \beta' - a)}{\sum_q k^{\text{in}}_q \int_{\beta_{\text{min}}}^{\beta_{\text{max}}} d\beta'' \; S(\beta_q - \beta'' - a)}, \tag{6.27}$$

which differs from the DSF equation only by the integrals of the form

$$I(\beta_j) = \int_{\beta_{\text{min}}}^{\beta_{\text{max}}} d\beta' \; S(\beta_j - \beta' - a). \tag{6.28}$$

This integral can be analysed by making the change of variables $x = \beta_j - \beta' - a$, leading to

$$I = -\int_{x_1}^{x_2} dx \; S(x), \tag{6.29}$$

where $x_1 = \beta_j - \beta_{\text{min}} - a$ and $x_2 = \beta_j - \beta_{\text{max}} - a$. x_1 and x_2 can be rewritten as multiples of the standard deviation of the normalised function $S(x)$ and the limits reversed to absorb the sign. This leads to

$$I = \int_{\theta_2 \sigma_f}^{\theta_1 \sigma_f} dx \; S(x), \tag{6.30}$$

where

$$\theta_1 = \frac{\beta_j - \beta_{\text{min}} - a}{\sigma_f} \tag{6.31}$$

and

$$\theta_2 = \frac{\beta_j - \beta_{\text{max}} - a}{\sigma_f}. \tag{6.32}$$

Due to the steup, θ_2 is always negative as $\beta_j \leq \beta_{\text{max}}$.

We wish to argue that the integral, I, is approximately a constant for the majority of values of β_j and hence will approximately cancel in the mean-field equations leading to the same set of equations as in the DSF model with fitness [287]. This can be done by considering the assumptions of the continuum approximation and the properties of the function, $S(x)$. One of the assumptions of mean-field theory is that the network size, $N >> 0$, as $t >> 0$ as such we can also assume that the network has many layers and there is a large number of trophic levels induced by a large range of uniformly distributed fitness values and that $\frac{\beta_{\text{max}}}{\sigma_f} >> 1$. We also assume that the mean-field theory only covers nodes in the bulk of the fitness range, nodes which are far from either the maximum or the minimum of the fitness. This means we can assume that $\theta_1 >> 1$ and $|\theta_2| >> 1$. As the fitness is uniformly distributed, the fraction of nodes not in this regime is the number of nodes within $2l$ standard deviations of the fitness endpoints at either β_{max} or β_{min}. This is given by

$$2l \frac{\sigma_f}{\beta_{\text{max}} - \beta_{\text{min}}} = 2l \frac{\frac{\sigma_f}{\beta_{\text{max}}}}{1 - \frac{\beta_{\text{min}}}{\beta_{\text{max}}}}, \tag{6.33}$$

where l is a finite positive parameter setting how close to the end points are nodes to be neglected. When the fitness span and number of levels becomes very large, $\frac{\beta_{\text{max}}}{\sigma_f} >> 1$, this quantity becomes very small and the contribution from these nodes to the degree distribution can be neglected. An alternative view of eq. (6.33) is that its LHS contains a ratio of the fitness spread (expressed as the standard deviation σ_f of the normalised fitness interaction function $S(x)$) and the β-value spread $\beta_{\text{max}} - \beta_{\text{min}}$. If the spread of β values is much larger than the fitness spread, the term (and hence the fraction of nodes not in the regime needed for our approximation) becomes negligible.

If the function $S(x)$ is uni-modal with finite mean and the function decays quickly enough for values away from the mean then as long as the fitness satisfies the constraints that $\theta_1 >> 1$ and $|\theta_2| >> 1$, the integral will give approximately the same value for any fitness β_j. This is due to the fact that the tails of the distribution contribute very little to the value of the integral as the fitness function goes to zero for large differences and we obtain the main contribution from the peak of $S(x)$. Meaning that the integral can be cancelled in the mean field equations and we return to the DSF case. This assumption works well if $S(x)$ is a Gaussian function for example, as the contributions to the integral become small after a few standard deviations. Some of examples of simple unnormalised unimodal functions, $\tilde{S}(x)$, are given in table 6.1, where it can be seen that the integral value quickly approaches a constant when the values of the limits move far away from zero.

$\tilde{S}(x)$	$\int_{\theta_2\sigma_f}^{\theta_1\sigma_f} dx\ \tilde{S}(x)$	$\int_{-\infty}^{+\infty} dx\ \tilde{S}(x)$
$e^{-\lvert x\rvert}$	$2 - e^{(-\theta_1\sigma_f)} - e^{(-\lvert\theta_2\rvert\sigma_f)}$	2
e^{-x^2}	$\frac{\sqrt{\pi}}{2}(\mathrm{erf}\,(\theta_1\sigma_f) + \mathrm{erf}\,(\lvert\theta_2\rvert\sigma_f))$	$\sqrt{\pi}$
$\frac{1}{1+x^2}$	$\tan^{-1}(\theta_1\sigma_f) + \tan^{-1}(\lvert\theta_2\rvert\sigma_f)$	π

Table 6.1: Examples of functions that when chosen as $\tilde{S}(x)$ satisfy the required property of converging to an approximate constant when integrated with the upper limit much greater than zero and the lower limit much less than zero.

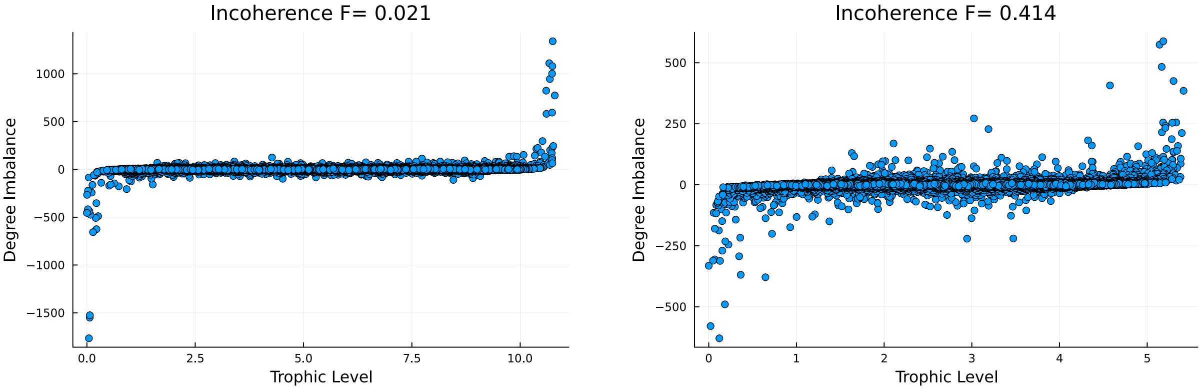
However, this can also be more rigorously quantified for a more general class of functions. If we assume that function $S(x)$ is normalised such that it represents a probability density function which gives the probability to observe a fitness difference, x, we can treat the analysis of the tails of the integral, I, as the probability of observing large fitness differences. In figure 6.9 we show that for a variety of fitness functions the empirically measured fitness difference distribution is well represented by the probability density, when $\alpha = 0$. $S(x)$ can be normalised by any constant as it cancels in the edge addition probability as previously stated. We can then use Chebyshev's inequality, which states that for a random variable X with mean μ_1 and standard deviation σ_1, the probability of making an observation κ times the standard deviation away from the mean is

$$\Pr(|X - \mu_1| \geq \kappa\sigma_1) \leq \frac{1}{\kappa^2}. \tag{6.34}$$

This means fitness differences which are many standard deviations away from the mean are very unlikely to be observed. If we assume the that integral, I, represents the integral over the probability density function of observing certain fitness differences then modification of the integral limits θ_1 and θ_2 when they are very large in absolute value is unlikely to impact the value of the integral and hence I can be said to be approximately constant for any fitness, β_j, far from the edge of the fitness range. An identical calculation can be done for the out-degree simply with the function arguments and labelling of the degrees swapped. This argument is simply an approximation to explain what we observe in the numerical data in particular we do not expect this argument to hold when the distribution of fitness is non-uniform, for model parameters resulting in $S(x)$ not having the properties detailed above or for all possible values of α. Even though this arguments is rough and approximate, as in the previous section, it makes sense that imposing a hierarchy in this way should not affect the degree distribution, aside form imposing finite size affects. Indeed, we do not impose any restriction on which nodes grow in degree - instead of a single large network the system is now organised through a linearly ordered fitness space where edges only connect within a specific region but degree-based preferential attachment can occur as normal in that range.

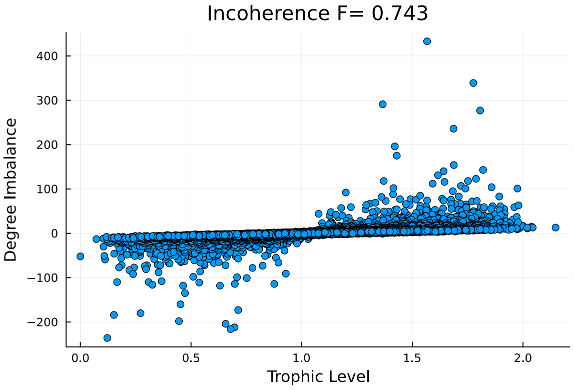
Degree Imbalance and Trophic Level

It has been observed previously that in some situations trophic level correlates with degree imbalance [2, 3] hence we investigated the relationship between trophic level and degree imbalance when the networks are constructed with degree-based preferential attachment and fitness interactions. When the network is highly coherent (i.e. the hierarchy is very strong), figure 6.3a, the trophic level is not strongly related to the degree imbalance apart from at the ends of the hierarchy. This is due to the uniform fitness and that position in the hierarchy is strongly enforced by fitness. This shows that this kind of hierarchy is distinct from hierarchy induced by degree imbalance. Nodes at the bottom of the hierarchy have no nodes below them which favourably connect into them so they have a higher out-degree than their in-degree while the nodes at the top of the hierarchy have nowhere to connect out to meaning they have high degree imbalance. This highlights a key feature of systems which display linear hierarchy - if the system is finite there will be “ends” which may have different behaviour compared to a node which lies in the middle of the hierarchy. This also puts a caveat on the results of the degree distribution mean-field and numerical tests as the analysis fails to take into account this inhomogeneity in the system. When the network becomes more incoherent, figure 6.3b, the trophic level starts to correlate more with the imbalance but we still observe the same behaviour in the tails with less sharp peaks. As the network becomes maximally incoherent for this variant of the model, standard deviation is much larger than the mean, shown in figure 6.3c, we see less sharp changes at the end of the distribution as the hierarchy is less strict and a there is a large regime where the degree imbalance and trophic level are correlated. This is a similar result to what would be found if the fitness function was set to a constant and the hierarchical ordering, as measured by trophic level, was not determined by fitness and a result of the degree imbalance in the system only. In the high standard deviation regime, figure 6.3c, we also see the spread of the trophic levels shrink and they do not span the full fitness regime as when the hierarchy was strongly enforced by fitness, figure 6.3a.



(a) Degree Imbalance (in-degree minus out-degree) with Trophic Level. Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 0.1$.

(b) Degree Imbalance (in-degree minus out-degree) with Trophic Level. Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 1$.



(c) Degree Imbalance (in-degree minus out-degree) with Trophic Level. Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 1000$.

Figure 6.3: Degree Imbalance with Trophic Level of evolving networks with Fitness Functions and Preferential Attachment. $N = 20000$, $m = 10$. Seed graph is a path of length $m = 10$. Degree-based preferential attachment exponent set to one.

6.4.2 Degree-based Preferential Attachment and Trophic Incoherence

Many networks can grow by simple degree-based preferential attachment and we investigate how this mechanism relates to the varied trophic incoherence we observe in these systems. This may also explain why we observe so many coherent and non-normal networks in nature [165, 18, 8, 19, 20]. We do this by investigating the impact of the preferential attachment exponent and the fraction of edges which go in and out of the newly added nodes on the trophic coherence.

Attachment Exponent and Trophic Incoherence

Firstly, we look at the relationship between the Trophic Incoherence and the preferential attachment exponent α to investigate if preferential attachment alone can act as an explanation for the appearance of coherent networks in nature. We take the fitness function $S(\beta_j - \beta_i) = 1$ and then use attachment functions of the form

$$\Pi_{\text{out}}(i, j) \propto (k_j^{\text{in}})^{\alpha}, \tag{6.35}$$

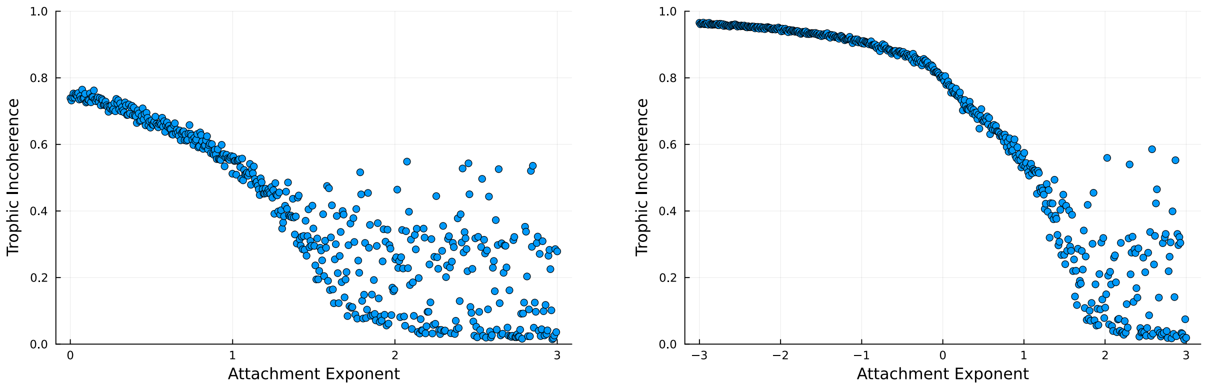
$$\Pi_{\text{in}}(j, i) \propto (k_j^{\text{out}})^{\alpha}. \tag{6.36}$$

We also study the functions

$$\Pi_{\text{out}}(i, j) \propto (k_j^{\text{in}} + \delta)^{\alpha}, \tag{6.37}$$

$$\Pi_{\text{in}}(j, i) \propto (k_j^{\text{out}} + \delta)^{\alpha}, \tag{6.38}$$

where δ is a small positive constant to allow the study of negative alpha.



(a) Trophic Incoherence and Preferential Attachment for positive exponent, α, which is evenly spaced between 0 and 3.

(b) Trophic Incoherence and degree-based attachment with a small positive constant added to the degree, $\delta = 10^{-6}$, to allow negative exponents. α is evenly spaced between -3 and 3.

Figure 6.4: Variation of Trophic Incoherence with preferential attachment exponent in standard preferential attachment and with a negative exponent. 500 networks were generated for each case with 1000 nodes and 5 edges added with each additional node. The seed network is a path of length 5. Edges have a probability 0.5 of being added as an incoming or outgoing edge of the newly added node.

Preferential attachment with varying exponent is shown in figure 6.4a. When $\alpha = 1$, this leads to networks which are more coherent than an ER random graph but not as coherent as a network which has a strong hierarchical ordering. In this case, much of the coherence comes from the large degree imbalance caused by the scale-free uncorrelated in and out degree distributions. This is expected as trophic level [3] and SpringRank [128] have both been shown to be related to degree imbalance in some cases. As well as the fact that in the extreme case a star graph with all edges pointing either in or outwards is completely coherent with $F = 0$.

When $\alpha = 0$, we get the same kind of incoherence you see in random graphs as there is no preference for where the edges are added and no strong degree imbalance created. When we send α to be larger than one we reach the regime of super-linear preferential attachment where a few nodes connect to all other nodes. This leads to lots of variability and lack of control of the incoherence as the network structure is dominated by a few nodes. Extremely high degree imbalance leads to very coherent networks as would be expected tending towards the extreme of a star graph.

This figure shows that preferential attachment can partially explain the emergence of coherent networks in nature. Preferential attachment with intermediate values of α leads to networks which are more coherent than random graphs explaining some of the networks we see in nature. Super-linear preferential attachment can lead to very coherent networks however it does this while enforcing degree distributions which are dominated by only a few nodes which is not the case in many real-world systems. It also comes with the additional constraint that the coherence is difficult to control in this regime.

In the case where we use the small constant to send α less than zero, figure 6.4b, when α is negative the networks become more incoherent than uniform random attachment as edges are added to the nodes with the smallest degree which leads to a network with more balanced in and out degrees leading to higher incoherence. This is again expected as we tend closer to the extreme case where the in degree equals the out degree for each vertex and we have a network where $F = 1$ [8].

In [104] it was also found that the behaviour of hierarchy, as measured by Reaching Centrality, could also be affected by the changing the degree distribution of scale-free networks with the size of the out-components of nodes, and Global Reaching Centrality being affected as the exponent varied.

Ratio of In and Out Edges Added and Trophic Incoherence

Trophic Incoherence and hence all the effects that depend on it [3, 2, 8, 34, 6, 5] can also be modified by varying the fraction of edges which attach into or out of the nodes as they are introduced, this is shown in figure 6.5. This figure shows that when edges strictly go only into or out of the newly added nodes this leads to networks which are very coherent at the ordering of the node addition implicitly leads to a directionality as nodes only connect to nodes which are younger or older (by node age). This explains why citation networks are very coherent as you can only cite papers which exist as the time of writing, creating a time ordering in the network. Figure 6.5 also shows how this process is symmetric about the point where the in/out probabilities are equal and this is where the networks are maximally coherent for the model as edges are equally likely to connect in any direction in terms of node age. In the cases where the fraction of edges added is between these extreme points we see that the network has coherence determined by the size of the majority and minority direction split. This behaviour can be interpreted by thinking about the age of nodes as a fitness parameter where new nodes connect a certain fraction of their edges from new nodes to older or from older nodes to the most recently added.

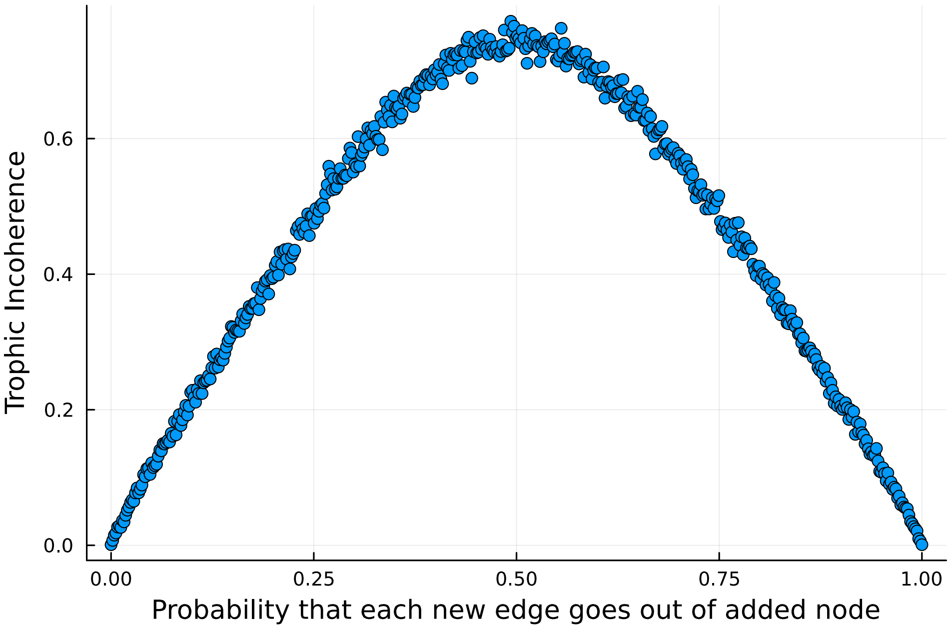
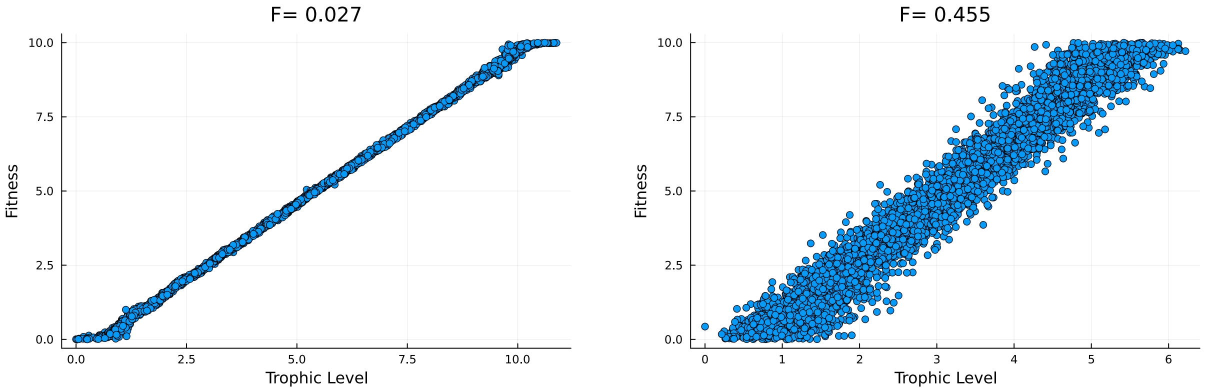


Figure 6.5: Variation of Trophic Incoherence with probability of new edges being attached into and out of new nodes. 500 networks were generated with 1000 nodes and 10 edges added with each additional node. The seed network is a path of length 10. Degree-based preferential attachment parameter, $\alpha = 1$.

The combination of the effects highlighted may partially explain the range of trophic incoherence we see in real networks [8, 2]. Preferential attachment can lead to more coherence than observed in random graphs due to the stronger degree imbalance which may be present in some systems. While if new nodes join the network and have an unequal probability to create incoming and outgoing edges this can lead to networks which are very coherent. For example, in citation networks where the age of the node acts as an ordering, limiting the range of connectivity structures available. The result in figure 6.5 agrees with the results found in the models of network non-normality [19, 166, 38, 20] where varying the probability of reciprocal edges and hence varying the probability that edges go against the ordering induced by the node arrival time modifies the non-normality and trophic incoherence.

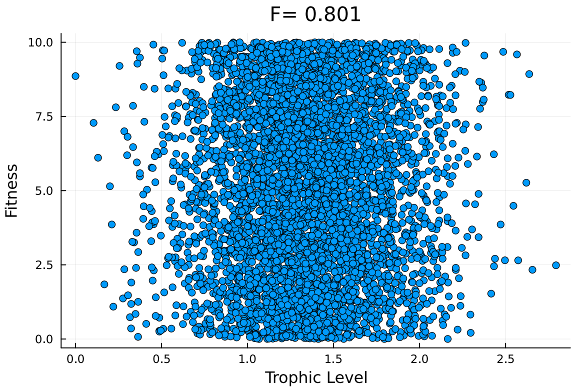
6.4.3 Correlation of Fitness and Trophic Level

We also investigate how the trophic level of node can be used to approximate the value of the fitness of a node in networks generated with only fitness interactions with varying success depending on the trophic incoherence of the network, figure 6.6. This is a useful feature as it highlights how the structural quantity trophic level relates to the node level fitness which was involved in the network generation.



(a) Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 0.1$ Pearson Correlation Coefficient approximately 1.0.

(b) Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 1$. Pearson Correlation Coefficient approximately 0.978.

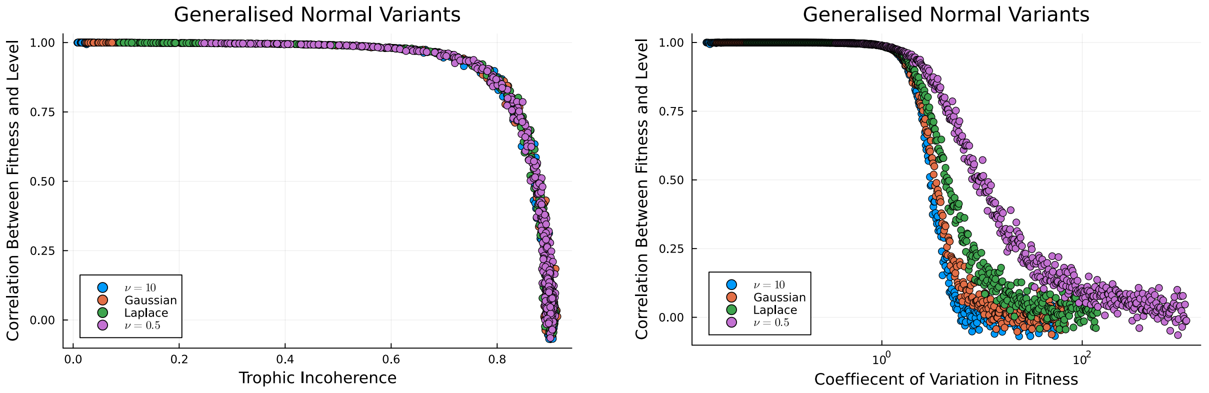


(c) Gaussian Function. Equation 6.14 $\mu_f = 1$, $\sigma_f = 1000$. Pearson Correlation Coefficient approximately 0.006.

Figure 6.6: N = 5000, Fitness is uniformly distributed between 0 and 10. Nodes are added with 5 new edges. Seed graph is a path of length 5. Degree-based preferential attachment exponent set to zero.

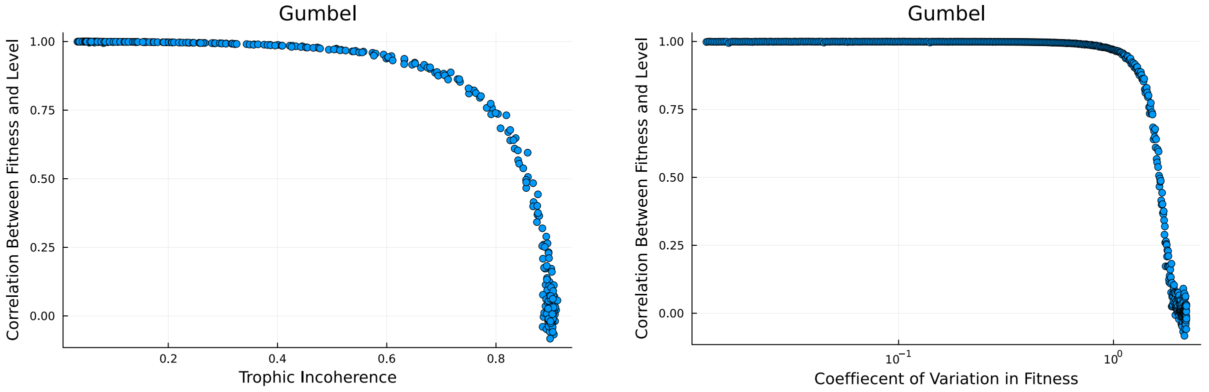
In figure 6.6a, we see a clear correlation between fitness and trophic level for the Gaussian networks of very low F showing that in this regime the level can be a good proxy for fitness. This is still maintained in figure 6.6b even as F reaches more intermediate values however with a broader spread of values at the same trophic level. This is due to that fact that as the network becomes more incoherent the range of trophic levels decreases and the maximum trophic level is now lower than the maximum of the fitness showing the hierarchy is less pronounced. This effect continues into the very high F regime, figure 6.6c, where there is no correlation between level and fitness and trophic level is no longer a useful parameter to predict the fitness and is likely be correlated with the degree imbalance [3, 128]. The level distribution again shrinks to spanning a very small range highlighting again that the impact of hierarchical structure is not very strong in this network. As the standard deviation is very large relative to the mean of the fitness differences, the behaviour in figure 6.6c is similar to the behaviour that would be found if the fitness function was a constant and the hierarchy was determined by the degree imbalance as in an ER random graph.

We investigate this phenomena in more detail by measuring the Pearson correlation coefficient between fitness and level for different fitness functions in networks of varying trophic incoherence, which we also plot in terms of the coefficient of variation (standard deviation divided by the mean) of the normalised fitness functions, in figure 6.7. The correlation is very good for coherent networks, which have clear hierarchical structure, but breaks down as the networks become more incoherent. A similar trend can also be seen in the coefficient of variation, figure 6.7. When this coefficient of variation is small, the standard deviation is less than the mean, there is good correlation between node fitness and trophic level. However, when the coefficient of variation is large, the mean is smaller than the standard deviation, the relationship between fitness and level breaks down. For all the functions we have roughly three regimes. When the coefficient of variation is much less than 1 then level acts as a good proxy for fitness as the correlation coefficient is near one. When the correlation coefficient approximately on the order of 1, then we are in an intermediate regime where it is some relationship between fitness and level but the correlation is weaker and then when the coefficient of variation is much larger than 1 the correlation between level and fitness breaks down. This gives a guide as to how the underlying properties of the fitness distribution shape the usefulness of trophic analysis as a network analysis tool.



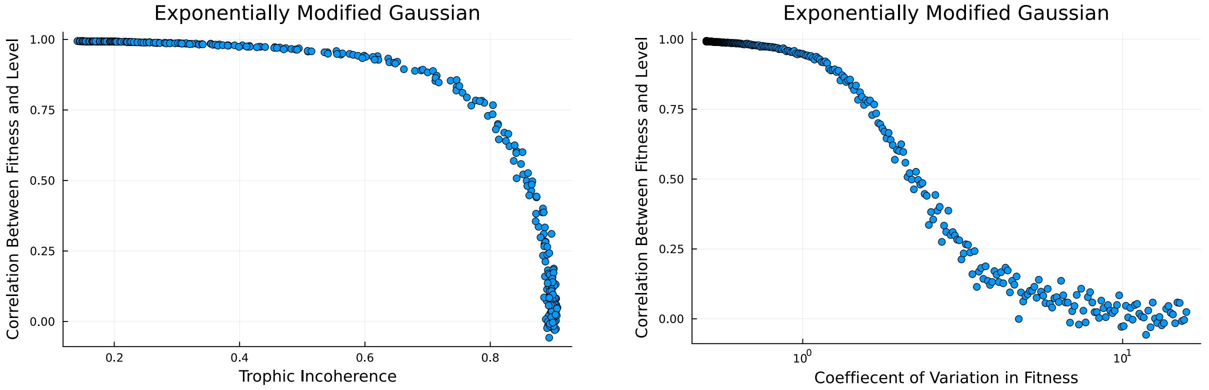
(a) Generalised Normal Variants. Equation 6.16 $\mu_f = 1$, Parameter b spaced from $10^{-1.5}$ to 10^2.

(b) Generalised Normal Variants.Equation 6.16 $\mu_f = 1$, Parameter b spaced from $10^{-1.5}$ to 10^2



(c) Gumbel. Equation 6.17 $\mu_f = 1$, Parameter b spaced between from 10^{-2} to 10^2.

(d) Gumbel. Equation 6.17 $\mu_f = 1$, Parameter b spaced between from 10^{-2} to 10^2.



(e) Exponentially Modified Gaussian. Equation 6.18 $\mu_f = 1$, $\lambda = 1$. Parameter σ_e, spaced between 10^{-2} to $10^{1.5}$.

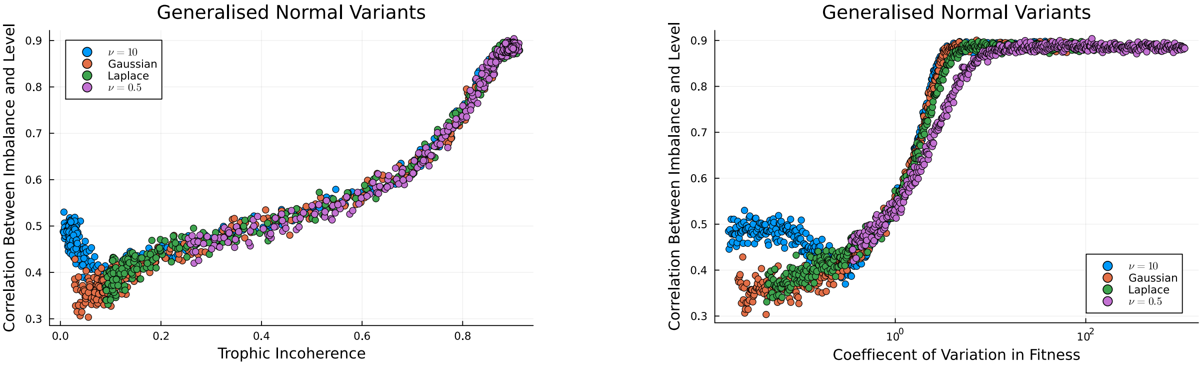
(f) Exponentially Modified Gaussian. Equation 6.18 $\mu_f = 1$, $\lambda = 1$. Parameter σ_e, spaced between 10^{-2} to $10^{1.5}$.

Figure 6.7: Correlation between trophic levels and fitness for different fitness functions with Trophic Incoherence and Coefficient of Variation. Networks are $N = 1000$ with a starting seed network which is a directed path of length 10. New nodes are added with 10 edges. 500 networks are generated for each case. Fitness is uniformly distributed between 0 and 10. Degree-based preferential attachment exponent set to zero.

The results in figure 6.7 extend the intuition found in [44] that calculated ranks in SpringRank are well correlated with the synthetic ranks. However, we extend it to edges which are created with non-Gaussian fitness difference functions, a growing network model with fixed edge number and relate the correlation to F which does not depend on knowing the parameters of the generative process and can be calculated directly from network structure.

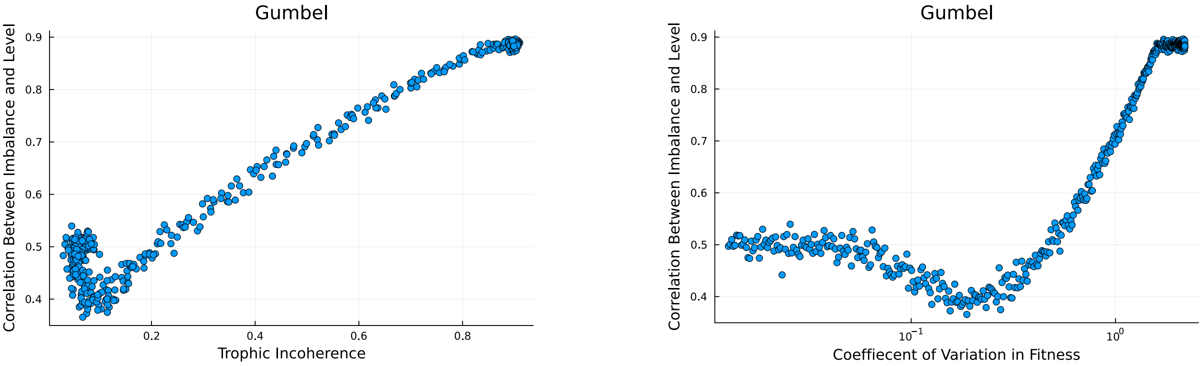
6.4.4 Degree Imbalance and Trophic Level Correlations

We also study the variation of the correlation between trophic level and degree imbalance with trophic incoherence and coefficient of variations of the fitness functions for networks generated with only fitness interactions. This allows us to understand the regimes in which trophic analysis gives information which is separate to information gained by looking at the degree imbalance and how trophic level relates to degree imbalance. This is shown in figure 6.8.



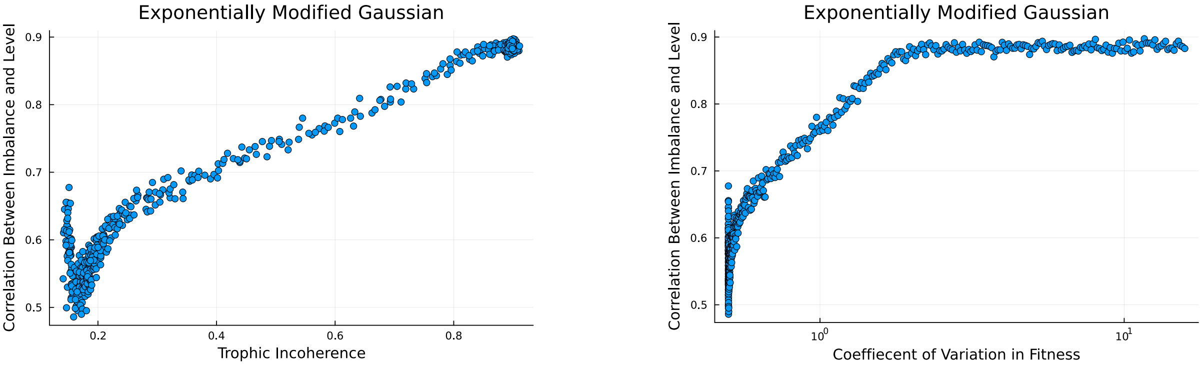
(a) Generalised Normal Variants. Equation 6.16 $\mu_f = 1$, Parameter b spaced from $10^{-1.5}$ to 10^2.

(b) Generalised Normal Variants.Equation 6.16 $\mu_f = 1$, Parameter b spaced from $10^{-1.5}$ to 10^2



(c) Gumbel. Equation 6.17 $\mu_f = 1$, Parameter b spaced between from 10^{-2} to 10^2.

(d) Gumbel. Equation 6.17 $\mu_f = 1$, Parameter b spaced between from 10^{-2} to 10^2.



(e) Exponentially Modified Gaussian. Equation 6.18 $\mu_f = 1$, $\lambda = 1$. Parameter σ_e, spaced between 10^{-2} to $10^{1.5}$.

(f) Exponentially Modified Gaussian. Equation 6.18 $\mu_f = 1$, $\lambda = 1$. Parameter σ_e, spaced between 10^{-2} to $10^{1.5}$.

Figure 6.8: Correlation between trophic levels and degree imbalance (in-degree minus out-degree) for different fitness functions with Trophic Incoherence and Coefficient of Variation. Networks are $N = 1000$ with a starting seed network which is a directed path of length 10. New nodes are added with 10 edges. 500 networks are generated for each case. Fitness is uniformly distributed between 0 and 10. Degree-based preferential attachment exponent set to zero.

In figure 6.8 we see that for all fitness functions used when the incoherence or coefficient of variation is very high, a regime where there is little correlation between fitness and level, we see a strong correlation between level and degree imbalance as this is the structural feature which trophic level picks out. When the trophic incoherence and coefficient of variation are low, a regime of high level fitness correlation, then the correlation between trophic level and degree imbalance is weaker. However, they are not completely uncorrelated. This makes sense as we expect nodes which sit at the ends of the fitness distribution, and have the highest and lowest trophic levels, to have degree imbalances related to their position caused by the sharp ends of the fitness hierarchy. As a result of there being no nodes above or below respectively which are preferred by the attachment function. There is however some non-monotonic behaviour in this regime where as the hierarchy becomes less strictly enforced the correlation decreases as the sharp edge effects are less impactful. There is some variability here between function choices depending how function behaves and how strictly it enforces hierarchy when the control parameter is reduced to very small values. The results in figure 6.8 again highlight how F is a useful tool to test if the hierarchy is likely to be impactful to a system and the effects that the ends of the fitness distribution can have on the behaviour of the system.

6.4.5 Trophic Level Differences Distributions

We also investigate the distribution of the trophic level and fitness differences for various fitness functions in order to understand if the measured fitness differences reflect the input fitness function and if the trophic level differences are reflective of the input fitness function.

This is shown in figure 6.9. For most of the fitness distributions the measured normalised fitness distribution is very similar to the probability density function implied by the fitness function. This is useful as it shows that using this generative method preserves the structure of the fitness function. The only cases where it fails are when the fitness function is a hyperbolic tangent or uniform, figures 6.9f and 6.9h, where the very large fitness differences are rare, as it is unlikely to pair the largest and smallest fitness together when randomly pairing nodes.

When networks are generated with a variety of non-Gaussian fitness distributions the trophic level difference distributions are all well approximated by a Gaussian probability distribution with parameters which can be directly calculated from F, shown in figure 6.9. This is done using results from [8] that the trophic incoherence can be written in terms of the average level difference, μ, and the standard deviation of the level difference, σ, as

$$F = \sigma^2 + \mu^2 - 2\mu + 1. \tag{6.39}$$

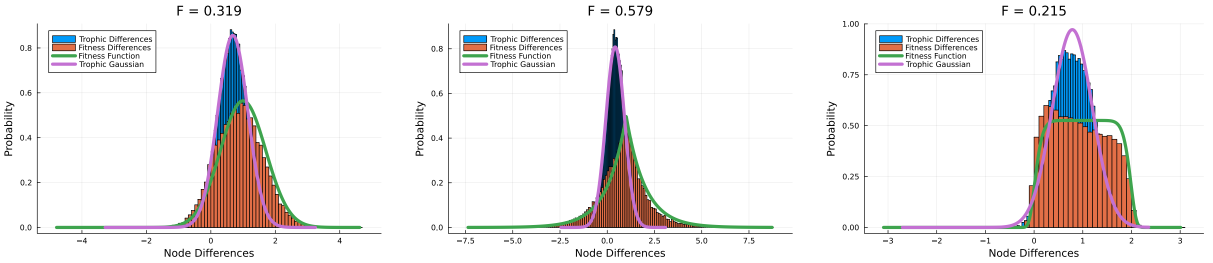
This is further analysed in [8] where it is shown that the expression for the average level difference can be written as

$$\mu = 1 - F, \tag{6.40}$$

which allows the standard deviation to be written as

$$\sigma = \sqrt{F}\sqrt{1 - F}. \tag{6.41}$$

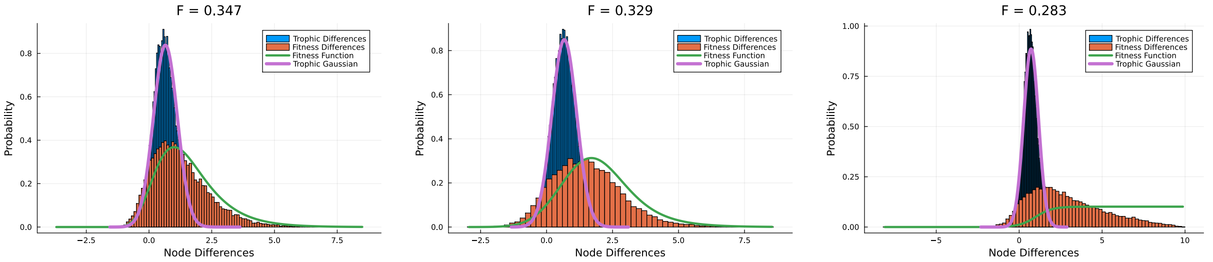
The good agreement between the level distribution and analytical Gaussian in figure 6.9 backs up arguments and assumptions in previous work [2, 6] that we expect the distribution of trophic level differences to be approximately Gaussian in real networks. However, it also demonstrates a limitation of the trophic analysis approach as information about the fitness distribution is lost in the calculation of the trophic level as all inputs are mapped to an approximate Gaussian.



(a) Gaussian. Equation 6.14 $\mu_f = 1, \sigma_f = \frac{1}{\sqrt{2}}$.

(b) Laplace. Equation 6.15 $\mu_f = 1, b = 1$

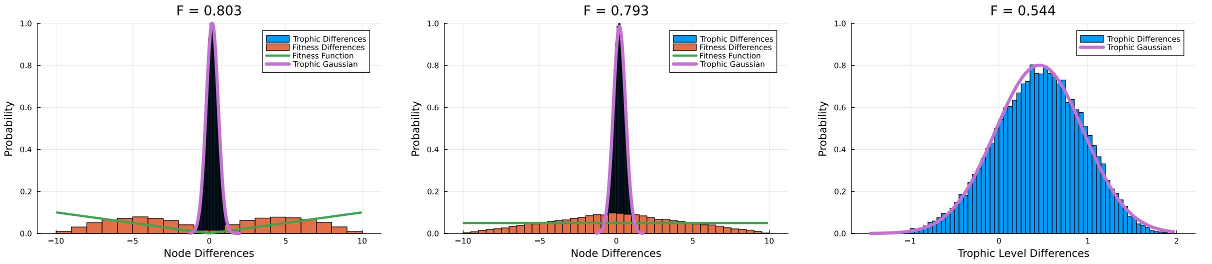
(c) Generalised Normal $\nu = 10$.Equation 6.16 $\mu_f = 1, b = 1, \nu = 10$.



(d) Gumbel. Equation 6.17 $\mu_f = 1, b = 1$.

(e) Exponentially Modified Gaussian. Equation 6.18 $\mu_f = 1, \sigma_e = 1, \lambda = 1$.

(f) Tanh. Equation 6.19 $a = 1, T_1 = 1$.



(g) Absolute Value. Equation 6.20 $T_2 = 1$.

(h) Uniform. Equation 6.21

(i) Scale Free. $\alpha = 1$. Constant fitness function.

Figure 6.9: Distributions of trophic level and fitness differences for different fitness functions, parameters and functions given in individual figure captions. Networks have $N = 5000$ nodes. Fitness is uniformly distributed between 0 and 10. Nodes are added with 5 new edges. Seed graph is a path of length 5. Degree-based preferential attachment exponent set to zero.

Potential Explanations for Gaussian Trophic Level Difference Distributions

The Gaussian distribution is one which arises in many different settings and as such there are many ways for it to appear, so there are several possible explanations for the behaviour of the trophic difference distribution. One possible argument is linked to the minimisation of the squared penalty function and its Bayesian interpretation as it is well known that minimising a squared loss function can be thought of as a Gaussian likelihood and that L_2 regularisation can be interpreted as a zero mean Gaussian prior.

Consider a set of networks with a given set of N nodes and a prescribed number of L edges. Each network can be uniquely characterised by the corresponding $N \times N$ adjacency matrix A of L non-zero elements, $A_{ij} = 1$ if and only if there is an edge from node i to node j, otherwise $A_{ij} = 0$. Given a vector Δh of trophic level differences over the L edges, where Δh_e is the trophic level of the destination node of an edge, e, minus the trophic level of the source node of the edge. The trophic level differences distribution yields a likelihood over possible edge topologies connecting the N nodes, $P(A|\Delta h)$. Given a prior $P(\Delta h)$ over possible trophic level difference vectors, if we are supplied with a particular network with edge structure A, the nodes will be expected to have trophic level differences Δh with posterior probability,

$$P(\Delta h|A) = \frac{P(A|\Delta h)P(\Delta h)}{P(A)}. \tag{6.42}$$

Let us adopt a Gaussian likelihood model stating a preference for the trophic level difference of two nodes connected by an edge to differ by 1 (trophic level of the child larger than that of the parent), modulated by a ‘tolerance’ scale parameter σ_Δ (standard deviation)

$$P(A|\Delta h) \propto \prod_{e=1}^{L} \exp\left[-\frac{1}{2}\left(\frac{\Delta h_e - 1}{\sigma_\Delta}\right)^2\right], \tag{6.43}$$

where each each label e represent as an edge which goes from node i to j.

Under the assumption of flat prior over trophic level difference vectors Δh, the maximum a-posteriori estimate of the level differences, given the network A, is equivalent to minimising trophic incoherence, equation 6.2, since the log-likelihood (up to constant terms) reads

$$\begin{aligned} \ln P(\Delta h|A) &= -\frac{1}{2\sigma_\Delta^2}\sum_{e=1}^{L}(\Delta h_e - 1)^2 + \text{constant} && (6.44)\\ &= -\frac{1}{2\sigma_\Delta^2}\sum_{ij} A_{ij}(h_j - h_i - 1)^2 + \text{constant}, && (6.45) \end{aligned}$$

using the fact that the adjacency matrix in this case is unweighted and it can be used to indicate the existence of an edge. By this construction, we show that the minimising of trophic incoherence can be interpreted as maximising the likelihood under the assumption of the Gaussian likelihood model for edge-based trophic differences, equation 6.43. Under the set of assumptions made, this may explain why we observe trophic level difference distrubtions which are well approximated by Gaussian distributions in this work and in real networks [2].

However, it is possible to come up with different generative models which lead to similar minimisation problem as a result of difference choices of likelihood functions and priors. For example, in [44] it was shown that using a Poisson likelihood model, with the mean being a Gaussian function of the level differences multiplied by a sparsity control parameter, a different generative model for levels (ranks) and no fixed edge number after certain assumptions (and discarding limiting terms) maximisation of the likelihood of this model is equivalent to minimising the SpringRank Hamiltonian [44]. It is also argued in [44] that the ranks in SpringRank are distributed as a multivariate Gaussian with variable noise levels. Additionally, it can be shown that minimising trophic incoherence can be related to the likelihood of another random graph model [53] which allows the relative importance of linear and periodic hierarchy to be studied. It was also shown in the study of node ranking in [80] that the assumption that each the rank of a node represents an average performance which is normally distributed leads to the probability of a set of ‘results’. These are a set of edge directions determined by competition between nodes imposed on an undirected graph of interactions, and can be written as a likelihood function which is a Gaussian of the rank differences where the maximisation leads to a minimisation of the energy of a network of directed springs [80], which is similar in concept to SpringRank or Trophic Analysis.

Of course in real systems, if the differences in trophic level of nodes represents a real physical quantity they could be well approximated as a Gaussian for various reason like the central limit theorem, approximation of a binomial or the fact that the Gaussian distribution is the maximum entropy distribution with specified mean and variance. However, what we show here is that due to the form of F its minimisation can be linked to a Gaussian likelihood model which may partially explain why the analytical Gaussian derived from trophic incoherence fits the level difference distrubtion so well.

Figure 6.9 and the link of trophic analysis to Gaussian distributions shows that trophic analysis may be less useful in situations where it is known the fitness differences are not distributed as a Gaussian. As a result, it may be useful to cast the ranking problem in terms of a different optimisation function which corresponds to a different specifically chosen likelihood maximisation problem and create a generalised version of trophic analysis which is something that we leave for future work.

The trophic level difference distribution also has some particular properties derived in [8]. The mean, μ, is equal to $\mu = 1 - F$, which means the mean is always between 0 and 1 and the variance, σ^2 can be written as $\sigma^2 = \mu(1 - \mu)$ which is very similar to the relationship between the mean and the variance of a Bernoulli distribution. This also means the variance is maximised when the mean level difference is 0.5. This makes sense as when the network is fully coherent, $F = 0$ all the level differences are $+1$ and then when the network is completely incoherent, $F = 1$ every node has exactly the same trophic level so the difference across all edges is 0 and the variance is zero.

6.4.6 Relating Trophic Incoherence to Fitness Difference Distribution

We would like to be able to relate the trophic incoherence of the network, which is a structural property, to the external parameters which make up the fitness function, which decides if nodes are connected based on an external node fitness. If the fitness distribution is ºvery tightly distributed around the mean and all the edges point upwards in fitness then it is likely that the network will be very coherent. The standard deviation and the mean of the trophic level difference distribution can both be expressed in terms of F [8]. However, we cannot directly match each of these structural properties to the fitness difference distribution as the fitness distribution can be any scale, while the mean level difference is bound between 0 and 1 [8]. However, we can use the coefficient of variation, ratio of standard deviation and the mean, to provide a measure of how coherent both the distribution of level differences is and how coherent the distribution of fitness differences is. The coefficient of variation gives a measure of the size of the standard deviation relative to the mean and acts as an alternative measure of coherence: when the network has $F = 0$ the coefficient of variation is zero as the mean is one and standard deviations is zero, and when $F = 1$ the coefficient of variation becomes infinite as the mean level difference is zero. The key thing about the coefficient of variation is that it is a dimensionless quantity so it allows comparison between the trophic level properties and the fitness properties of real-world systems which could be off any scale and have fitness steps of any size.

By assuming the coefficient of variation of the trophic level distribution matches the coefficient of variation of the distribution of fitness differences,

$$\frac{\sigma}{\mu} \approx \frac{\sigma_f}{\mu_f}, \tag{6.46}$$

we can derive an expression for the Trophic Incoherence in terms of parameters of the fitness distribution only. Where this approximation is made on the basis that even though the trophic level difference distribution is on a different scale to the fitness difference distribution the variability of the fitness difference distribution should affect the measured trophic incoherence and the coefficient of variation gives us a way to compare the distributions using a dimensionless parameter.

Using results from [8] that the average trophic level difference is

$$\mu = 1 - F \tag{6.47}$$

and the standard deviation is given by

$$\sigma = \sqrt{F}\sqrt{1 - F}. \tag{6.48}$$

This leads to the expression

$$\sqrt{\frac{F}{1 - F}} = \frac{\sigma_f}{\mu_f}, \tag{6.49}$$

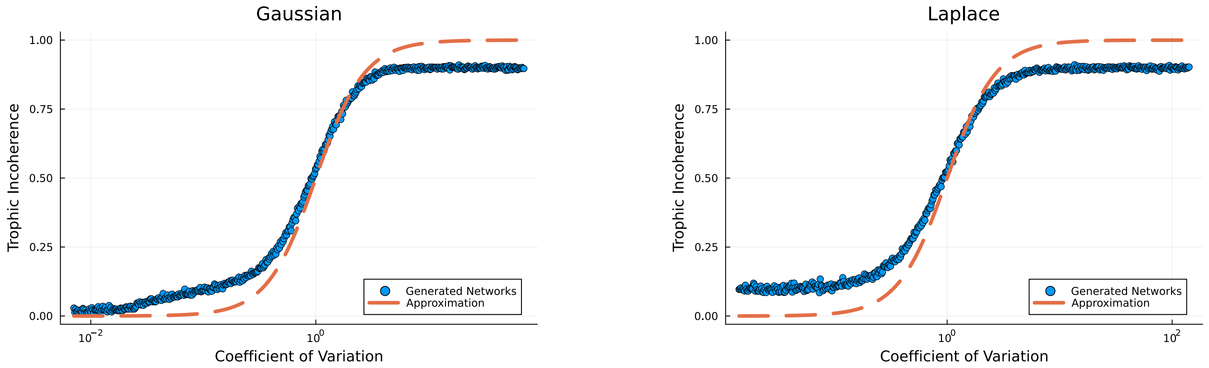
which can be rearranged to give the result

$$F = \frac{\sigma_f^2}{\sigma_f^2 + \mu_f^2}. \tag{6.50}$$

This can also can also be expressed directly in terms of the coefficient of variation as

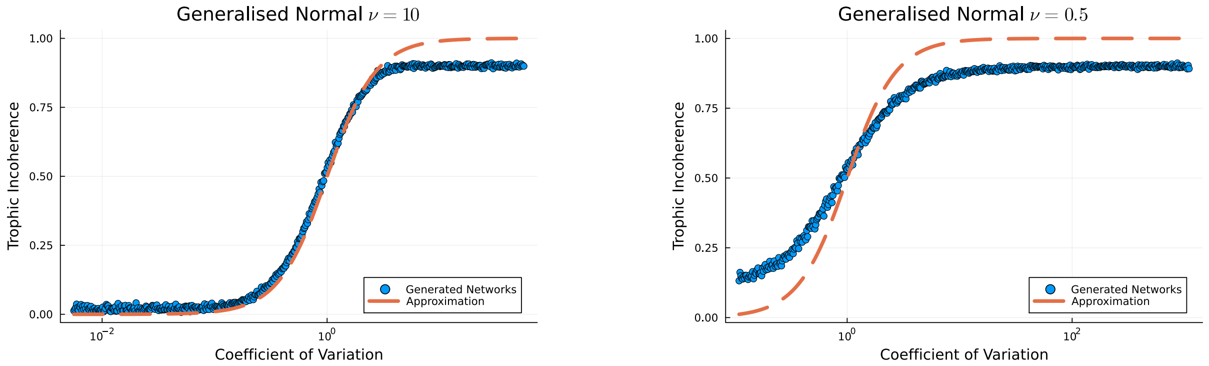
$$F = \frac{(\frac{\sigma_f}{\mu_f})^2}{(\frac{\sigma_f}{\mu_f})^2 + 1}. \tag{6.51}$$

This is a useful prediction as it allows the incoherence to be expressed as function of the fitness distribution which is an external property imposed on the network and not a structural property like incoherence. The accuracy of this prediction, equation 6.50, is shown in figure 6.10. This prediction works reasonably well, even for networks which are generated with a non-Gaussian fitness functions, which shows how trophic incoherence depends on how the tightly the network follows the defined fitness hierarchy. It fails slightly at very low incoherence as the specific functions and finite networks may not generate networks of extremely low coherence as predicted by the approximation and similarly at high incoherence, the generative model does not produce the balanced networks which correspond to maximally incoherent networks, instead producing variants of random graphs where the trophic incoherence plateaus below $F = 1$.



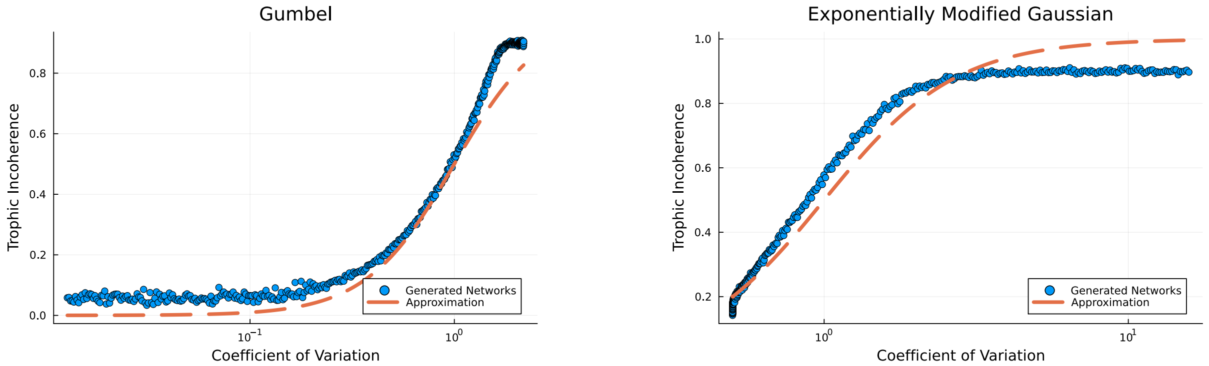
(a) Gaussian. Equation 6.14 $\mu_f = 1$, σ_f spaced $\frac{10^{-2}}{\sqrt{2}}$ and $\frac{10^{2}}{\sqrt{2}}$

(b) Laplace. Equation 6.15 $\mu_f = 1$. Parameter b spaced between from 10^{-2} to 10^{2}.



(c) Generalised Normal $\nu = 10$. Equation 6.16 $\mu_f = 1$, $\nu = 10$. Parameter b spaced between from 10^{-2} to 10^{2}.

(d) Generalised Normal $\nu = 0.5$.Equation 6.16 $\mu_f = 1$, $\nu = 0.5$. Parameter b spaced between from 10^{-2} to 10^{2}.



(e) Gumbel. Equation 6.17 $\mu_f = 1$, Parameter b spaced between from 10^{-2} to 10^{2}.

(f) Exponentially Modified Gaussian. Equation 6.18 $\mu_f = 1$, $\lambda = 1$. Parameter σ_e spaced between 10^{-2} to $10^{1.5}$.

Figure 6.10: Trophic incoherence and analytical approximation of trophic incoherence based on the mean and standard deviation of the fitness difference via equation 6.50. Each network has $N = 1000$ nodes. 10 edges are added with every new node with equal probability of being an in or out edge of the new node. Seed graph is a path of length 10. Fitness uniformly distributed between 0 and 10. Parameters and functions given in each sub-figure caption with the spacing of all varied parameters being logarithmic. Degree-based preferential attachment exponent set to zero.

The relationship between trophic incoherence and the coefficient of variation follows a sigmoid shaped curve when plotted on a logarithmic axis and can be thought of as three distinct regions. Firstly, the sigmoid shape of the curves when plotting on a logarithmic axis, figure 6.10 can be explained by equation 6.50 which can be reparameterised such that $(\frac{\sigma_f}{\mu_f}) = 10^x$. This leads to

$$F = \frac{1}{1 + 10^{-2x}}, \tag{6.52}$$

which is a sigmoid curve in log coefficient of variation in fitness. When the coefficient of variation of the network is much less than 1 we are in the region where we predict a very coherent network with clear hierarchy, when the coefficient of variation is much larger than 1 we expect the network to be very incoherent and there to be little hierarchy determined by fitness; and when the coefficient of variation is around the order of 1, we are in an intermediate regime where moderate incoherence is expected and there is some hierarchy and ordering but not as strict as in a very coherent network.

Moreover, the approximation also works for the more complicated functions like the Gumbel, figure 6.10e, and Exponentially Modified Gaussian 6.10f where the coefficient of variation tends to a constant as the standard deviation grows large in the case of Gumbel and to constant as the standard deviation becomes very small in the case of the exponentially modified Gaussian. This figure demonstrate how measuring the trophic incoherence can give you information about the parameters used to generate the network and information about the fitness distribution, even if the actual distribution information is lost when the trophic levels are calculated.

In this work, we have varied the coefficient of variation by modifying the standard deviation but an alternative approach could modify the mean and fix the standard deviation instead. However, care would need to taken with zero mean and it may be necessary to work with the inverse of the coefficient of variation. This could link to other work on Trophic Analysis where the trophic incoherence has been shown to equal to one minus the mean trophic level difference [8].

6.4.7 Interplay of Fitness Interactions and Degree-based Preferential Attachment

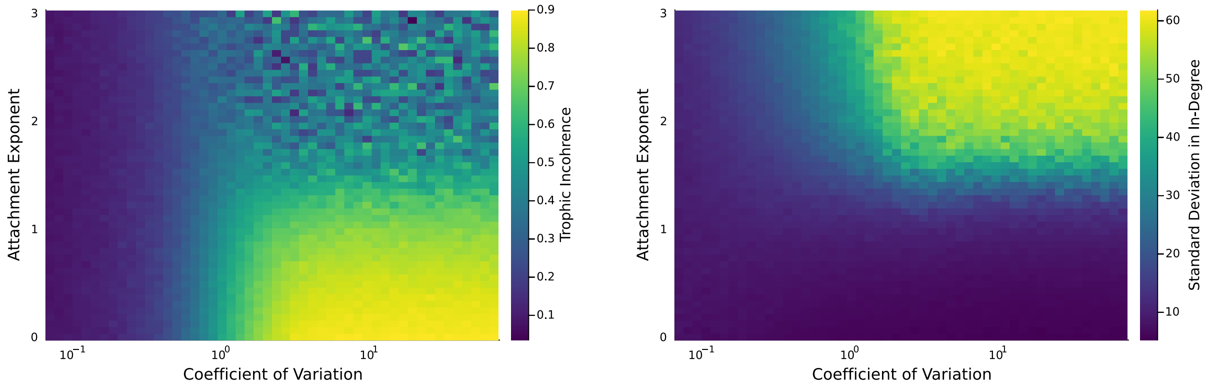
The final way we can explain the ubiquity of coherent networks in nature as well as understand the relationship between trophic level and fitness is to look at the interplay of degree-based preferential attachment and connection based on fitness hierarchy. This is done by using an addition probability which is formed by a Gaussian fitness interaction, of which we vary the standard deviation, that we multiply by degree-based preferential attachment, where we vary the attachment exponent.

We plot the changes in trophic incoherence and other network properties as networks are generated with varying exponent, α, and coefficient of variation of the Gaussian fitness function in figure 6.11. In figure 6.11a, we see that there are three distinct regimes. When the coefficient of variation of fitness is small the networks are very coherent as the hierarchy is strongly enforced by the fitness function. When the coefficient of variation of the fitness function is high we have two behaviours. A smooth regime, where the incoherence increases as α gets closer to 0 and a regime where α is greater than 1 and the preferential attachment reaches the super-linear regime. In this region, the networks become more coherent but the behaviour is much more variable as the networks are dominated by a few super-hubs. This can be understood by looking at figure 6.11b which shows the standard deviation of the in-degree distribution for the same sample of networks. The standard deviation in the degree distribution grows large when $\alpha > 1$ and the coefficient of variation of the fitness function is large. This is due to hubs with very large degree being formed by the strong degree-based preferential attachment and this not being restricted by a fitness function which limits the range of nodes which can be connected to. In figure 6.11c, we show how interplay of the degree-based preferential attachment and fitness functions affect the correlation coefficient of the trophic level and the fitness. The results show a similar trend to when the preferential attachments is fixed, figure 6.7. With the correlation being very strong when the coefficient of variation is low and network is coherent and the correlation being weak when the coefficient of variation is high and the network is incoherent. This shows that even with additional degree-based preferential attachment contribution that the trophic level can be taken as a good proxy for the network fitness, when the coefficient of variation of the fitness function is low. Figure 6.11c also demonstrates an interesting feature that the line separating the two regimes of high and low correlation between fitness and level is diagonal, as when the preferential attachment is weaker the correlation of fitness and level is maintained for fitness functions which are less strict, while when the preferential attachment exponent is higher the correlation is more quickly destroyed. A similar trend can also be seen if we take one of the quantities which is related to trophic incoherence such as matrix normality [8, 20] which is measured following the convention of [8], where normality, y, is measured by

$$y = \frac{\sum_j |\lambda_j|^2}{||A||_F^2}. \tag{6.53}$$

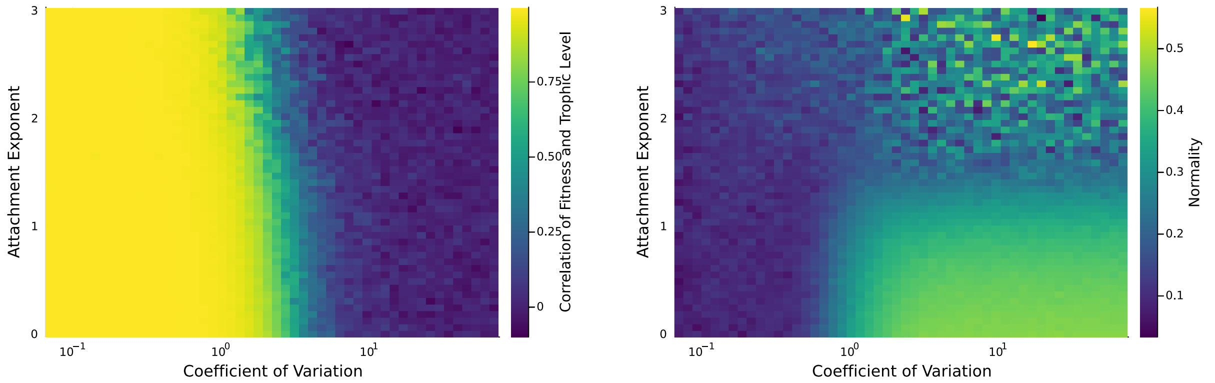
Here, λ_j are the eigenvalues of the adjacency matrix and $||A||_F$ is the Frobenius norm of the matrix A defined as $||A||_F = \sqrt{\sum_{ij} |A_{ij}|^2}$. The full justification and explanation of this measure are given in [8].

Figure 6.11d shows a similar trend in normality as 6.11a does for trophic incoherence. This fits with the close relationship between non-normality and trophic coherence described previously [18, 8].



(a) Trophic Incoherence

(b) Standard Deviation of In-Degree



(c) Correlation of Fitness and level

(d) Matrix Normality measured using convention in [8], equation 6.53.

Figure 6.11: Impact of varying coefficient of variation of a Gaussian fitness function and degree-based preferential attachment exponent on network properties. Each networks has 1000 nodes with 10 edges added with each new node with equal probability connecting in or out of the newly added node. The seed graph is a path of length 10. Fitness is uniformly distributed between zero and 10. We use a 50 by 50 grid of points with the preferential attachment evenly spaced between 0 and 3 and the fitness standard deviations logarithmically spaced between $\frac{10^{-1}}{\sqrt{2}}$ and $\frac{10^{2}}{\sqrt{2}}$. The mean fitness difference, $\mu_f = 1$, for all points.

The fact that a combination of these effects can lead to many different values of trophic coherence suggests and explanation for why we observe non-trivial trophic coherence in many real-world systems. It can also give us information about how the networks are formed as the prevalence of large degree imbalance and its association with the trophic level can be an indication as to whether the trophic coherence derives from an underlying fitness interaction or strong degree-based preferential attachment. Figure 6.11c also shows how trophic analysis can be useful as a tool to predict fitness variables as there is a good correlation between fitness and level in the low coefficient of variation regime even when the degree-based preferential attachment is strong.

6.4.8 Example Application to Historical Network of Ragusan Nobility

To highlight how our methods can be used to study real systems, we demonstrate with an example of a real network. The family tree of the nobility from the Republic of Ragusa from the 12th to the 16th century, data from [310] and converted using [311], with metadata which roughly corresponds to node fitness which we compare to the quantities found via trophic analysis. The Republic of Ragusa was a merchant republic located in Dubrovnik, Croatia and ruled by a number of noble merchant families. We construct a network containing 5,999 people and draw 9315 edges from parent to child and making no distinction between males and females in the network. We compute the trophic levels of the nodes in this network and compare with the birth dates of the nodes for which this is known (3065 individuals). This is shown in figure 6.12. Here we find a good correlation between the year in which someone was born and their trophic level. This is to be expected as the year you are born can only be a within a range after your patents birth, hence we expect trophic analysis of the network to detect this structure. The size of each trophic level roughly corresponds to generation of people which shows that trophic analysis is detecting some real features of the network. There are some issues in the correlation around the mid 14th century however there are several factors which could explain this. The structure of the nobility was changing between the 12th and 14th centuries and was established by stature in 1332 [310] with no new families accepted after this time. So the changing legal basis of who is included and recorded in the nobility is likely to explain the lack of correlation at this time. This is also the time of the ‘Black Death’ plague in Europe so we expect a loss of population to occur at that time.

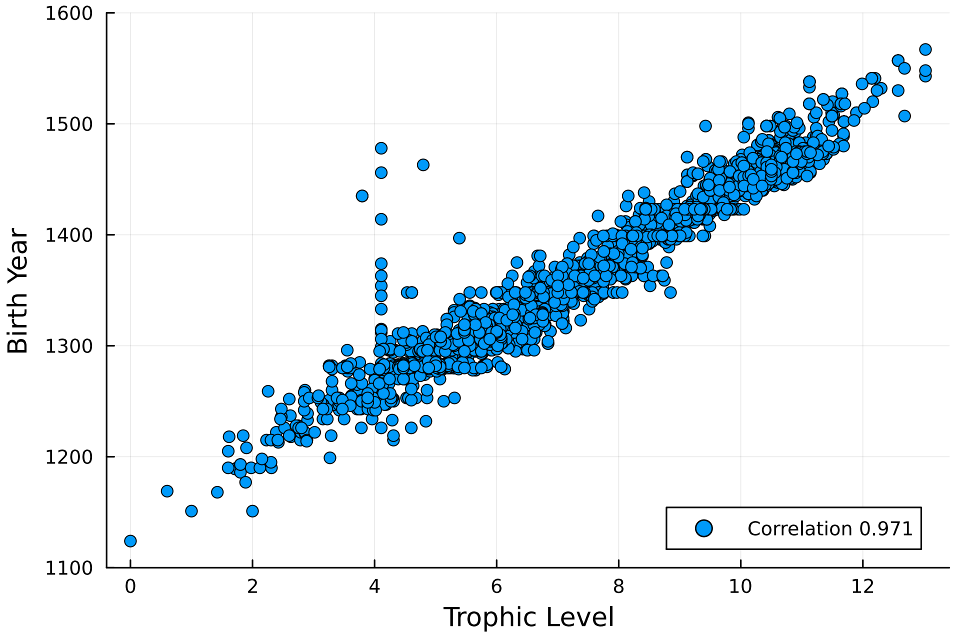
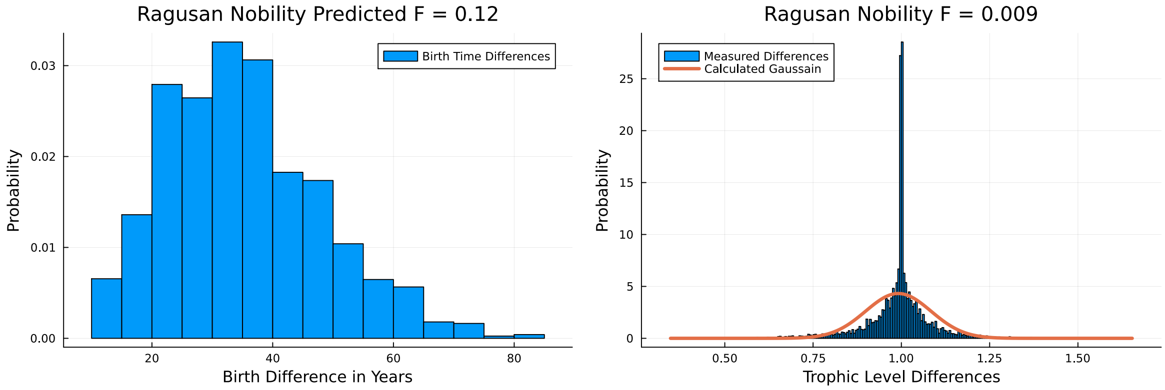


Figure 6.12: Known Birth Dates (3065 individuals) of Members of the Ragusan Nobility, [310], against Trophic Level with Pearson correlation coefficient given in the legend.

We also note that for this network the data may be “missing not at random". This means that the fact the birth dates for certain nodes is missing may be correlated with the time period the node is from, events that were ongoing at that time or another property of the node. In figure 6.13a, we present the differences in birth time for the parent-child pairs where we have data for both parties. This constrains how much we can say definitively as this is a small subset of the network data. We prune the data-set of obvious errors, making sure that the differences are positive to preserve causality, that you are born after your parents, as well as removing any differences outside what is biologically possible to exist (birth time differences smaller than 10 and greater than 120). This data is also a mixture of the mother-child and father-child differences which may be different for biological reasons and due to the patriarchal society from which we draw the data. Based on this difference distribution, we predict a Trophic incoherence of $F = 0.12$ which makes sense. We predict a very coherent network as edges are constrained to only go forward in time in this network. This is more than the measured trophic incoherence of $F = 0.009$. This is not surprising as there is a large variation in birth difference between parent and child as well as the fact that the full network is sparse, the number of children and parents you can have is limited, and acyclic so it is not surprising that F is very low. The two values do not agree very closely but do imply the same kind of regime where the network is very hierarchical and ordered which is what we expect when analysing this network. Additionally, we do not know the birth year difference across all nodes in the network as this data is missing for some pairs so the trophic incoherence is being measured over a much larger samples so this may account for some of the differences as the sample size could affect the ratio of mean and standard deviation for the birth year differences.



(a) Birth Year difference between parent and child in Ragusan Nobility Network [310]. Across 2442 edges where this is known for both nodes.

(b) Trophic level differences between nodes in Ragusan Nobility Network [310] across the whole network.

Figure 6.13: Comparison of trophic level differences and birth year differences in real historical network [310]

Additionally, Trophic level has been used to analyse another historical network of Islamic scholars and infer missing data. [52]. Our work explains why this was possible and justifies the assumption that trophic level could be used as a good approximation for the relevant “fitness” parameter in that network. We also analyse the difference in death dates between individuals and the relationship between degree imbalance and birth year in the network in appendix 6.7.1, where we show how both of these are not useful factors for predicting the network structure and how understanding the trophic structure shows that certain factors do not contribute to the formation of a network. The study of this historical network is not meant to unveil new information as the process of how family trees form is well understood. However, we demonstrate how the technique of trophic analysis can be linked to node properties, used to infer missing data and analyse network structure. We hope that techniques in this work can be extend to study real-world systems which are not as well understood.

6.5 Discussion

In this work, a uniform fitness distribution was used as we wished to create the simplest possible structures where the number of nodes are equally distributed across the fitness spectrum. However, this need not be the case and many fitness distributions could be used. If the fitness is thought to represent a property of a real system it may be more realistic if this is a Pareto or Gaussian distribution for example. Modifying the fitness distribution may impact the degree distribution and arrangement of levels which could be the subject of future work. Changing the range of the fitness distribution and the size of the preferred fitness difference will affect the maximum number of levels with the fitness density in a particular regime translating into the number of nodes of a particular trophic level. The number of levels and the fitness distance between them could reflect an underlying feature of a real system, such as the “ depth of competition” of a game or range of social status of individuals [125]. The effects associated with the sharp end of the uniform distribution could also be mitigated by having a distribution which decays of towards the maximum and minimum fitness; although, in some circumstances, the fitness edge affects may be a realistic behaviour which is important to the dynamics of the system. For example, consider a network of sports teams where edges represent player transfers between teams. The top teams clearly have different dynamics as there are no “better” teams for their players to move to compared to a team which buys players from lower leagues but also sells to better teams. A similar effect can be imagined in food-webs or production networks, where the nodes which consume the raw material or energy input to the system behave differently to nodes in the bulk of the system. Related to this, it is known that the presence of source/sink nodes [166] can be related to non-normality and that nodes at the ends of the trophic hierarchy are important for influencing the network [3]. It is also possible to have a fitness which is multi-dimensional, where different functions act on different fitness aspects. This could allow a mixing of heterophilic and homophilic behaviour where a different interaction could be present in each fitness. Our model provides a natural way to move between linear hierarchy and homophillic behaviour with a single fitness as the difference parameter can be decreased to zero. Community structure could also be studied through fitness functions and distributions as densely connected groups with few connections between groups could be modelled. And in some systems there can be an interaction of the hierarchical structure of the network with organisation of the network into communities [175, 128].

Another possible extension of this work would be to use a fitness space which is not linear. For example, the node fitness could be an angle on a circle and used to study periodic structures [53]. It may also be possible to link network hierarchy and fitness, linear or periodic, to the field of network geometry which has recently been extend to the directed case [136] where the topological features found in these models, such as reciprocity and the prevalence of different types of directed cycle, may be analysed through various tools associated with network hierarchy [53, 128, 44, 8, 20].

In this work, we present a model to explain how a simple fitness-based mechanism can lead to a hierarchical network structure. However, it is also possible to view the emergence of directed hierarchy as the result of dynamics taking place which alter the network structure [60, 109, 105]. Faculty hiring dynamics were studied in [57] where hierarchy steepness, fraction of edges pointing up in rank, and other network measures were analysed as the institution hiring preference functions were varied. This has also being studied in time varying endorsement networks where the probability to endorse depends on the preference for endorsing up the hierarchy and preference for endorsing nodes close in the hierarchy [60]. Hierarchy linked dynamics can also take place in animal social interactions [312] with position in the hierarchy affecting the behaviour of individuals. These works link to the kind of dynamics which could be built into extensions of our growing fitness model where hierarchy can be mixed with other interactions. As the network evolves in time, it may be possible to analyse the time evolution of the network hierarchy either using standard trophic level or the recent reformulation of

SpringRank for ranking in temporal networks [62]. Inspiration for creating a temporal network could also be taken from the approach of [313] where the network structure updates according to interaction between dynamic hidden variables assigned to each node. In the directed hierarchical case, a model could be constructed where the fitness of a node varies over time and edges are broken and formed as it moves through the hierarchy.

This work is also closely related to the study of non-normality [165, 19, 20] in networks and provides a generative model to create networks with varying degrees of normality while controlling how the levels are formed by varying the fitness distribution. It also provides a justification for the ubiquity of non-normal networks by creating a model for them which does not only depend on ordering by node arrival time and reciprocal edges [166, 38, 20]. The fact that it was observed in a real network in [38] that the number of reciprocal edges varies with level is something that could be built into the fitness function we use, showing the flexibility of the model. The model we present also comes with the advantage that the number of edges and nodes is fixed and that the model always generates connected networks which may not be the case in some static fitness models. Due to the similarities between trophic analysis and the study of non-normality it is hoped that trophic analysis and models of the type presented in this work could be a useful tool to augment areas where non-normality is being applied such as has been done in [20].

One of the key results of this work is that it provides some explanation of why coherent networks are common in nature as they can arise by multiple mechanisms which act simultaneously. We have shown that coherence can be induced by the fraction of edges which go in and out of newly introduced nodes, by the strong degree imbalance induced by degree-based preferential attachment or by the node ordering induced by fitness interactions. These simple effects could combine in many real-world systems to create the varied spectrum of trophic incoherence observed in real networks [6, 8]. The general model we provide captures both the hierarchy induced by time ordering as in citation networks and the niche-based hierarchy studied in ecology.

This work also provides some insight into the utility and limitations of trophic analysis as a tool. We have shown that when incoherence is low trophic analysis can be taken as good proxy for node level fitness and can be useful to infer some properties about the nodes. However, when a network is very incoherent this is not the case and trophic level gives you no information about the node fitness and simply correlates with degree imbalance. We also show how trophic analysis does not fully capture the underlying fitness distribution as all the trophic level differences are approximately mapped to Gaussian even when the underlying fitness distribution is not a Gaussian. We do however show that trophic incoherence can be used as a good proxy for estimating the scale of the coefficient of variation of the underlying fitness distribution, if the network is built using a fitness hierarchy. Linking trophic analysis to node fitness and the properties of the fitness distribution also allows the fitness properties to be linked to the network properties which have been shown to be related to trophic structure [8, 6, 5, 3, 2]. Another limitation of this work is that we assume that each edge represents one type of interaction whereas in real systems the ranking of elements may depend on the interplay between different types of edge interactions [174]. It is also true in some systems that being at the top of the ranking may not represent some intrinsic skill or ability but could just be related to luck [171]. For such systems, we could use a variant of our model where some edges can be added without respect for fitness or hierarchy representing luck or intrinsic variability in the system taking inspiration from the work of [125], where luck-based variability was incorporated into their model of rankings based on pairwise comparisons.

In this work, we have also shown the interplay between trophic analysis and degree imbalance. In some circumstances, this is useful as it has been shown that there is a relationship between non-normality and degree imbalance and that both are prevalent in nature [165]. However, there may be situations where this degree imbalance just arises from randomness like in an ER random graph and then trophic level simply correlates with this feature. This may be useful in some cases if the degree imbalance is an important feature in your dynamics however this is something to be aware of when using methods like Trophic Analysis or SpringRank [44]. Alternative ranking methods exist which mitigate this affect based on the stochastic block model [128]. This allows the statistical significance of the observed structure to be understood. The approach of [128] is very useful for understanding hierarchy and we recommend that it is used when trying to understand the significance of ranks in an application. In Trophic Analysis, the incoherence, F, can be used as a guide to understand the importance of hierarchy to the system and we would argue that ranks should always be given with a parameter like F or another quantification of the importance of hierarchy like the normality or significance of the ranks [128]. A stochastic block model framework has also been used to study the ability of “agony” to detect planted ranks [115]. F and other parameters which involves an average over the network structure do however have some limitations. For example, if we used a fitness function which creates a very strict hierarchy in one fitness region and no significant hierarchy in the other we lose the information about the fact that the network has two distinct behaviours as F takes a value based on the average across both. This means that we also need to look at the distribution of levels to fully understand the hierarchy in a network and the incoherence has an implicit assumption of the hierarchical behaviour being homogeneous across the system. Additionally, source/sink nodes which always have non-zero degree imbalance play a unique role in the network [166] with their number potentially affecting the dynamics.

Our results may also be affected by varying the sparsity of the networks used. If a networks is extremely dense, with the precise threshold depending on the fitness function and expected number of levels implied by the fitness function, it may be impossible to build very coherent networks as there are too many edges to have only edges which go up by exactly one trophic level. Additionally, depending on the generative process, compared to dense networks, very sparse networks may have fewer cycles and more nodes of zero in or out-degree. Hence these are generally more coherent, as there is more likely to exist an arrangement such that the trophic level differences are close to one across all edges.

This work could also prompt further examination of the relationship between trophic analysis and models of ecological network formation, as has been studied using a previous definition of trophic level which required basal nodes and a network formation model which was not based on fitness interactions [32]. Our work explains features like how the hierarchical arrangement and level structure change as the fitness mean and standard deviation are varied [285]. Our model could also be extended in a similar way to in the probabilistic niche model [131, 314]: we could assign the preferred fitness difference and fitness function standard deviation to each node individually to account for the fact that in some systems, such as food webs, different nodes may be able to interact over different fitness distances with different standard deviations, which may change the structure of the network formed, depending on the distributions of parameters chosen.

Trophic coherence has also been found to affect opinion dynamics in social network models [7]. These results could be linked to social network formation via the work of [130], where it was shown that there is a hierarchical structure present in some social networks, due to a phenomenon that edges going from lower to higher status individuals are less likely to be reciprocated. This concept could be incorporated into a variant of our model with a reciprocity parameter and analysed via Trophic Analysis.

6.6 Conclusion

In conclusion, we have presented a model of growing directed networks based on the principle of assigning nodes fitness and the network being built from a mixture of degree-based preferential attachment and fitness interactions. We have shown how these simple effects can produce a wide range of values of trophic incoherence which may explain the ubiquity of trophic coherence in real-world systems. We have shown how the properties of the networks, as measured with trophic analysis, can be related to the properties of the fitness function used in the generative model. In addition, we have shown how preferential attachment interacts with the trophic structure of the network and how fitness hierarchy affects the degree distribution in networks generated with our model. We have provided a variety of possible extensions and use cases of this model and other models of this type, in the hope that it can generate ideas for more work on the interplay between network hierarchy and both the structure and dynamics of directed networks.

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Data Availability Statement

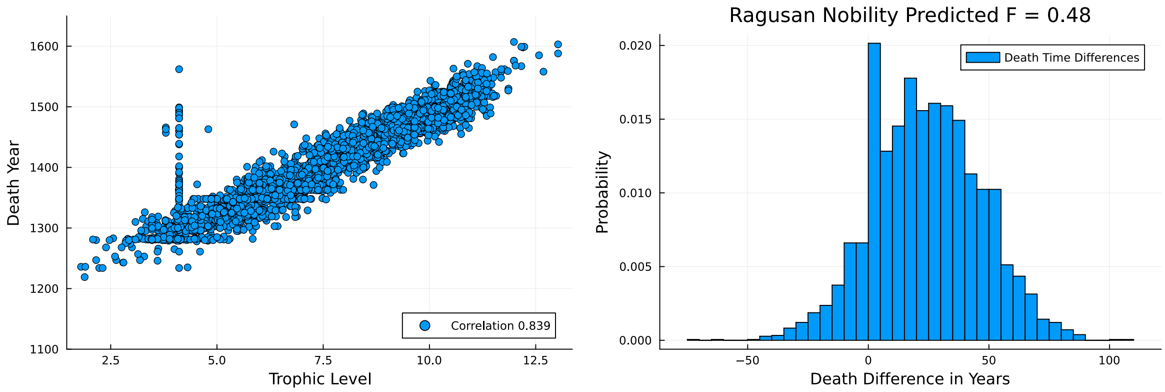
The data and code used as part of this work can be found at https://github.com/nrodgers1/directed_networks_with_fitness_and_hierarchy. Original network data can be found at [310].

6.7 Appendix

6.7.1 Additional Analysis of Historical Network Data

We also extract from the historical network, [310], the death year of the individuals and the difference in death year between individuals and their parents. The death years were found to be related to the trophic level however the difference distribution predicts a different kind of network structure than the one we observe. Showing that not all network metadata can be used to understand the hierarchical nature of network formation.

In figure 6.14 we analyse the relationship between the trophic parameters and the other data we have from this network which is the date of death of some of the individuals (3043). There is a strong correlation between the year an individual dies, figure 6.14a, which makes sense as we expect individuals who die later in time to be further along the family tree. However, the correlation is not as strong as in the case of birth times which makes sense when we consider figure 6.14b. We see that the difference in death year (year of child death minus year of parent death) can be negative which is not the case of the birth difference. Hence based on death differences you would not predict an acyclic and very coherent network as seen in the real data so this rules this out as a generative mechanism for the network. Also, it explains why the correlation between death times and trophic level is worse than the birth-level correlation as there is much more variability in the difference in death times as it can be negative and there is a large spike at zero which is not the case in the birth year difference. We assume this is the affect of disease and high childbirth mortality in the historical era in which this data is taken from. This highlights how trophic analysis can be used to understand the parameters that contribute to network formation in a simple real-world example but we hope this can be extended to more complex real world systems where the answers are less obvious.



(a) Death Year against Trophic Level of nodes in Ragusan Nobility Network [310] for 3043 nodes where this is known.

(b) Death Time differences between nodes in Ragusan Nobility Network [310] across the 3633 edges where the year is known for both nodes.

Figure 6.14: Comparison of trophic level differences and birth year differences in real historical network [310]

It can also be demonstrated, figure 6.15, that degree imbalance is not a useful metric to predict birth year as you would expect in the low incoherence regime as there is little correlation between the two quantities unlike was observed with trophic level. We also see that as the network is a network of parent-child relationships the maximum degree imbalance is two from having two parents and no children and the minimum is constrained by the number of children someone can have minus two for their parents.

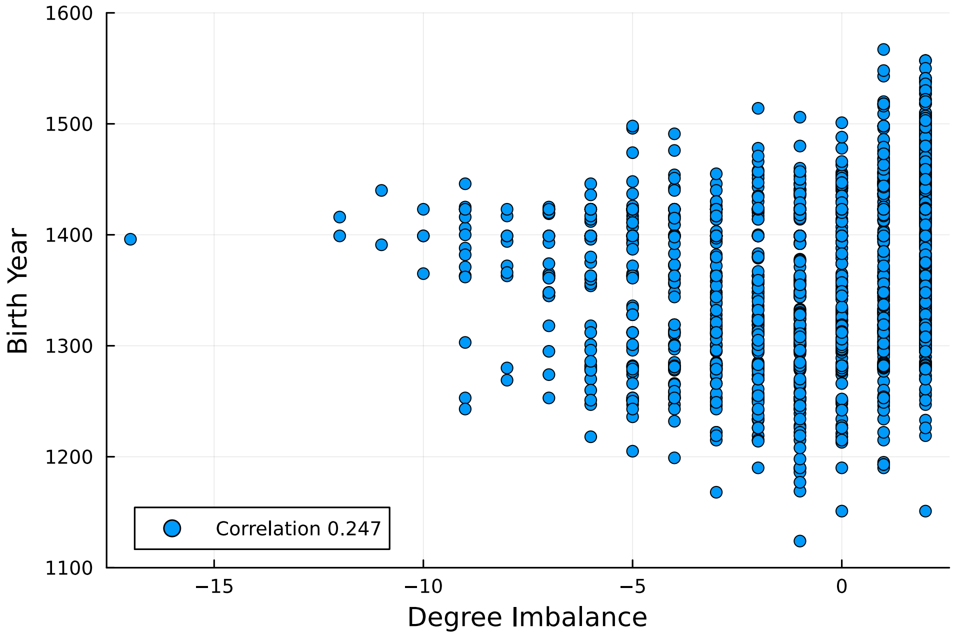


Figure 6.15: Known Birth Date (3065 individuals) of Members of the Ragusan Nobility, [310], against Degree Imbalance (in-degree minus out-degree) with Pearson correlation coefficient given in the legend.

CHAPTER

7

DISCUSSION AND OUTLOOK

7.1 Discussion of Work Presented

In this thesis, we have presented how Trophic Analysis can be used to understand various features of real and generated directed networks. In this section, we review the common threads and key findings of all work presented, with discussion of the individual works found in the section they were presented.

Throughout this thesis, we have taken a consistent approach to understanding hierarchy via Trophic Analysis. This approach has highlighted how Trophic Analysis can be used to understand many features of networks related to hierarchy and highlights how the papers presented can be viewed as a single body of work related to this methodology. All the results in this thesis draw on the same underlying fact that many real directed networks have a hierarchical structure, as measured by Trophic Analysis, and that this hierarchy is important for the dynamics and structural features of these systems. This work provides a well rounded studied of hierarchy in directed networks as we looked at how it impacts dynamics on networks, the structure of these networks and studied how networks with hierarchy can be generated and simple rules that lead to their emergence. All the results are also consistent with each other. Similar phenomena are observed in the work on Hopfield-like networks [1] and when studying network influence [3] which make sense in the context of the results found on the emergence of strongly connected components in [2]. While the results on fitness based generative model [4] attempt to explain why the features observed arise in real networks. This thesis furthers our understanding of how the hierarchical structure of directed networks affects many aspects of their function, while also serving to promote this idea to the wider network science community.

7.2 Outlook and Future Work

Having presented a study of Trophic Analysis and how it can be used study various phenomena related to directed networks we now give an overview of potential extensions to this work. In addition, we give an outlook of potential future developments and trends in the study of directed networks and general network science.

7.2.1 Outlook of Trophic Analysis

Since its inception in [5], Trophic Analysis has been utilised in many applications and the unique features of directed networks have become increasingly commonly understood [18, 20, 8]. It is hoped that this trend continues with more systems and dynamics identified which can be studied by analysis of their hierarchical structure. This could potentially span a huge range of fields corresponding to any area where the object of study can be represented as a directed graph. Work is currently ongoing on a potential paper, which I have contributed towards, to extend the results of [6] linking the spectral radius of the adjacency matrix to trophic incoherence using a "coherence ensemble" to the MacKay definition of Trophic Analysis and to devise new algorithms to sample from this ensemble.

One of the key achievements of the original proposal of Trophic Coherence was relating it to the longstanding May's paradox in ecology [5]. Similarly, a key step which would improve the visibility of the new version of Trophic Analysis [8] would be to find another system in which considering the hierarchical structure provides insight and answers to a long-standing question about the workings of a real-world phenomena. However, this is clearly not simple and it would be a large research step to come up with such a system. There are still many types of dynamics where Trophic Analysis could be applied and we would expect to see similar behaviour to as found in the dynamics studied in this work. Selecting other types of dynamics on which to perform a similar analysis and potentially running the dynamics on a real network structure could be a fruitful avenue of further work. In this PhD, the possibility of a data analysis based project surrounding the analysis a specific network dataset was considered, however we did not have access to appropriate data, collaborators to provide it or a clear research questions to answer. If this was the case in the future, it may also become a fruitful area of research, as demonstrated in [51].

One of potential extensions of this work is to focus on temporal networks. This could be using an specific adaption of the Trophic Analysis framework in a similar way to how SpringRank was extended to temporal networks in [62] or it could be simply applying standard Trophic Analysis to temporal data. In [62], a term is added to the minimisation problem which imbues a cost to updating the ranking to something which is different to the ranking at the previous temporal snapshot to smooth the changes in rankings over time as the network evolves, giving the rankings a dependence on the history of the network. In temporal networks, how the hierarchical structure and global directionality change with time could be analysed as well as the factors which lead to changes in this structure. In addition, a network could be setup where the structure and dynamics are coupled to each other which results in the incoherence of a network varying. For example, the network could be more likely to reorganise itself to become more coherent and sensitive to perturbations if it has not recently changed state but stabilise by adding more feedback if the state has changed recently. This type of approach was something which was considered during my PhD but other projects took priority and we had difficultly identifying real systems where this type of dynamics and evolution could take place. However, if a system is identified in which the changes in hierarchical structure over time are a key part of its behaviour Trophic Analysis or related methodologies could be a useful tool to study it.

Modifying the objective function used in Trophic Analysis by adding extra terms or changing the norm used is another potential outlet of future work. A regularisation term was included in the original definition of SpringRank [44] and there have been attempts to modify SpringRank [63] and other related methods [76] to deal with outliers by expressing them as a Huber Loss. During my PhD, some experimentation was conducted on changing the norm used in the definition of Trophic Incoherence. We found that this may modify the levels found by the algorithm as expected but we had no strong reason to give up on the current definition as it leads to a simple minimisation problem. If a justification was found to change the minimisation problem related to the study of specific features, such as temporal evolution [62], outliers [63, 76] or underlying fitness interactions [4], it may be an interesting avenue of future work. However, for the purpose of this thesis the current definition worked as well as required.

Another useful facet of Trophic Analysis, has been the connection of Trophic Analysis to various global network quantities such as the spectral radius [6, 8] and non-normality [8, 18, 20]. Future work could involving trying to analyse what other network quantities can be related to Trophic Incoherence as was done in [3, 2]. As well trying to link the results expressed in terms of Trophic Incoherence to the wider literature on non-normal networks and the phenomena they exhibit. This has been begun by other groups such as in [20] where both trophic analysis and non-normality were used to analyse dynamics on directed networks and the features captured by each measure analysed. It may be possible to relate further spectral properties of the adjacency matrix to the hierarchy and directionality of the network it represents.

Additionally, work could be undertaken to relate Trophic Analysis to the other methods of hierarchy present in the literature and to provide a unified view which brings together differing views of hierarchy and ranking. The review conducted earlier in this thesis represents a start of this process. It could be extended by comparing in more detail some of the many different methodologies and their application to studying dynamics or real data and comparing their mathematical formulation and properties. However, this is a very extensive task given the range of techniques and approaches which may be considered. Any work of this nature could further draw attention to the close relationship between Trophic Analysis and the related methodologies [45, 44] describing the relationship between the different formulations and interpretations in precise detail and linking to the very large literature which methods based on Helmholtz-Hodge Decomposition draw on.

In chapter 2, we highlighted the myriad examples of how to study and measure hierarchy in directed networks. Of course, in the future one of these methods could become the default way for the network science community to view hierarchy which would change the development of the field. For example, it may be possible that one of the methods related to Trophic Analysis highlighted in chapter 2 such as SpringRank [44] or Hodge Decomposition [45] gain in popularity much more than any of the others so that it becomes that standard way to refer to this type of methodology, while the terminology contained within that method becomes the literature standard. On the other hand, this type of standardisation may not occur and there will remain many different ways to describe hierarchy in the literature for a long time. One particular methodology which may see lots of use in the future is [128] and potential future work derived from this. The framework of [128] uses a modified stochastic block model to measure the hierarchical structure. This allows quantification of the significance of the structures found and can separate out the correlations with degree imbalance observed in Trophic Analysis. This framework is also available in the popular and well maintained `graph-tool` library [129] which may aide in widespread adoption. We would recommend the development of this framework [128] is followed as it allows analysis of the interplay between community structure and hierarchy as well as being easily accessible for use in application and visualisation. Unfortunately, it seems like the clash in terminology between flow hierarchy and cluster or modular hierarchy is a feature of the literature with both terminologies well established and something that researchers will need to be aware of.

There may also be methods outwith the type of one-dimensional hierarchy used in this work which may become widely used to quantify the structure of directed networks. For example, the directed extensions of the network geometry framework [136]. Additionally, some system may not be well represented by a one-dimensional linear hierarchy. There may be systems which feature a periodic hierarchy [53] which could be studied using the Magnetic Laplacian methods [53, 138, 140], also used to study community structure [137, 138]. In particular, a useful approach could be to measure simultaneously the flow and periodic hierarchy [54] allowing the nodes to be embedded using two dimensional polar coordinates and more of the network structure captured [54]. Another potential future avenue of work is applying Trophic Analysis or a related methodology [172] to signed directed networks either by adapting the framework to deal with negative edges or by working on the absolute value of the edges and then analysing the role that the negative edges play in the hierarchy. This could link to recent work in directed networks which has analysed the amount of reciprocity and frustration observed in signed directed networks [173]. It may also be the case that systems exist with a range of nodes types and edge types which follow different hierarchical rules and patterns. As well as systems with large variations in how strictly the hierarchy is followed in different parts of the network. It may be in future that specific methodologies can be developed to quantify these more complex structures. Trophic Analysis may capture some of this information through the distribution of levels and edge differences but as the incoherence is an average over the whole network this kind of local information can be lost. In future, it is hoped there will be more widespread understanding on the prevalence and importance of hierarchy and ranking in directed networks and it will be of great interest to see where this type of methodology can be applied, the questions it can answer and the insight it can inspire.

7.2.2 Trends in Network Science

During the course of my studies, there was also significant developments within network science and science more generally which may shape how research into complex systems develops in the years to follow. One exciting and developing area of research not covered by this thesis has been the field of higher-order networks [315, 316, 317] which has attracted much interest in recent years and is the topic of numerous reviews [315, 316, 317]. The networks covered in this work all feature pairwise interactions but in some real systems this may not be adequate to fully describe them and higher-order interactions involving more elements of the system may be required to fully capture their behaviour [317]. In the field of higher-order networks this is done by representing the systems through either a hypergraph or simplicial complex. Both of these approaches allow the representation of interactions which are beyond pairwise and much work has gone into understanding dynamical process on these systems [316, 317, 315]. Recent work has highlighted the interplay between higher-order network structures, directed interactions and dynamics [318, 319, 320, 321] by using various frameworks for the study of directed hypergraphs. Additionally, the work of [322] has considered how higher-order Laplacians can be constructed to study directed simplicial complexes. As the field of higher-order networks further develops it will be interesting to see the insight this framework can give into real-world systems and the role directed interactions may play in this framework. It will be also of great interest to see the future uses of the frameworks such as network geometry [136] or renormalisation methods [147] which were extended to directed networks during the course of my PhD. Additionally, it will be of interest to see how ideas around the low-rank nature of complex systems [323], using dimension reduction based on singular value decomposition develop in future. Moreover, their may be future scientific developments based on expanding areas of interdisciplinary research such as linking complex networks and dynamical systems using Koopman Operators [324] or research on quantum networks [325] linking network science and quantum physics, which may include directed quantum networks [326].

During the course of my PhD, there has also been significant advances in AI and machine learning applied to a vast range of topics in network science and beyond. In the middle of my PhD, large language models entered the public consciousness and become easily accessible with huge improvements made in the capabilities of generative AI. There has also been great interest in how machine learning can be used to study complex dynamical systems such as the data-driven approach to dynamical systems of [327]. To give some recent examples in closer relation to this work, it was shown in [89] how a Graph Neural Networks (GNN) could be used to rank elements in a directed networks and in [328] how a GNN framework can be used to study the evolution of the structure of a network. Overall, it will be of great interest to see in the years following this thesis how machine learning approaches interact with the study of complex systems and network science, see [329] for a review and outlook on the applications of AI to study complex networks. It will be of great interest to see how science is affected in the years after my PhD by the rapid progress in AI which took place during the course of it.

7.3 Conclusion

In conclusion, we have presented a detailed study of how Trophic Analysis can be used to understand the properties of directed networks. We have shown how hierarchy can be used to understand the emergence of strongly connected components, how it affects the performance of Hopfield-like networks and how it can be used to understand network influence. In addition, we have shown how hierarchy can be created using preferential attachment models based on node fitness interactions. We hope this thesis provides a basis for future work involving directed networks and furthers our understanding of these systems.

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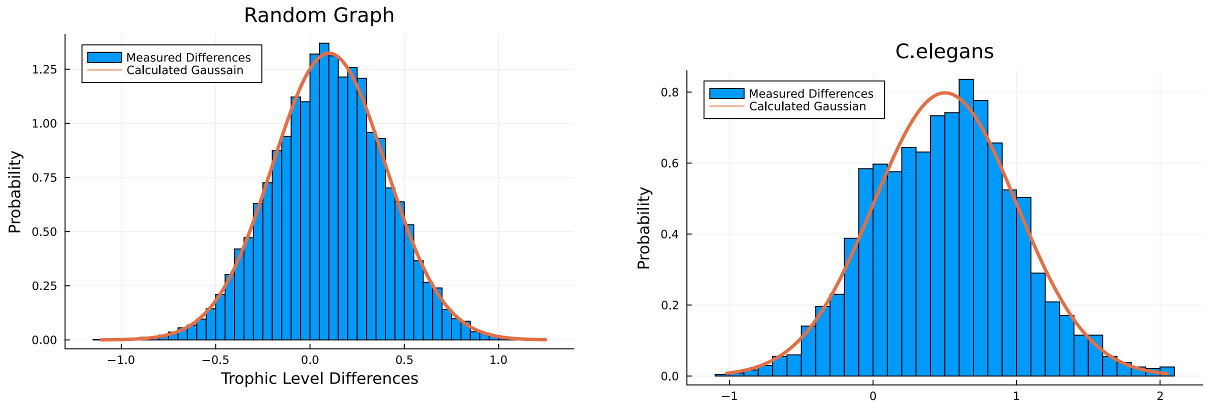
APPENDIX

A

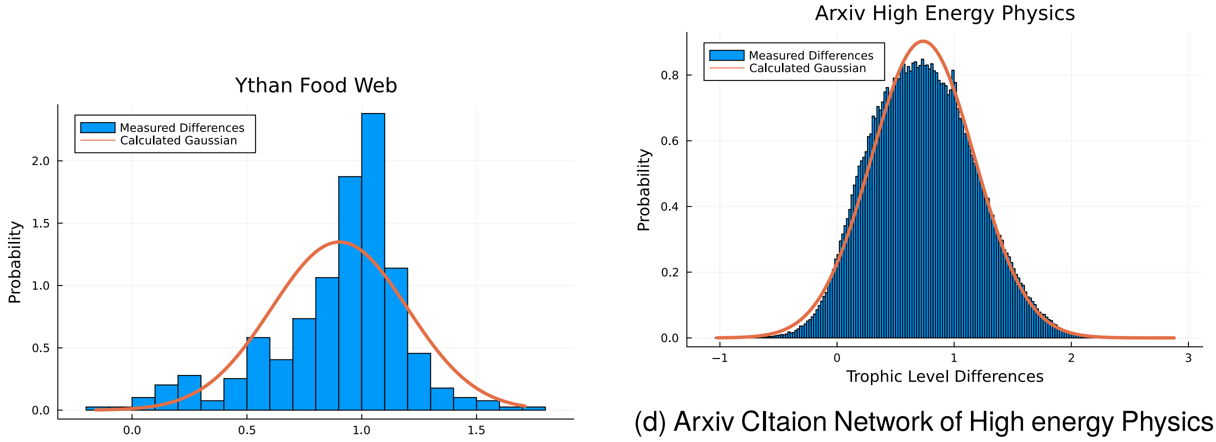
SUPPLEMENTARY INFORMATION FOR CHAPTER 3

A.1 Level Distribution of Example Real Networks



(a) ER random graphs with $N = 1000$ and $\langle k \rangle = 10$

(b) *C.Elegans* connectome [240]



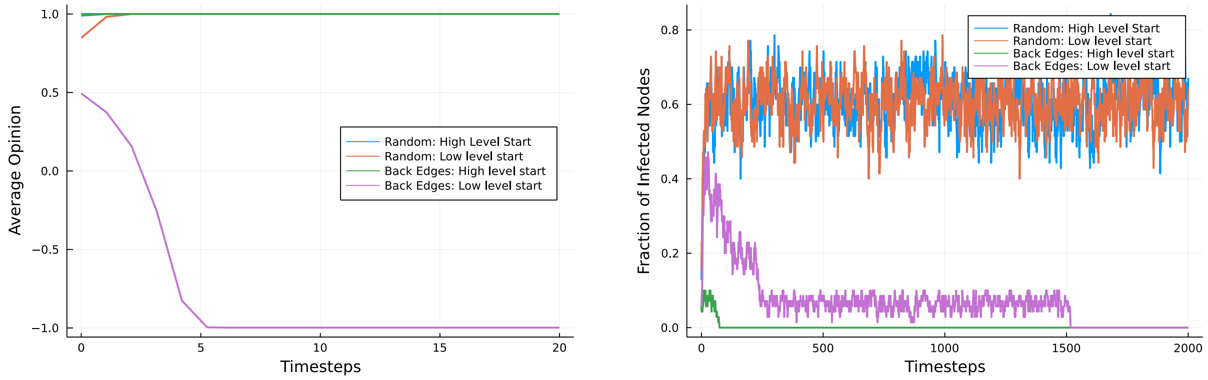
(c) Ythan Estuary Food Web

(d) Arxiv CItaion Network of High energy Physics with approx 35,000 nodes [330]. Downloaded from [331].

Figure A.1: Level difference distributions of real networks of a variety of sizes and function which can roughly be approximated as Gaussian's.

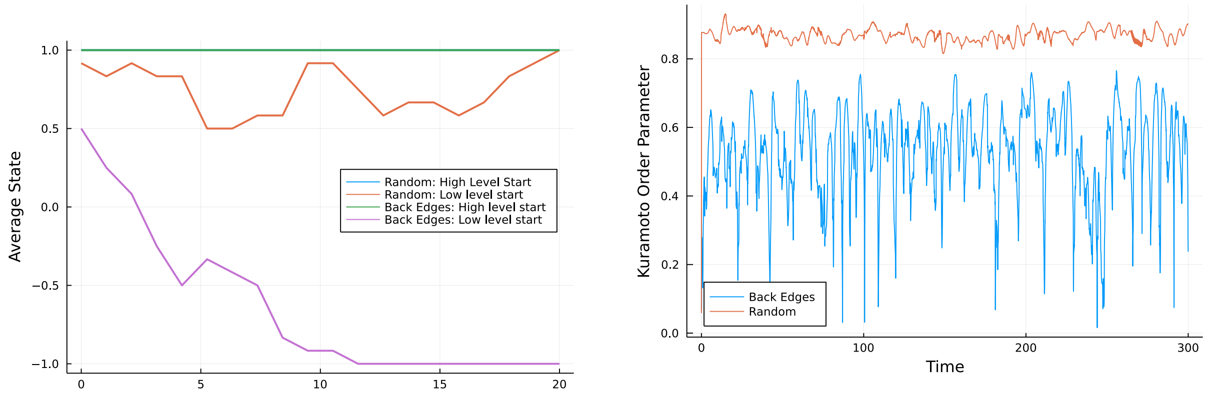
We show the level difference distributions for a variety of real world networks, figure A.1. The Gaussian approximation is calculated from using mean, $\bar{z}$ and standard deviation $\bar{z}\eta$ as defined in the main text and as in [8]. All the distributions are reasonably well approximated by a Gaussian. The random graph, figure A.1a is well approximated even though it has no hierarchical structure and so is the *C.elegans* connectome figure A.1b which has a more complex structure. The approximation is not perfect for all networks for the small food web, figure A.1b, as the network is very coherent the peak at one is larger than the Gaussian predicts and the network is quite small so we expect fluctuations and noise. However the approximation works well on very large networks such as the Arxiv Higher Energy Physics citation network.This network is very structured as more popular papers are cited more and it has an ordering imposed by time as you can only cite papers written before you. However the trophic level distribution is still well approximated by a Gaussian which depends only on F.

A.2 Importance of Attacks on Backwards Edges for Dynamical Processes



(a) Majority Vote Dynamics with Opinion Inertia on ER random graphs with $N = 1000$ and $\langle k \rangle = 10$ with 20% of most backwards edges targeted or random edges targeted with different starting locations in the hierarchy of with a fifth of nodes taking a new opinion.

(b) Spread of infection with time in SIS model on High School Social Network [332] with 20% of most backwards or random edges targeted with different starting locations in the hierarchy and an initial infection in 5% of the students. $pI = 0.2$, $pR = 0.1$.



(c) Voter Model on Trade Network [333] with 33% of most backwards or random edges targeted with different starting locations in the hierarchy and 5% of nodes taking the new state.

(d) Synchronisation of Continuous Kuramoto Oscillators on the *C.Elegans* connectome [240] with 20% of most backwards edges targeted and random edges targeted starting from random phase between zero and 2π.

Figure A.2: Dynamics of Real-World Networks after targeted attack on Backwards edges and Random Edge Attacks. All real-world data sets can be found at [185] or [333] for the trade network.

Strong connectivity is very important for many real-world networks and their dynamics. For illustrative purposes we demonstrate how a spreading process defined by a Susceptible-Infected-Susceptible (SIS) model dynamics; Opinion formation governed by Majority Vote

Dynamics; changes in states of nodes governed by the the Voter Model and Synchronisation of Continuous Kuramoto Oscillators all change after a targeted attack on the backwards edges calculated using Trophic Analysis and random attack. These are all demonstrated in figure A.2.

Majority vote is a very simple model of opinion formation which is demonstrated in figure A.2a. Each agent in the model is given an opinion and then updates their opinion if the majority of their neighbours have a different opinion. It is very simple but shares some similarities with other discrete dynamics widely used in complex networks such as the SIS epidemic model [204], Hopfield neural network model [1], the Ising model of magnetisation [205] and the Moran process describing evolution of populations [206]. The simplest way to define majority vote dynamics is a system where there are two opinions denoted as +1 and -1. Each agent holds either of the two options and updates their state according to the majority opinion of their neighbours. In the case of a draw the new state can be randomly selected or remain in the previous state. We choose to fix the system in the previous state to prevent random opinions filtering through the system from the nodes with in-degree 0 when the backwards edges are removed. This update rule can be written as

$$S_i(t+\Delta t) = \text{sgn}\left(\sum_j A_{ij} S_j(t) + \delta S_i(t)\right). \tag{A.1}$$

Where δ is a small positive constant less than one to account for balanced opinions. We also update the state of the system in parallel. In this setup, for maximum simplicity, we take an Erdős–Rényi random graph, with $N = 1000$ and $\langle k \rangle = 10$, and give one fifth of the nodes a new opinion, labelled -1, and observe how that opinion spreads over time. This could represent a political belief or taking part in a social trend. Figure A.2a shows that how the opinion forms depends on where in the hierarchy the opinion starts and how much feedback there is in the system driven by the backwards edges. When the new opinion starts at the bottom of the hierarchy and the backwards edges have been attacked it can spread through the whole system and it becomes a majority opinion amongst the nodes. When the opinions starts at the bottom of the hierarchy after a random attack it can still slightly spread up through the system but since there is still feedback in the system the affect of the new opinion is damped so it quickly dies out. When the opinions starts at the top of the system and the back edges have been attacked it can not propagate back down the system so the new trend quickly dies out. When the opinions starts at the top of the system after a random attack it is also quickly replaced by the opinion from the lower trophic level nodes. This also demonstrates that hierarchical structure can be found and exploited even in networks like random graphs where little structure is expected.

The SIS model, figure A.2b, is a simple spreading process which could be imagined to represent in the simplest way the spreading of an infection which you can catch multiple times and lack immunity like the common cold or sexually transmitted disease; the spreading of a meme in a social network; selling in a trading network or activation in a neural network. In this model each node can either be susceptible or infected. If a node is susceptible it becomes infected if any of its in-neighbours are infected with probability pI, at each time step. If a node is infected it loses the infection and transitions to the susceptible state with probability pR. There are many possible variations of this model however we use the simplest case for demonstration [334]. Using parallel updates we start the system with 5% of the nodes infected and the rest susceptible. This is shown in figure A.2b where the dynamics take place on a High School Social Network. If random edges are removed the backwards edges remain and then the infection can cycle round the network and the infection becomes endemic. If the network is strongly connected the final state is not affected by where in the the network the infection appears however the initial spread can be affected by where in the hierarchy it starts. When the backwards edges are removed there is no strongly connected component to maintain the infection so it eventually dies out. However the hierarchy induces an asymmetry in the network. If the infection starts in the low trophic level nodes it can spread through a large part of the network before it dies out so many nodes see the infection while if the infection begins in the high level nodes it has nowhere to spread to so quickly dies out, figure A.2b. This is very important to understand as each of these scenarios can have very different consequences depending on the nature of the spreading agent and the system in question.

A voter model, figure A.2c, is another simple model which can represent opinion formation or general updating of states of the agents in a network [335]. We take two discrete states labelled $+1$ and -1 and update the system in parallel such that at each time step a node selects one of it's in-neighbours at random and copies the state of the chosen neighbour. This model is very simple however variants of this model can be used in modelling real voting processes [215], economics [216] and chemistry [217, 218]. In our example dynamics we simulate the simple voter model on a trade network. Where the new state can represent any relevant binary change in the function of an entity for example if the agent suffers a delay or shortage in production or begins selling off particular assets. We start the system with 5% of the nodes in the new state and destroy one third of the edges, more edges have to be attacked due to the network being small and dense as well as quite incoherent. When the perturbation is made to the high level nodes the new state can not take hold and the system maintains it's previous state, figure A.2c. However when the new state is introduced to the low level nodes it can gain a foothold. When it is presented at the low level nodes after a random attack it survives for some time before disappearing while after an attack on the backwards edges the new state is able to overtake the entire system.

The Kuramoto model is a very important model of synchronisation [209] used in a wide variety of setting in particular in Neuroscience [210, 211]. In figure A.2d we simulate Kuramoto oscillators on the neural structure of the nematode *C.Elegans* after random and targeted attack. It can be treated analytically in simple network topologies but in complex networks the model must be solved numerically. We use NetworkDyanmics.jl [213] to solve the system of differential equations used in our variant of the model. Each oscillator has a phase, θ, which evolves according to the equation

$$\frac{d\theta_i}{dt} = \frac{K}{k_i^{\text{in}}} \sum_{j=1}^{N} A_{ji} \sin\left(\theta_j - \theta_i\right) + \omega_i. \tag{A.2}$$

Where K is the coupling constant, k_i^{in} is the in-degree of node i and ω_i is the natural frequency of node i. We use the form normalised by in-degree so that the oscillators update at similar rates even if they have many input nodes. K is taken to be 50 to ensure synchronisation and the natural frequency of each node is drawn from a normal distribution with mean 0 and standard deviation 1. The synchronisation of the oscillators is shown in figure A.2d and measured by the order parameter

$$r = \frac{1}{N}|\sum_{i=1}^{N} e^{i\theta_i}|. \tag{A.3}$$

This reaches 1 when all the oscillators are fully in phase. Starting from each oscillator having an initial phase between 0 and 2π under a random attack the system is still able to synchronise. However when the backwards edges are attacked the synchronisation is less strong, A.2d, and the system is disrupted.

These results tie into existing literature on directionality, spreading [336] and epidemic thresholds in directed networks [114]. Where the epidemic threshold can be considered a function of the spectral radius and driven by the directionality as measured by the fraction of bidirectional edges [114]. Our results are in agreement with this as a bidirectional edge pair must count at least one edge where the trophic level difference is less than or equal to zero. We extend the definition of directionality to make it more general and complete rather than simply the fraction of edges which are bidirectional [114]. Our results can also be restated in terms of the spectral radius of the adjacency matrix as there is an analytical estimate of the spectral radius as a function of F [8]. Similar results demonstrating the affect of directionality and hierarchy on the performance of Hopfield-like neural networks can be found in [1]. The results demonstrate the importance of the backwards edges to the system across a variety of dynamics and scales which we expect to hold in a variety of other systems. However it should be stressed that the importance of the backwards edges to dynamics depends on a variety of factors. Firstly the impact of attacking the strongly connected component depends on the initial size and distribution of that component as if the component is initially very small destroying it may have little affect. Degree distribution can also interplay very strongly with dynamics both in the sense that hub nodes of very high degree can play in important role in controlling the dynamics and that directed networks can potentially have many nodes which have in-degree zero [193]. Nodes which have in-degree zero have no input from the system so internally set their own state so can play a large role in controlling the system dependant on their placement in the hierarchy, out-degree and the specifics of their internal dynamics. In addition this could be repeated with another measure of the hierarchical ordering and targeting of the backwards edges however you could not analytically estimate the number of edges you would need to target before enumerating all the backwards edges and would also lack the link to the global directionality.

A.3 Network Data-sets

The majority of the networks used in this study are stored at [185] where they were previously used in the results surrounding the relationship between trophic structure and spectral radius [6]. Information about the original sources of the networks as well as additional network information about the structure can be found in the supplementary information of [6] or online at [185].

We also supplement this data-set with some additional networks from [182], https://networks.skewed.de/, in order to sample the parameter space as best as we could which are listed in the table below. The links provide more detailed information about the network structure and origin and the original source as listed in [182] is referenced in the last column.

Network Name	Retrieved From	Source
FAA Preferred Routes	https://networks.skewed.de/net/faa_routes	[236]
Dutch school friendships (all 6 connected networks)	https://networks.skewed.de/net/dutch_school	[337]
Abu Sayyaf kidnappings	https://networks.skewed.de/net/kidnappings	[338]
Papuan gift-giving	https://networks.skewed.de/net/moreno_taro	[339]
Swingers and parties	https://networks.skewed.de/net/swingers	[340]
Email network (Uni. R-V, Spain, 2003)	https://networks.skewed.de/net/uni_email	[341]
Political blogs network	https://networks.skewed.de/net/polblogs	[342]

A.4 Strong Connectivity By Network Type

In the main text we give the result for predicting the strong connectivity for real networks where all the networks of different types are shown in the same figure. Here we break down the networks by the categories included in the data set [185, 6]. All the networks are collected in different ways so there may be uncertainty associated with how well networks of each type represent the underlying real world system.

Food-webs, figure A.3, are unlikely to be strongly connected as expected as they have a very hierarchical structure as result of the interactions between species and the flow of energy up the food chain. It is interesting to note that some food webs have high degrees where previous work on random directed networks [177] would expect the network to be strongly connected.

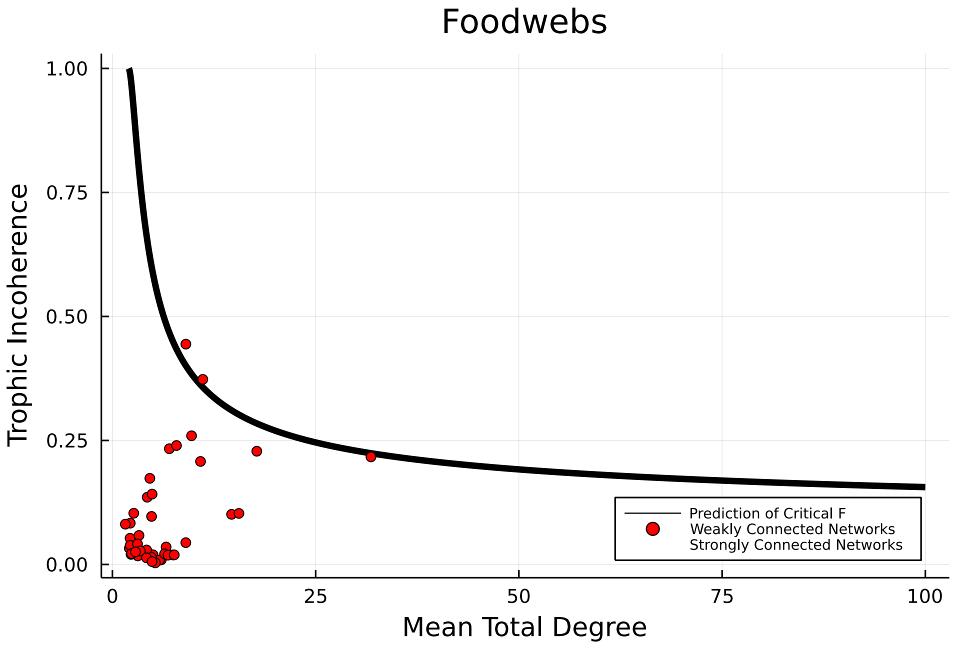


Figure A.3: Prediction of Strong Connectivity in Food webs from [185]

The genetic networks in our data set, figure A.4, are all very coherent and lack a strongly connected component.

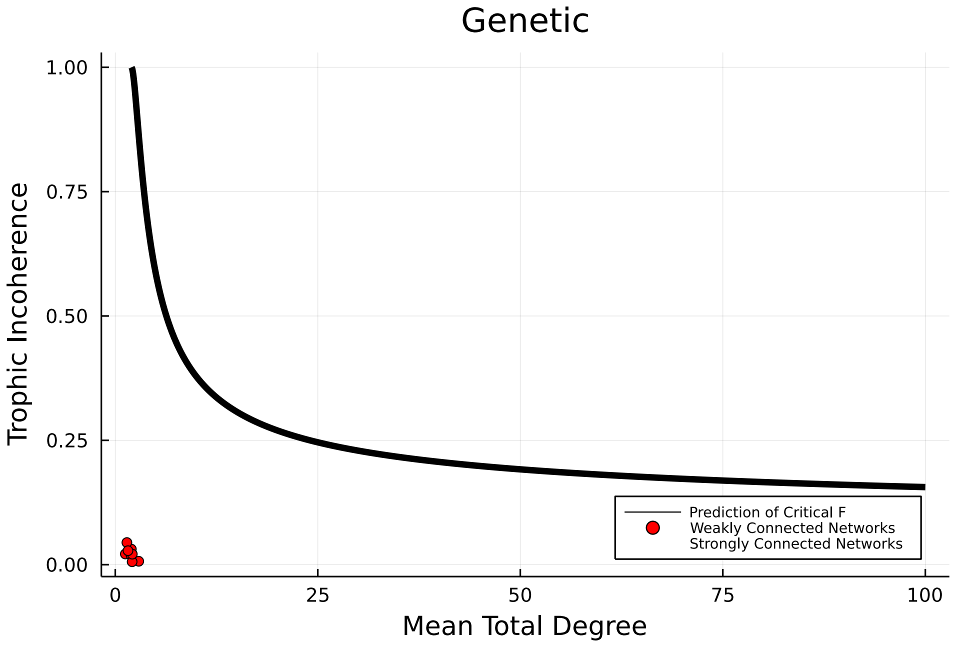


Figure A.4: Prediction of Strong Connectivity in Genetic Networks from [185]

The singular language network, figure A.5, is quite incoherent but lies close to the transition line.

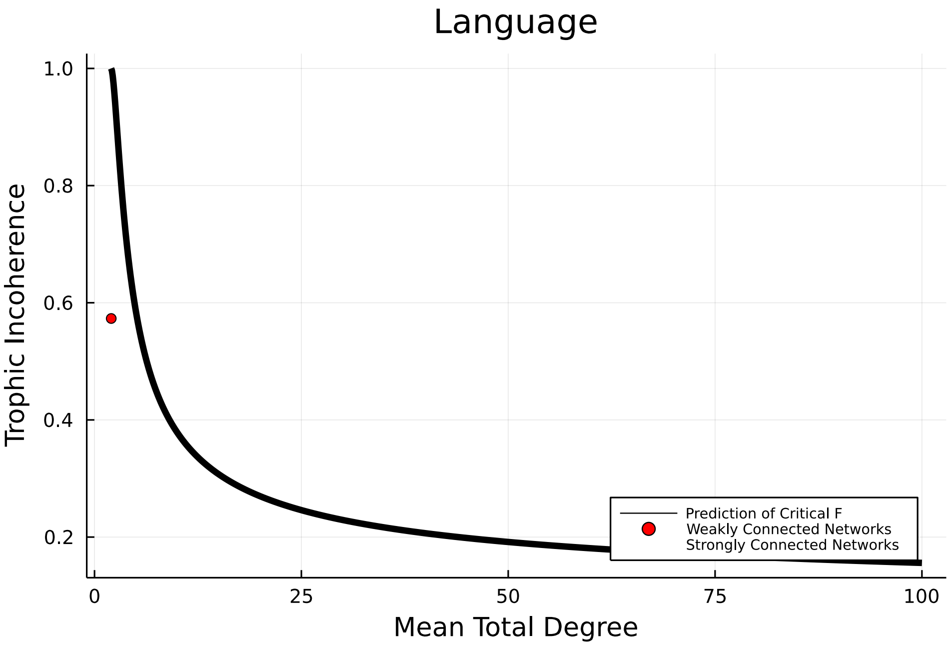


Figure A.5: Prediction of Strong Connectivity in Language Networks from [185]

The metabolic networks, A.6, all lie very close to the transition line and are very incoherent so have a little global hierarchical structure but still enough to make our analysis relevant.

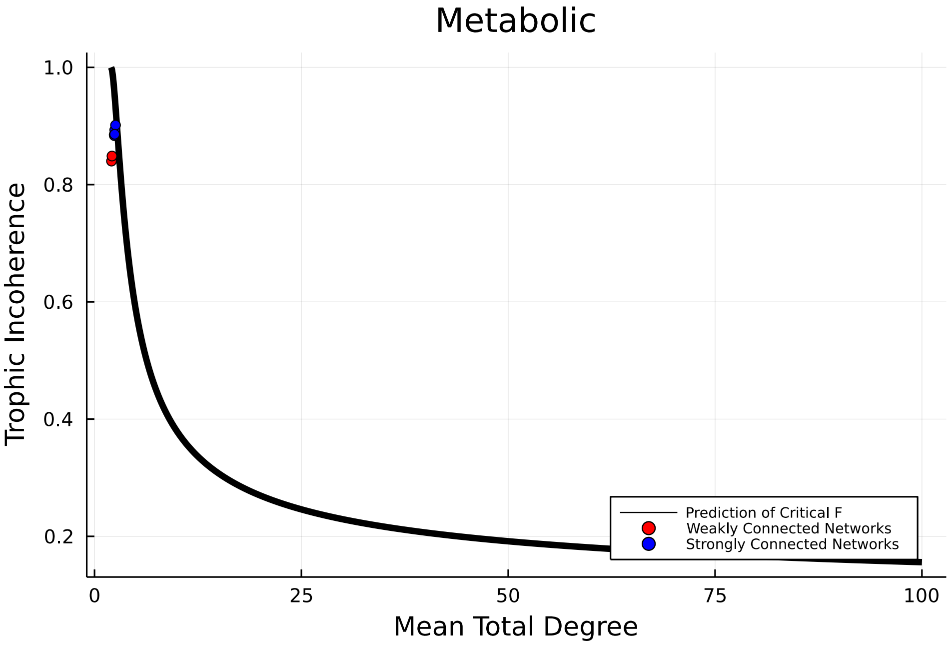


Figure A.6: Prediction of Strong Connectivity in Metabolic Networks from [185]

There is large variation in the neural network data set, figure A.7, this is due to the variety of data types and methods employed in this field. This data includes the connectome of

C.Elegans as well as functional brain networks for a variety of species.

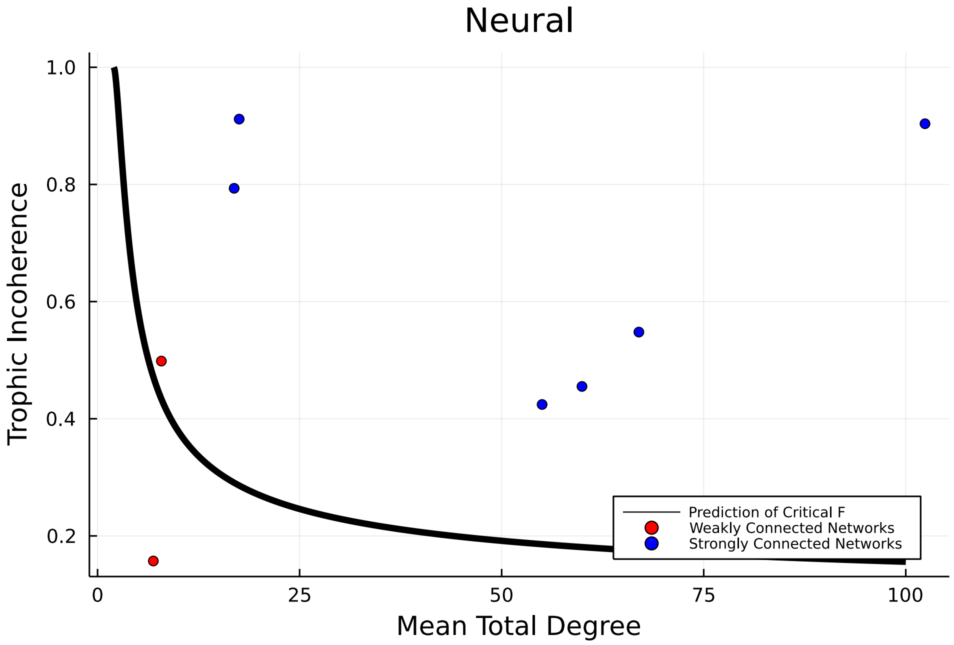


Figure A.7: Prediction of Strong Connectivity in Neural Networks from [185]

The social network comprised of in-person friendships all lie close to the transition line, figure A.8, between strong and weak connectivity. Again social networks are a type of real network where you might initially expect there to be very little hierarchy and ordering.

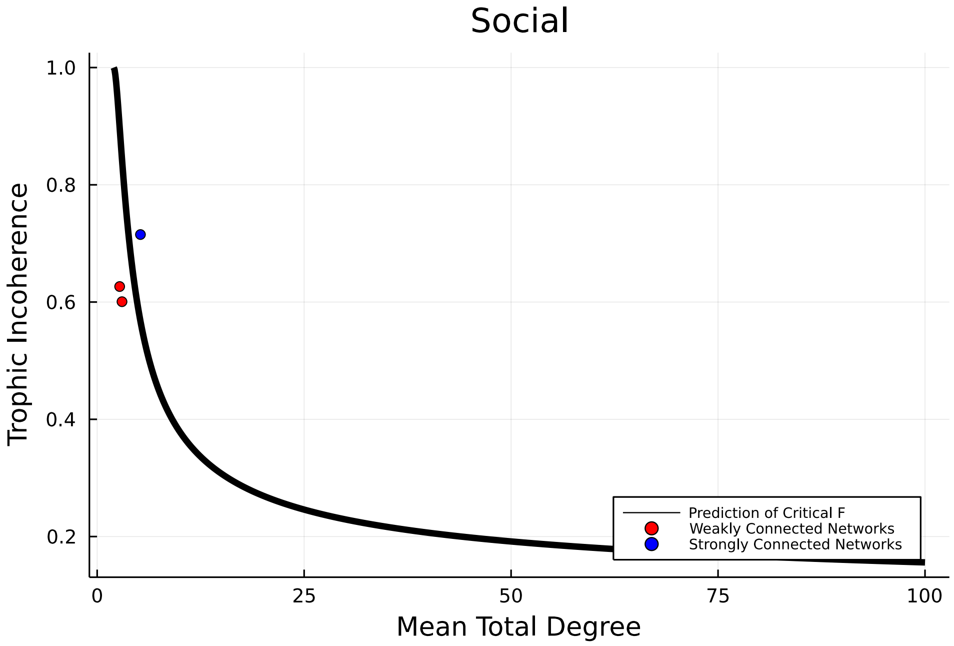


Figure A.8: Prediction of Strong Connectivity in Social Networks from [185]

The trade networks in our data set, figure A.9, are all in a similar region which is mostly strongly connected but still exhibits some hierarchy.

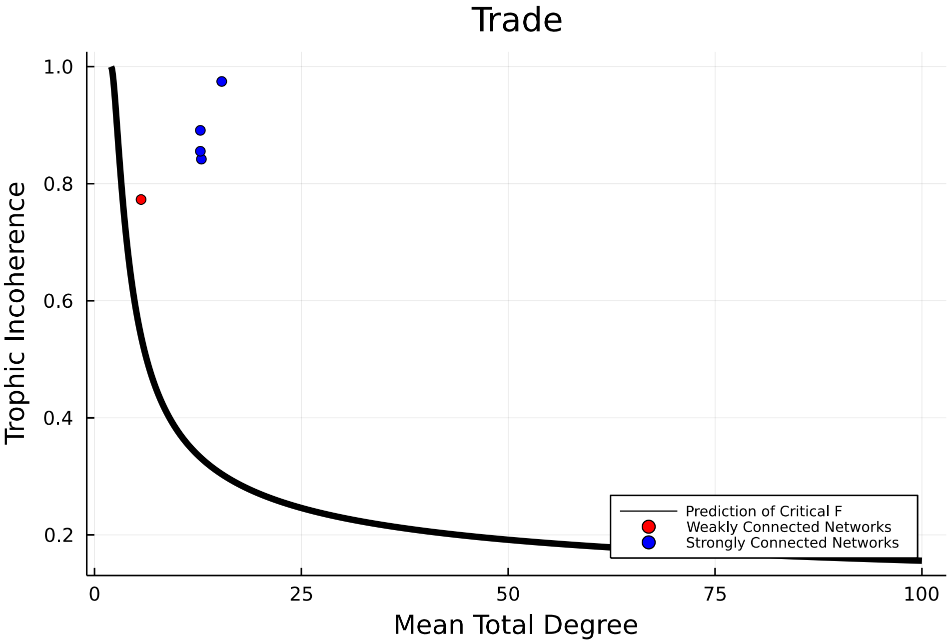


Figure A.9: Prediction of Strong Connectivity in Trade Networks from [185]

A.5 Branching Factor for all Networks

The branching factor is shown for all the from [185] networks in figure A.10. Again it is clear the the transition is missed when not considering the hierarchy and methods derived from random graphs [177] are not enough to explain the behaviour of real networks.

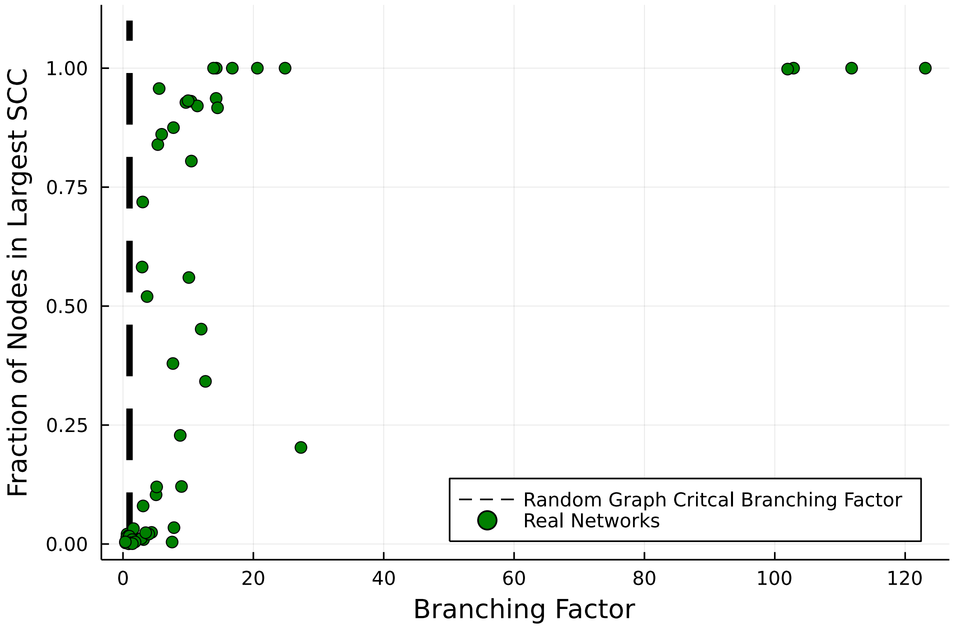


Figure A.10: Prediction of Strong Connectivity using the Branching Factor for Real Networks [185].