Physical network structure and robustness

by Luka Blagojević

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Supervisor: Márton Pósfai

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Abstract

Physical networks are networks composed of interconnected, volume-occupying objects, embedded in three-dimensional space. For example, a biological neural network is composed of neurons, which are physical objects, connected via synaptic connections, thus forming a network. Due to technological advances, data describing the three-dimensional layout and network connectivity of physical networks is becoming increasingly available, which provides an opportunity to ask fundamental questions about the relationship between their physical and network structure. In my thesis, I contribute to the emerging field of physical network research by extending network science tools to incorporate physical structure and using these novel tools to characterize the structure and dynamics of empirical and model physical networks. Chapter 1 introduces the topic, and Chapter 2 reviews the literature. The main results are presented in the following chapters:

In Chapter 3, I extend the so-called meta-graph to analyze empirical physical networks. The meta-graph was originally introduced to capture physical conflicts in growing linear physical models (i.e. networks where nodes are spheres and links are straight cylinders). Here, I generalize the meta-graph to study the spatial proximity of general physical nodes and links. Applying this tool to empirical networks, I find a strong correlation between the layout and the combinatorial network describing the system, highlighting the need to study the co-evolution of networks and their physical shape.

In Chapter 4, I standardize and analyze 15 physical networks from different domains, each consisting of tube-like objects (links) connected at junction points (nodes). The networks are categorized into three types: lattice-like networks, trees, and linked trees; most nodes exhibit degrees of one or three. To characterize their layout, among other physical descriptors, I introduce a quantity that captures how physically confined links are, showing that while most links follow straight paths, some take winding trajectories through dense network regions. The shape and connectivity of these networks are intertwined: for some data sets, highly confined links tend to have high network centralities, confirming that important links in the network are also confined in space.

In Chapter 5, I investigate the robustness of networks against physical damage. To simulate spatially correlated damage, physical networks are tiled with equally sized boxes, which are sequentially removed. Whenever a tile is damaged, all links intersecting the tile are removed from the network, leading to a percolation transition. Using numerical simulations and analytical calculations, I systematically investigate how physical and network structures affect the location of this transition for both random and targeted tile removal. I show, for example, that the presence of long physical links renders networks extremely vulnerable to random tile damage. Even scale-free networks robust against random link damage are dismantled after removing a vanishing fraction of the tiles.

This thesis contributes to the emergent field of physical network theory, with the overarching goal of identifying principles valid for a wide class of physical networks. My results revealed that the shape and connectivity of physical networks are intertwined and that their interaction strongly affects their behavior. Therefore, to fully understand such systems, both physical and network structures must be taken into account.

CEU eTD Collection

Every living being is an engine geared to the wheelwork of the universe. Though seemingly affected only by its immediate surroundings, the sphere of external influence extends to infinite distance.

- Nikola Tesla (1856-1943)

Serbian Engineer, Futurist, and Inventor

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Love never fails.

But where there are prophecies, they will cease; where there are tongues, they will be stilled; where there is knowledge, it will pass away. For we know in part and we prophesy in part, but when completeness comes, what is in part disappears. When I was a child, I talked like a child, I thought like a child, I reasoned like a child. When I became a man, I put the ways of childhood behind me. For now, we see only a reflection as in a mirror; then we shall see face to face. Now I know in part; then I shall know fully, even as I am fully known. And now these three remain: faith, hope, and love. But the greatest of these is love.

— Corinthians 13:8–13

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Chapter 1

Introduction

1.1 Background and Problem Statement

Network science seeks to uncover principles governing complex systems by studying connections between their constituents represented as a graph. This thesis focuses on *physical networks*, which represent a diverse class of systems in which nodes and links are physical entities embedded in three-dimensional space. Examples include molecular networks in metamaterials [1], the hard-wiring of computer chips [2], vascular systems [3, 4], and the brain neural networks [5]. Apart from being representable as combinatorial graphs (i.e. they have an abstract network structure), physical networks [6, 7, 8, 9, 10, 11] are also spatially embedded, their nodes and links have complex three-dimensional shapes and these nodes and links interact physically, for example, they obey volume exclusion [12, 13]. To understand how these characteristics influence their structure, evolution, and functionality, in addition to their abstract structure, their three-dimensional layout must also be taken into account.

Recent advances in mapping technologies provided detailed three-dimensional representations of physical networks, offering opportunities to investigate the relation between their layout and network structure. Examples of available large-scale data sets include neuronlevel maps of biological neural networks [14, 15], high-resolution MRI maps of vascular systems [4], and mycelia network mappings of fungi [16]. Representing the detailed shape of physical networks requires large quantities of data, and data of such volume and type is rarely studied within network science. Therefore, a suitable generalization of the toolset of network science is necessary to describe such systems and to understand how spatial embedding and physical constraints shape network connectivity, evolution, and robustness. This thesis contributes to this effort by introducing novel computational and analytical tools. By integrating spatial and physical constraints with traditional network science, my work aims to explore the interplay between network properties and physical structure. While my research foremost aims to advance network science, it potentially provides insights for applied areas studying specific physical networks.

1.2 Significance of the Problem

Physical networks perform central functions in both natural and artificial systems. For example, the human brain is composed of billions of interconnected neurons exchanging electrochemical impulses [5]; vascular networks regulate blood flow, lymph circulation, and oxygen transport [3, 4]; and computer chip wiring enables the functioning of modern technology [2]. These networks are not abstract graphs; their physical structure and spatial embedding significantly impact their structure, robustness, and evolution.

Therefore, the broader significance of physical network theory lies in its potential to influence a wide range of adjacent fields by offering generalizable methods and principles. By integrating physicality into network science, we not only deepen theoretical understanding but also we also provide practical tools for analyzing and designing complex systems. These insights, down the line, may find applications in biological systems and medicine. They could also extend to technological advancements, including bio-inspired neural networks for neuromorphic computing, the development of network materials with custom properties, and the design of infrastructure systems.

1.3 Contributions

Research on physical networks bridges network science and physical sciences by incorporating spatial embedding and physical constraints. This interdisciplinary approach uncovers new phenomena that emerge when networks occupy space and cannot overlap, offering insights into how physical properties influence network structure, dynamics, and robustness.

This thesis contributes to the emergent field of physical network research by introducing

computational and analytical tools to characterize physical networks, along with data compiled from different domains, and data representation and processing methods. Leveraging this empirical data and novel toolset, I present findings in three chapters: i) In Chapter 3, I provide evidence that shows that volume exclusion and physical shape significantly impact the growth and functionality of real physical networks ii) In Chapter 4, I quantify the physical and network structure for a collection of empirical networks, providing insights to inform model development. iii) In Chapter 5, I study the robustness of networks against physical damage through percolation analysis, showing that network layout encodes vulnerabilities that we are unable to capture relying on traditional methods of network science.

These results expand the scope of physical network research within network science and potentially provide a fresh perspective in fields studying physical networks, such as neuroscience or metamaterials.

1.4 Thesis structure

This thesis is built upon three research articles, each of which is discussed in a separate chapter [8, 17, 11]. While there is some overlap in notations, definitions, and datasets, each chapter is intended to be self-contained. The structure of the thesis is as follows:

- Chapter 2: A literature review of both relevant research fields culminating in the emerging field of physical network research. This chapter provides the broad background and immediate context for the thesis.
- Chapter 3: Introduction of the generalized meta-graph formalism, a tool that analyzes spatial proximity and highlights the correlation between physical layout and network structure.
- Chapter 4: A systematic analysis of physical network properties across 15 empirical datasets from various domains. This chapter introduces novel physical descriptors, including a measure of link confinement, and explores the relationship between physical and network structures.
- Chapter 5: Investigation of the robustness of physical networks under spatially correlated damage using percolation analysis. This chapter identifies the role of physical link length and other structural features in determining network vulnerability.
- Chapter 6: A conclusion summarizing the key findings, discussing their implications, and suggesting directions for future research.

Chapter 2

Literature review

In this chapter, I present a chronological development of relevant scientific fields that have given rise to the field of physical networks. Although physical network theory is a nascent field within network science, it builds on a long history of research-related topics and on specific physical networks. I will start by reviewing relevant areas of graph theory, and I continue with polymer physics and neuroscience. Then I cover related areas within network science: transport networks, spatial networks, and network-of-networks. Finally, I summarize the recent development of physical network research.

2.1 Graph theory

Physical network connectivity can be represented with combinatorial graphs [8] (also called the abstract network representation [17]), making graph theory a cornerstone of physical network research. Furthermore, subfields of graph theory, such as planar graphs, graph drawing, and spatial graph theory, explore how mathematical and geometrical constraints are explicitly or implicitly tied to the connectivity, size, or other graph properties. A similar notion is present in physical network research, which explores how spatial embedding and the thickness of the links affect the network growth and structure. In this section, I discuss these three areas of graph theory, relevant to physical network research - planar graphs, graph drawing problems, and spatial graphs.

Planar graphs [18] are graphs embedded in two-dimensional space whose edges do not intersect, hence planar graphs can be thought of as two-dimensional physical networks without the edge thickness. A typical problem in this subfield can be paraphrased as "If we have a graph with certain properties, a specific number of vertices, or edge connections, can it be embedded without any edges intersecting (i.e. is it a planar graph)?". One of the fundamental results from this field is Euler's formula [18], which states that the number of vertices v, number of edges e, and number of faces f (regions) abides by the following equation v + f = e + 2, illustrating how the non-intersecting condition intricately constraints the combinatorial network's structure. Another famous result is the Kuratwoski theorem [18, 19], which determines if a graph is planar, by analyzing its subgraphs, again revealing a connection between the layout and the network structure. The results from planar graph theory are not directly generalizable to three dimensions, as embedding the edges without crossing becomes a trivial task in d > 2 dimensions. Nevertheless, by introducing other types of constraints, such as adding thickness to edges and restricting the embedding volume, or avoiding edge entanglements, similar problems are studied for graphs embedded in three dimensions.

A graph drawing [20] is an embedding of a combinatorial network into some metric space; it is said that a drawing is a geometric realization of a graph. If a graph is drawn with no overlap between the edges, the graph drawing is called "crossing-free", which is a property possessed by all physical networks as well, due to physical repulsion forces [6, 21, 17]. As mentioned in the last paragraph, avoiding edge crossing of lines in three dimensions is a trivial task, unless additional constraints are imposed, such as turning edges into threedimensional objects by adding a thickness to them. Such three-dimensional drawings are also investigated within the graph drawing literature [20]. One of the foundational papers of the field is "On the Realization of Networks in Three-Dimensional Space" [22], by Kolomogrov and Barzdin, published in 1967. Inspired by the real physical networks (i.e. biological neural networks) [23] and how to construct them, they investigated how to embed combinatorial graphs in three-dimensional space, given certain constraints. Specifically, they draw graphs such that the nodes and links are restricted to follow an underlying orthogonal grid and they investigate how the minimum volume needed to draw the network depends on network size. Thus the result connects a property of the three-dimensional layout to a property of the combinatorial network. Later work on three-dimensional graph drawings investigated similar questions: connecting combinatorial graph invariants, (e.g. graph colorability) to the volume of the drawings (for a short overview see Ref. [20]). Even though the drawing algorithms do not evolve the network, rather, they are trying to embed a predefined combinatorial graph, they still might be used to inspire physical network growth models. For example, algorithms used for the problem of orthogonal grid drawings [20], where all edges are drawn on a grid, can be considered relevant for physical networks grown via random walkers on a grid [9].

Spatial graphs are spatial representations of graphs (i.e. embedding) in Euclidean space R^3 [24]. One of the extensively studied problems in the subfield of spatial graph theory can be paraphrased as: "Can a graph be embedded in space without the formation of entanglements?" [25]. Notable results are tied to entangled links (at least two disjoint cycles, that are not individually knotted and cannot be separated without cutting them) and entangled knots (a single loop in space, entangled in such a way that it cannot be untangled into a simple loop without cutting it). For example, there are combinatorial graphs in S^3 that cannot be embedded in physical space without forming an entanglement link or an entanglement knot, which are called intrinsically linked [26, 27] or intrinsically knotted graphs [28]. Recent physical network research has shown that entanglements can arise in the network growth process (for both model and empirical networks) and are shown to be connected to their network structure [7, 29].

The graph drawing literature and spatial graph theory are useful for physical network research in several ways: (i) the graph drawings can be used as representations of physical networks, providing a mathematical tool set to describe layouts, and (ii) theorems on embedding combinatorial networks reveal fundamental constraints on network layout imposed by combinatorial structure. However, graph drawing primarily focuses on realizations of a given graph, physical network research is interested in understanding how network and physical structure evolve together and how the interaction of the two leads to emergent phenomena [8, 9].

2.2 Polymer physics

Polymer physics [12] studies chains of covalently linked molecules, called polymers and other macromolecules [30]. Its main aim is to model and bridge the micro-level properties of the polymer chains, to the macro-level behavior of materials like plastics, rubbers, or biological macromolecules such as DNA. Polymer physics is relevant for physical network research for several reasons: First, some physical networks are composed of macro-molecules, like mitochondrial [31] or DNA contact networks [32]. Second, similarly to polymers, physical networks are made of elongated objects that physically interact with each other, e.g., they obey volume exclusion. Therefore, the mathematical characterization and models developed for polymer systems, such as self-avoiding random walks or

sequential deposition, are often adapted to general physical networks [9, 10].

To quantify the geometrical aspects of polymer systems and macromolecules, mathematical quantities such as persistence length [33, 34], radius of gyration [35, 34] and fractal dimensions [36] have been used. To quantify the rigidity of polymers at different scales, the persistence length l_p is introduced, as a way to measure how much the directions of subsequent chain segments are correlated. In other words, if one were to walk l_p length along the chain, the starting and ending points would, on average, be uncorrelated. As physical networks can be represented as a series of subsequently connected segments (i.e. a chain of segments), the persistence length was used as a physical intuition behind the parameter choice for the skeleton representation of network layouts. [8, 17]. The radius of gyration describes the distribution of a polymer's components around its center of mass, thus giving insight into the size and compactness of the polymer structure in solution. It is a scalar quantity that describes the three-dimensional spatial configuration of a polymer, thus providing a good tool for model comparison or analytical calculations, which were also adapted for physical network research [8]. Fractal dimension describes the space-filling of a physical object on multiple scales [37, 38, 39] and it has been used to characterize the shape of polymers [40] and also, empirical physical networks [17].

Since the introduction of self-avoiding random walks by Flory in the 1940s [41], random walk trajectories have been used to study the spatial configurations of macromolecules and polymers. As real macromolecules are objects that physically cannot overlap with each other or themselves (i.e. they obey the excluded volume effect [34]), a random walk that cannot intersect its trajectory (i.e., self-avoiding walk or SAW) has been utilized to recreate their spatial configurations [12]. As simple as random walk models are, self-avoiding walks and their variants have successfully characterized the macroscopic behavior of polymer systems, such as the size and shape parameters of random-flight chains, the determination of the distribution of end-to-end distance from moments, and polymer-chain adsorption at surfaces [42]. Recent work used random walks to model growing physical networks [9] and are used as null models to study empirical physical networks [17].

From the initial investigations of the car parking problem by Alfréd Rényi [43] and onedimensional polymer chain growth by Flory [44] in the 1950s, the field of random sequential deposition (also called addition or adsorption) [45, 46], has studied processes in which particles are sequentially introduced into a system, without physical overlaps. The key quantity of interest in random sequential deposition is the maximum packing density [47, 48], which represents the highest fraction of space that can be covered by the addition of objects to the system, without violating volume exclusion. As random sequential deposition respects the non-crossing condition, it was used as a foundational mechanism for physical network growth models, such as linear physical networks [8] and bundle formation model [10].

Overall, due to the similarity of the studied objects, polymer physics adds to the toolset of methods and measures that are useful for physical network research [6, 9, 8]. In polymer physics, the focus is on the collective properties of mostly disconnected, elongated objects, while in physical network research, the main focus is on the collection of objects that realize a complex network and lead to new types of phenomena, related both to the physical and the network structure.

2.3 Neuroscience

Neuroscience [49] is devoted to studying the nervous system and its function, which includes the biological neural networks, one of the largest and the most complex physical networks. For example, the human brain contains the order of magnitude $\approx 10^{11}$ neurons and glial cells [50], making it very difficult to fully map and analyze. In addition to the sheer size of these networks, there are individual and developmental differences [51] - each human has a unique brain, which changes and develops during their lifetime, thus adding to the complexity. Here, I briefly discuss three subfields of neuroscience relevant to physical network research - neuromorphology, neural development, and network neuroscience.

Neuromorphology [52, 53] studies the shape and structure of the nervous system. In a recent review study [54], 23 different open-source tools have been identified, which in total, provide 150 unique morphometric features of the neuron shape. From the perspective of physical network research, relevant results from this subfield show the relationship between the neuron morphology and their function [55, 56]. For example, Peter's rule [57], predicts the number of synapses between two neurons, based on the overlap of axonal and dendritic branches. Although they are not directly applicable to every physical network, some of the applied measures and principles could be generalized for the quantification of physical network shape and structure [17].

Neural development [58, 59] studies the processes that grow, develop, and change nervous systems. One of the ways these naturally occurring processes are researched is by simulation using computational models [60, 61, 62], which encapsulate physical and chemical processes of neural growth and guidance. Although the growth of neurons and the formation of biological neural networks occur within a specific context, the developed

mathematical models and principles could be generalized for physical network research as well.

Network neuroscience encompasses the application of network science methods to the study of nervous systems [63, 64]. In recent years, there has been a surge of high-quality data, which has allowed for network representation and analysis [63] of connectomes (neurons connected via synapses) [65, 66] and functional brain networks [67] (connected and dynamically active brain regions). Specifically, the availability of high-resolution morphological mappings of different species has allowed for the discovery of the geometric scaling law between neuron connection probability and their distance [68], along with the validation of the exponential decay pattern in axonal length distribution (exponential distance rule) [69, 70]. These large data sets with morphological information are important empirical examples of physical networks, that drive the development of a general theory of physical networks.

2.4 Transportation networks

Transporation [71] or transport networks [72] are networks through which material or mass flows between nodes in the network. They can be man man-made, such as gas pipelines [73] or naturally occurring, like vascular systems [74] of different species - from leaf veneration of plants [75, 76] to blood vessels of animals [4, 77]. Real transport networks are necessarily physical networks, composed of links and nodes that carry physical material, hence physical network research can also build on the principles and methods of transport network analysis, such as flow optimization, transport robustness, and scaling laws.

Flow optimization or optimal design [78] seeks to minimize resource costs while maintaining efficient transport of the material within the network. This is particularly crucial in biological networks [79], which must grow and adapt, as energy efficiency is vital for their survival. Techniques such as minimizing path redundancy or optimizing the network structure to reduce global energy loss are central to this approach [80, 81], thus, similar models optimizing the tradeoff between function and the cost of building and maintaining physical connections represent an important, but mostly unexplored direction in physical network research.

Transport network robustness [82] is the ability of the network to continue transporting material, despite failures or disruptions. Robustness is important for both man-made networks like road systems [83], which must withstand accidents or closures, and biological

networks, where physical damage or disease might damage the living tissue [84]. Studies on robustness often model the effect of damage as a percolation process [85] or eventbased attacks that stress-test the networks [86] to understand how much disturbance they can tolerate before a system-wide collapse occurs. Naturally, physical network robustness can be explored in the same manner, but also taking spatial embedding or geometrical properties into account [11].

Scaling laws describe how the properties of the network change with its size. These laws are useful in predicting how large-scale systems—whether natural, like ecosystems, or engineered, like cities—behave as they grow. For example, scaling laws help explain how the length and density of transport routes must adjust as the system expands [87]. In general, uncovering the scaling laws characterizing physical networks is an important step in understanding and predicting their evolution and organization. For example, recent work explored the scaling properties of a physical network model [8], showing that volume-exclusion and thickness of the networks impact their growth. Another recent work investigated the scaling between physical node size and degree, also exploring how this correlation affects diffusive dynamics on the network [9].

Overall, transport networks are an important example of physical networks, with the central theme in this research field being the tradeoff between cost and transportation efficiency. Studying similar tradeoffs, in a more general way, is a goal of physical network research as well, therefore it is important to incorporate the knowledge and principles from the field of transport networks

2.5 Spatial networks

Spatial networks [88] are networks embedded in real space; therefore, all physical networks are necessarily spatial networks, but not all spatially embedded networks are physical. For example, an online social network can be considered as a spatial network: users have a home location that can affect how they form connections in the online space; however, the links of the network are not physical objects [89]. A spatial network is typically described by its combinatorial network (i.e., the list of connections between node pairs) and the spatial coordinates of the nodes. In contrast, the characterization of a physical network requires much more data: in addition to the combinatorial network, we also need to describe the three-dimensional shape of each node and link. This difference in level of description means that the results of spatial network theory do not always translate to physical network research. In this section, I highlight concepts and methods developed for spatial networks that directly apply to or inspire physical network research.

Long links (i.e. measured by their Euclidean path length, compared to the system size or typical link length) in spatial networks are generally costly to build and maintain in terms of resources. For example, in transportation networks, longer connections, like highways, require more materials, higher energy consumption, and ongoing maintenance expenses. However, these long links are also crucial for the overall function of the network, as they often provide shortcuts that optimize flow and reduce the number of intermediary nodes [88]. This duality also holds for physical networks [17], which should be incorporated in physical network models [6]. Moreover, long links impact both the abstract and physical structure of a network - for some physical networks, longer links can provide more connectivity in the abstract network structure (i.e. long links tend to have high link degree or link betweenness centrality) [17], but for some other physical networks, they might lead to more entanglements or congestion in their layout [29].

The robustness of networks against external damage is a central question of network science, and it is often modeled as a percolation process. Spatial features in percolation are considered in three main ways: (i) Spatial embedding affects the structure of the network and hence affects its critical properties. For example, controlling the typical length of links leads to a crossover between mean-field-like to lattice percolation [90] (ii) Damage may spread in the network depending on space, through spatially restricted interdependence links [91]. (iii) The external damage applied to the network may depend on space. Examples of this method include the simulations of earthquakes [92], space weather events [93], or hurricanes [94] used to model the damage they might cause to the road or electricity transmission networks. Therefore, this approach can be extended to physical networks, where damage is modeled by removing links that pass through a certain volume in threedimensional space [11], which is elaborated in more detail in Chapter 5.

Spatial network theory mostly focuses on whether it is sufficient to know the location of the nodes, while other spatial features can be neglected. Physical networks on the other hand focus on the case when physical interactions between nodes and links cannot be ignored [8, 17]. This distinction requires us to extend the toolset of network science and thus extend to scope of spatial network theory.

2.6 Network-of-networks

Network visualization and spatial network research typically focus on network embeddings where nodes are points in space connected by straight lines. In the case of physical networks, however, it is often useful to consider nodes that are extended objects with complex shapes and links that are point-like connections between them. To capture the complex shape of nodes, we can represent the individual nodes as spatially embedded networks that are bound together with physical links, thus forming a network-of-networks [95]. For example, a biological neuron can be represented as a spatially embedded network where branching points are nodes and links are tube-like connections between them, and these networks representing individual neurons are then bound together by synapses, thus creating a network-of-networks [8]. This approach mirrors the primary and dual representations of road networks: the former treats road junctions as nodes and road sections connecting junctions as links, while the latter treats entire roads as nodes and connects them if they share a junction point [96]. The network-of-networks representation establishes a formal connection between multi-layer network theory and physical networks. In this section, I review how methods developed to analyze network-of-networks (including multi-layer, multiplex, and interdependent networks) are and could be adopted to characterize physical networks.

The supra-Lapacian matrix, an extension of the Laplacian matrix, was used to model diffusion processes and connectivity on multi-layer networks [97, 98, 99]. This method has inspired the introduction of the so-called physical Laplacian describing diffusion-like dynamics on the network-of-networks representation of physical networks [9] and it has been used to show that node volume, a physical characteristic, impacts the diffusion dynamics. Following this approach, future work investigates other ways physical properties of the systems affect dynamics on the network, for example, understanding the role of hubs in spreading dynamics or going beyond linear dynamics [100, 101].

The robustness of multi-layer and interdependent networks is a well-studied topic, for example, percolation [102] has been previously performed on spatially embbeded networksof-networks [103] to asses their robustness [104, 105]. Interdependent network percolation considers spatially embedded multi-layer networks, where nodes in different layers are connected by interdependency links. If a node in a layer fails, it causes nodes in other layers to fail in its proximity. Such events may trigger large cascades of node failure, leading to abrupt percolation transitions. Analogously, physical network damage may spread between nodes and links in each other's spatial proximity even if they are not connected in the abstract network [11]. Therefore, the results and methods of interdependent network percolation can be used to understand and model the spread of physical damage [106].

Multi-layer extensions of network centralities [107] make it possible to assign a centrality measure not just to individual nodes, but network layers too. Future work, therefore, adapting multi-layer centralities to the network-of-networks representation of physical networks can characterize the importance of physical nodes in a way that incorporates their physical structure. Furthermore, one may partition the bounding box of a physical network into equally sized regions [11], and then treat each region as a layer to form a multi-layer network. Applying multi-layer centralities to this representation would allow us to assign an importance not to individual nodes, but to spatial regions of the network.

The formal connection between networks-of-networks and physical networks provides a rich set of tools for physical network research. However, these tools must be adapted for use, since networks-of-networks literature typically focuses on systems with a few layers that are similar in size, while networks representing individual physical nodes focus on subnetworks that are large in number and have heterogeneous size distributions [8, 17]. While in my thesis, with a few exceptions, I mostly focus on physical network representations where nodes are spherical or point-like, future work should leverage the connection between the two research areas [9].

2.7 Physical networks

The term *physical network* is used in a number of contexts from computer hardware to chemical reaction networks [108, 109]. Here, I use it to mean networks of objects embedded in three-dimensional space, where physical constraints apply to nodes and links (e.g. non-crossing conditions), following the convention of Dehmamy et al [6] from 2018. The rise of available data describing the three-dimensional structure of networks spurred an effort to understand the fundamental principles of physical networks building on the framework of network science. In this section, I focus on the recent developments in this field to which my thesis also aims to contribute. I summarize three topics: tractable models of network formation, three-dimensional link organization, and dynamical processes on physical networks.

The influential Barabási-Albert and Erdős-Rényi models of traditional network science are minimal tractable models that aim to strip away the system-dependent, and often complicated details of network formation, and focus on processes present in a wide range of systems. Such models allow us to understand general mechanisms shaping networks, serve as null models to compare empirical data, and as a starting point for more complex models. Several recent works introduced such minimal models for physical networks; what they have in common is that all models incorporate volume exclusion to model physicality, i.e., nodes and links are not allowed to intersect each other. The model of Dehmamy et al [6] generated abstract networks using the classic BA and ER models and found a threedimensional layout that minimizes the length of links while obeying volume exclusion. By changing the diameter of nodes and links, the authors discovered when physicality affects the layout and how this physical region depends on the characteristics of the combinatorial network. The approach of Dehmamy et al first generates a combinatorial network and then a realistic layout, mimicking the approach of graph drawing problems; therefore, it is unable to capture how the layout can affect network structure. To overcome this limitation, Posfai et al [8] introduced a model where physical layout and network structure evolve together. In this work, the linear physical network (LPN) model is generated by sequentially depositing straight rods into the unit cube, respecting the non-crossing condition. Given the minimal assumptions behind this model, it can be also considered the "ER model for physical networks". The results of this research show how link thickness and the number of links, due to their physicality, limit which type of network structures can be realized. Additionally, there is an emergent correlation between the layout and network structure, as it is encoded in the spectrum of the adjacency matrix, which carries the information about the layout. The aforementioned models had nodes as spheres or point-like objects, where links are the tubes that connect them. In reality, links may have a more complex shape, where for example, a neuron might be considered a node, while a synaptic connection might be considered a link. Defining extended objects as nodes and their contact points as links, a minimal random walk model on a grid has also been employed to generate physical networks [9]. Due to the effect of physicality (i.e. random walkers avoid each other), the emergent network structure has a broad degree distribution and node degree and node volume correlation. Readapting models from other fields or the introduction of new physical network models is still a promising area of research, which would help in answering fundamental questions about the importance of physicality to network structure.

The three-dimensional organization of physical networks is another significant area of investigation. For example, utilizing knot theory, researchers measured the entanglement of physical links in model networks and real systems [7, 29]. Findings reveal that the intertwined structure of non-crossing networks carries physical energy and undergoes transitions between different states of intertwining, quantified by measures such as the graph linking number [7]. Additionally, Bonamassa et al [10] explored link bundling, where physical links follow trajectories parallel to each other, and have demonstrated, using a simple linear physical network model, that due to volume exclusion alone, link bundles can be formed.

Understanding the relationship between the physical properties of nodes and links and their role in the abstract network is a crucial step in understanding the effect of physicality on networks. For example, our recent work [17] has shown using model networks and empirical data that a positive correlation between node volume and degree is prevalent in physical networks, and that such correlations can have a strong effect on both network evolution and dynamics on networks. Concepts like the generalized meta-graph and the link confinement, discussed in Chapters 3 and 4, reveal that spatially confined physical nodes and links tend to be central in the abstract network. The meta-graph representation serves as an efficient tool for physical networks [8], which can capture the interactions and collisions resulting from physical constraints, for both model and empirical networks, deepening our understanding of how physical properties influence network growth and function.

Physicality does not only affect network structure, but can also influence its function or dynamical behavior, including diffusion processes governed by the Laplacian operator, which were studied to understand how physical constraints impact the flow or the spread of information, energy, or materials through a physical network [9]. Investigations into spatial percolation processes (i.e. sequential spatially correlated attacks), discussed in Chapter 5, have revealed that robustness and connectivity are affected by the three-dimensional layout, highlighting differences from traditional percolation in abstract networks [11].

Overall, research on physical networks bridges the gap between network science and the physical sciences, and by incorporating spatial embedding and physical constraints, it explores new phenomena and properties that arise when networks occupy space and cannot overlap. This interdisciplinary approach has led to significant insights into how physical properties and constraints influence network structure, dynamics, and robustness, expanding our understanding of complex systems in natural and engineered contexts.

Chapter 3

Generalized meta-graphs on real networks

3.1 Introduction

Recent experimental advances provide increasingly accurate three-dimensional maps of physical networks; however, network science lacks the tools to understand how physicality affects the structure and the evolution of their abstract networks. In this chapter, I introduce one such tool called the generalized meta-graph based on my contributions to Pósfai et al [8]. In this work, the impact of physicality was studied using a simple physical network model, where nodes are spheres and links are straight cylinders. The authors introduced the so-called meta-graph to keep track of potential conflicts between physical links, this meta-graph provided a framework to characterize the model analytically. Crucially, the meta-graph relies on the fact that the links are straight in the model. However, real physical networks are typically not linear [17], meaning a link cannot be accurately represented with a straight rod. Furthermore, if we add a new non-straight physical link to a network, we can route it infinitely many ways; therefore, it is impossible to keep track of emerging physical conflicts relying on the original definition of the meta-graph. Despite this limitation, we show that it is possible to define a generalized version of the meta-graph that is useful to characterize the physical structure of any existing physical network, which can be used to predict their functional features, like synapse formation in the brain.

In this chapter, I introduce linear physical networks and the original meta-graph in Section 3.2, followed by the definitions of the skeleton representation in Section 3.3 and generalized meta-graph in Section 3.4. Finally, the restricted meta-graph is introduced in Section 3.5, applied in Section 3.6, with results being discussed in Section 3.7.

3.2 Linear physical networks and the metagraph

In this section, I briefly introduce the simple network model studied in Pósfai et al [8] and the related meta-graph formalism.

A linear physical network (LPN) is a network embedded in three-dimensional Euclidean space such that each node in the network is a sphere and each link is a capped cylinder with diameter λ . The nodes and links satisfy volume exclusion, meaning that they cannot overlap in space. To avoid restricting the maximum node degree, we allow a node to overlap with the links that are connected to it, and we allow links to overlap with each other if they share an endpoint, leading to the following formal definition:

Definition 3.2.1. A λ -linear physical network (LPN) in its strictest sense is a graph \mathcal{G} such that the vertex set of \mathcal{G} is a point set $\mathcal{P} \subset \mathbb{R}^3$ and the edges $(p_1, p_2) \in \mathcal{E} \subset \mathcal{P}_2$ are straight segments connecting these points, where \mathcal{P}_2 is every unordered pair formed of elements of \mathcal{P} . We require that the distance is at least λ between

- 1. every point pair $p_1, p_2 \in \mathcal{P}$, with $p_1 \neq p_2$ (node-node interaction);
- 2. every point p_1 and every edge $(p_2, p_3) \in \mathcal{E}$, with $\{p_1\} \cap \{p_2, p_3\} = \emptyset$ (node-link interaction);
- 3. every pair of edges $(p_1, p_2), (p_3, p_4)$, respectively, with $\{p_1, p_2\} \cap \{p_3, p_4\} = \emptyset$ (link-link interaction).

Here we define the meta-graph $\mathcal{M}(\mathcal{P}, \lambda)$, which is an auxiliary graph that captures the physical constraints between link candidates connecting point pairs $(p, q) \in \mathcal{P} \times \mathcal{P}$.

Definition 3.2.2. The meta-graph $\mathcal{M}(\mathcal{P}, \lambda)$ is a graph defined for a $\lambda > 0$ and point set \mathcal{P} , such that

1. the vertex set of $\mathcal{M}(\mathcal{P}, \lambda)$ is the set of link candidates that do not overlap with nodes, i.e.,

$$\mathcal{V}_{\text{meta}} = \{ (p,q) \in \mathcal{P}_2 : d((p,q),r) \ge \lambda \ \forall \ r \in \mathcal{P} \setminus \{p,q\} \}$$

2. and the edges of $\mathcal{M}(\mathcal{P}, \lambda)$ connect link candidates that overlap in space, i.e.,

$$\mathcal{E}_{\text{meta}} = \frac{\{((p,q), (r,s)) \in \mathcal{V}_{\text{meta}} \times \mathcal{V}_{\text{meta}} : d((p,q), (r,s)) < \lambda \\ \forall (r,s) \in \mathcal{P} \times \mathcal{P} \text{ and } \{p,q\} \cap \{r,s\} = \emptyset\}.$$

If link-node interaction is not considered, the vertex set of the meta-graph contains all possible point pairs, i.e., $\mathcal{V}_{\text{meta}} = (p,q) \in \mathcal{P} \times \mathcal{P}$ and $N_{\text{meta}} = N(N-1)/2$, where $N_{\text{meta}} = |\mathcal{V}_{\text{meta}}|$ and $N = |\mathcal{P}|$.

To illustrate both the LPN and the meta-graph, Fig. 3.1 presents an example of an 8-node LPN. Once a linear physical network has been generated, its corresponding meta-graph can be constructed by identifying all possible links and their physical constraints. The figure showcases two examples: a low link diameter of $\lambda = 0.01$ in Fig. 3.1a, where most links are allowed, and a higher diameter of $\lambda = 0.2$ in Fig. 3.1c, where many links are restricted due to volume exclusion. The corresponding meta-graphs are shown in Fig. 3.1b and Fig. 3.1d, where each vertex represents a candidate link, and edges indicate mutual exclusion due to spatial overlap. This visualization highlights how increasing λ reduces the feasible connectivity of the linear physical network by enforcing stricter geometric constraints, which is reflected in the structure of its meta-graph.

In the following sections, I will generalize the meta-graph to study networks where the links have arbitrary shapes.



Figure 3.1: Linear physical networks (LPN) (a,c) A linear physical network (LPN) with eight nodes, showing its structure for two different λ values. While for the small λ in (a) most links are allowed, for $\lambda = 0.2$ in (b) many links are forbidden, as they would overlap with other links. (b,d) The 28 vertices of the meta-graph represent the candidate links of the physical network, each labeled by the node numbers they attempt to connect. Two vertices are connected if the corresponding links overlap, hence they cannot coexist in a physical network. Figure adapted from co-authors [8].

3.3 Skeletonized representation of physical networks

To generalize the meta-graph, we introduce an appropriate representation of the layout - skeletonized representation, which allows for the generalization of formalism applied to linear links or nodes, to the non-linear cases. For example, this representation would allow to generalize of the meta-graph formalism on physical networks where nodes are not just straight rods, but more complex, extended objects [17, 9].

Most real physical networks, from neural or vascular networks to rock fissures, are obtained as volumetric data from experiments. Volumetric representation of a physical network means that the three-dimensional space is divided into voxels, the three-dimensional equivalent of pixels, and the voxels are labeled to be inside or outside the physical network. While such representation provides the most accurate description of the shape of a physical network that is available, it is both computational and analytically demanding to analyze. Therefore volumetric data is routinely approximated by skeletonization, capturing less details, but providing a more concise description [110].

The skeleton of a physical network is in fact a variant of a linear physical network: a skeletonization algorithm approximates the shape of a physical network with vertices and straight segments inside the physical network and associates a radius to each vertex. Multiple segments in the skeleton can correspond to what is considered a separate entity in the original network, e.g., a single neuron in a neural network or a non-branching section of a vessel in the vascular network is represented by a collection of straight segments in the skeleton. Therefore it is common to associate a label with each segment connecting it to the original object it represents. Altogether, a skeleton representation for our purposes must have the following properties

Definition 3.3.1. A skeleton representation S is a graph with vertex set V and edge set \mathcal{E} together with

- a position $\mathbf{r}: \mathcal{V} \to \mathbb{R}^3$ and a radius $\rho: \mathcal{V} \to \mathbb{R}^+$ associated to each vertex,
- and a label $\sigma : \mathcal{E} \to \mathbb{Z}$ associated to each edge.

Note that the skeleton S is a physical realization of the abstract network G, where the node set of G is the set of labels in S.

To recover an approximate volume of a physical network from a skeleton, we take the union of spheres centered at $\mathbf{r}(v)$ with radius $\rho(v)$ for each vertex $v \in \mathcal{V}$, and truncated cones that have axis corresponding to the segment $(\mathbf{r}(v), \mathbf{r}(w))$ and parallel faces with

radii $\rho(v)$ and $\rho(w)$ for each edge $(v, w) \in \mathcal{E}$. Alternatively, a less accurate but simpler approximate volume can be obtained by substituting each edge with a cylinder with axis $(\mathbf{r}(v), \mathbf{r}(w))$ and radius $(\rho(v) + \rho(w))/2$.

The quality of the approximation can be controlled by the number of vertices in the skeleton. There is, however, no single definition of the cost function that characterizes how good an approximation is, and there are a large number of skeletonization algorithms available and used in various scientific disciplines [111]. We obtained the data that we work with already in a skeleton representation unless otherwise noted.

3.4 The generalized meta-graph

Having defined the skeletonized representation, we can generalize the metagraph, whose goal is to characterize a given physical network by identifying components that are in a physically confined space. Specifically, we define the generalized meta-graph \mathcal{M}_g for a skeleton representation of a physical network.

Definition 3.4.1. Given a skeleton representation S and a parameter $\Delta \lambda$, the associated generalized meta-graph $\mathcal{M}_g(\Delta \lambda, S)$ is a graph with vertex set corresponding to the edge labels of S. We increase the diameter of each skeleton-vertex by $\Delta \lambda$, and meta-vertices l_1 and l_2 are connected if the approximate volume corresponding to the labels l_1 and l_2 now overlap.

The labels l_i of a skeleton representation S correspond to separate nodes or links of a physical network, for example, a label can identify the skeleton of a single neuron in a neural network or a vessel segment in a vascular network. The degree of a neuron or vessel in $\mathcal{M}_g(\lambda, S)$ quantifies its physical confinement: it counts the neurons or vessels that surround it in space.

3.5 Empirical networks and the restricted meta-graph

A skeleton S is a physical realization of an abstract network G, such as the synaptic network for neurons or the network of vessel segments connected together by junction points. There are, however, many alternative skeletons S' that realize the same abstract network, prompting the question: What are the properties of S that are common in all realizations and what are the differences? Two neurons that are connected in the synaptic network or two vessels bound together at a junction point are necessarily adjacent in physical space, hence they become connected in the generalized meta-graph for low $\Delta\lambda$ for any possible physical layout S' realizing the abstract network. To measure the excess confinement of a neuron, i.e., the confinement beyond what is necessitated by the synaptic network, we define the restricted meta-graph, where we exclude all edges in the generalized meta-graph that are between neurons that are synaptic partners or vessel segments bound together.

Definition 3.5.1. Given a generalized meta-graph $\mathcal{M}_g(\Delta\lambda, S)$ and a corresponding abstract network \mathcal{G} , the restricted meta-graph $\mathcal{M}_r(\Delta\lambda, S)$ is obtained by removing each edge $e = (l_1, l_2)$ from $\mathcal{M}_g(\Delta\lambda, S)$ if l_1 and l_2 are adjacent in \mathcal{G} .

Figure 3.2 shows an example comparing the generalized and the restricted meta-graph.

Note that the original meta-graph $\mathcal{M}(\lambda, \mathcal{P})$ is a special case of the restricted meta-graph. We start from a skeleton S corresponding to a complete graph on \mathcal{P} with uniform link thickness 0, and labeling each link uniquely. The restricted meta-graph $\mathcal{M}_r(\lambda, S)$ obtained by thickening each link by λ is equivalent to the original meta-graph $\mathcal{M}(\lambda, \mathcal{P})$.

We calculate the restricted meta-graph for the four real physical networks (for more details about the data sets, see SI 3.8.2) as a function of $\Delta\lambda$, where we measure $\Delta\lambda$ in units of the average radius of the original network. As a reference, we also generate a jammed random linear physical network with N = 300 nodes and $\lambda = N^{-1/2}$ and calculate its restricted meta-graph by thickening the links present in the jammed state. Figure 3.3f shows the average meta-degree $\langle k_{\text{meta}} \rangle$ as a function of $\Delta\lambda$ for each network, revealing two distinct patterns: for the brain network, we observe an initial fast increase in the average metadegree followed by a slower, steady growth. Such rapid growth is absent in the vascular, mitochondrial, and root system networks, and is also absent in random linear networks.

This different behavior represents the differences in the building blocks: the connectome consists of highly intertwined neurons with complex shapes, while the other three networks consist of tube-like components, such as vessels, molecular chains, and roots. Indeed, if we subdivide each neuron into smaller non-branching segments before constructing the meta-graph, we recover the superlinear behavior without the initial rapid growth of of $\langle k_{\text{meta}} \rangle$ (Fig. 3.3e).


Figure 3.2: The generalized and the restricted meta-graph. (a) The schematic layout of five neurons. The black neuron must be physically adjacent with its synaptic partners (purple and orange) and depending on the layout may be confined by other neurons it does not synapse with (green and blue). (b) In the synaptic network realized by the physical layout (a), the black neuron has degree two. (c) In the generalized meta-graph a neuron is connected with all neurons it overlaps with after thickening its branches by $\Delta\lambda$; therefore the generalized meta-degree of the black neuron is four. (d) In the restricted meta-graph, we remove edges representing an overlap between synaptic partners; therefore, the restricted meta-degree of the black neuron is two.



Figure 3.3: The restricted meta-graph of real networks. (a-d) Three-dimensional rendering of the skeletonized description of the four real physical networks. (e) For the vascular, mitochondrial, and root system networks, we label non-branching sections uniquely, i.e., paths connecting skeleton vertices with degree not equal to two (color-coded sections). In the generalized and restricted meta-graph the vertices represent these non-branching sections. (f) Average degree of the restricted meta-graph $\langle k_{\text{meta}} \rangle$ as the thickness of the network is increased by $\Delta \lambda$, where $\Delta \lambda$ is measured in units equal to the average radius of the original physical network. Dots represent real physical networks and the dashed line represents a linear physical network with N = 300 nodes and $\lambda = N^{-1/2}$. To show that the complex shape of the neurons is responsible for the shape of $\langle k_{\text{meta}} \rangle$ ($\Delta \lambda$) we divide the neurons into smaller non-branching sections and we calculate $\langle k_{\text{meta}} \rangle$ treating these sections as the vertices of the restricted meta-graph.

3.6 The meta-graph of the neural network

In the previous section, we calculated the meta-graph of four real networks. Here, we take a closer look at one of the case studies, the network representing the brain region of a fruit fly, and we investigate correlations between the node's position in the meta-graph and in the synaptic network.

We illustrate the process in Fig. 3.4a, which shows the meta-graph $\mathcal{M}_{\mathfrak{s}}(\Delta\lambda)$ of the fruit fly connectome, consisting of N = 2,970 neurons and M = 35,707 synapses serving as links. According to Peter's rule, neurons can only form synapses if their axons and dendrites are in close physical proximity [57, 112]. Hence we expect and find a strong correlation between the meta-degree and the number of synapses. To abstract from these obvious correlations between the generalized meta-graph and synapse formation, we focus only on conflicts between neurons that are not connected by synapses and therefore are the result of the packing of the neurons in the brain. We achieve this by building a restricted meta-graph, where we remove the synaptically connected links from the metagraph (for more details, see SI 3.8.1). Figure 3.4a highlights the vertex with the highest restricted meta-graph degree $k_{\rm A} = 13$, corresponding to the most physically confined neuron, bordered by 13 other neurons that it does not synapse with (Fig. 3.4b,c). This prompts the question: Is the most confined neuron also the most central in the synaptic network? To find an answer, we performed a linear regression between the restricted meta-degree and the logarithm of synapses, revealing a positive association between the physical confinement and the functional role of neurons (Fig. 3.4e, slope $a = 0.356 \pm 0.022$ and $R^2 = 0.26$). Our result indicates that synaptically central neurons in the connectome are tightly confined in the brain by non-synaptic partners.

This is non-obvious, as we can construct physical networks that have negative correlations between the number of synapses and the restricted meta-degree: consider a physical network with N nodes where each neuron is physically adjacent to all N - 1 other neurons, as shown in Fig. 3.5. If a neuron *i* has k synaptic partners, it has N - 1 - k meta-degree, resulting in a perfect anticorrelation between the number of synapses and the meta-degree. Additionally, some studies show that in dense neural circuits, neurons that are physically close to each other are more likely to form synaptic connections, as spatial proximity increases the chance of their axons and dendrites coming into contact [113]. However, other studies highlight the prevalence of non-local connections guided by molecular cues and functional specificity, indicating that spatial proximity alone does not universally determine synaptic connectivity [114, 115]. This complexity is further explored in a study [57] critically examining Peter's Rule—the idea that synapse formation is largely determined by axo-dendritic overlap. While the study confirms that overlap is a strong predictor at the cell-type level (between the neuron types), it also shows that many potential connections remain unrealized due to selective wiring rules. Therefore, in a brain network where physical proximity does not guarantee connectivity, the persistence of a positive correlation—even after removing direct synaptic partners suggests a deeper structural or developmental constraint. The persistent positive correlation also confirms that the generalized meta-graph captures important properties of the physical layout and can be used to systematically study the connection between physical and abstract network structure.

As connectome mapping aspires to scale up to the 10^{11} neurons of the human brain [50], new mathematical and computational formalisms, like the one offered by the meta-graph, are needed to unveil the predictive power of these exceptionally large physical network maps. A full description of the layout of a physical network requires copious amounts of data that is difficult to handle computationally and also limits analytical advances. For example, the Hemibrain dataset describes the 3D trajectory of approximately 25000 neurons of a fruit fly using 117 million linear segments [5]. Naïve identification of physical conflicts, therefore, requires 10^{16} distance computations, a prohibitive computational burden for most researchers. In contrast, the 25000×25000 adjacency matrix of the generalized meta-graph can be represented using a few hundred MB of data, hence publishing it together with the adjacency of the connectome would allow the computationally efficient study of the relation between physical and abstract network structure.



Figure 3.4: Meta-graph of a real neural network. (a) Each vertex of the restricted meta-graph represents a neuron in the fruit fly connectome [5]. A link between two vertices of the restricted meta-graph implies that the corresponding neurons overlap if we increase their thickness by $\Delta\lambda \approx 0.028$ but they are not connected by synapses. The neuron with the highest restricted meta-degree, A, has 13 connections, while 1469 isolated vertices (not shown) correspond to neurons that are conflict-free for $\Delta \lambda \approx 0.028$. (b) A three-dimensional rendering of neuron A (red) and its neighbors, shown here as a twodimensional projection for visualization purposes, highlights that neuron A exhibits the most excess confinement. Displayed alongside are the 13 neurons within distance $\Delta \lambda$ of A, which are connected to A in the restricted meta-graph and highlighted in (a). Neuron colors correspond to the meta-vertices in (a). (c) Neuron A, being an extended physical object, exhibits spatial conflicts with other neurons that are localized to specific regions of the physical network, as illustrated in its three-dimensional structure (projected in 2D for this figure). (d) The degree distribution of the restricted meta-graph for $\Delta \lambda \approx 0.028$. Vertices with degree zero correspond to conflict-free neurons, i.e., lack proximity within $\Delta\lambda$ with other neurons that are not connected to them via synapses. Physically confined neurons have high restricted meta-degree, indicative of a large number of physical conflicts. (e) The dependence of the restricted meta-degree on the number of synapses of each neuron indicates that the restricted meta-degree is predictive of synapse formation. The dashed line corresponds to linear regression between the restricted meta-degree and the logarithm of the number of synapses for each neuron. Small markers represent individual neurons, large markers are binned averages. For illustration purposes we chose $\Delta\lambda$ such that the meta-graph is sparse. In SI 3.8.1, we repeat the above analysis for various $\Delta\lambda$ values, finding that the positive association between the restricted meta-graph and the synaptic network is robust.



Figure 3.5: Physical layout with negative correlation between restricted meta-degree and abstract network degree. (a) A physical network with N = 5 nodes, each color corresponds to a separate node. We construct the network by placing five parallel logs in one layer, then we place another five parallel logs on top of them rotated by 90 degrees. (b) Logs of the same color are bound together, meaning that each physical node is a cross. (c) In this construction, each physical node touches every other node; therefore, the corresponding generalized meta-graph is fully connected, each node has generalized meta-degree 4. Since all physical nodes are adjacent in space, this physical layout can realize any abstract network. For example, if nodes represent neurons, the physical layout can support any synaptic network. If neuron i in the synaptic network is connected to k_i other neurons, its restricted meta-degree is $N - k_i$, meaning that there is a perfect negative correlation between the degree in the synaptic network and the restricted meta-degree.

3.7 Discussion

Recent experimental advances, driven by connectomics and high-resolution MRI, have offered detailed and accurate maps of a wide range of physical networks, from the structure of individual neurons in a brain, to 3D maps of large vascular systems. These advances unveiled an important gap in network science: the lack of understanding of how physicality affects the network structure. The need for a quantitative and conceptual framework goes beyond biology: complex metamaterials, combining random and repetitive local structures [116, 1, 117], offer other manifestations of physical networks, and so do computer chips that pack billions of transistors.

In this chapter, I introduced a formalism designed to systematically explore the structure of real physical networks, which are characterized by non-uniform node density, heterogeneous link diameters, and bent links [17]. The impact of these features can be studied by using the generalized meta-graphs, where for example, the link confinement measure, also introduced in the following Chapter 4, can be considered an adaptation of the meta-graph formalism. Other issues are less straightforward extensions of this work but may benefit from the meta-graph framework, such as understanding the effect of the physical architectures on network robustness [118, 119, 11], which is investigated in Chapter 5, or on dynamics on networks [120, 121, 122, 123, 124, 9].

A quantitative understanding of physicality can directly impact multiple areas of science. For example, at this point it is unclear to what degree the observed brain connectomes are driven by the genetic processes that govern their developmental biology [125], or by physical constraints that the neurons and their interactions must obey, limiting a neuron's ability to synapse with desired target neurons in a very dense environment. Answers require a modeling and analytical platform that helps us systematically explore the competing role of genetics and physicality.

3.8 Supplementary Information

3.8.1 The generalized and the restricted meta-graph of the fruit fly brain network

Neurons can only form synapses if their axons and dendrites are in close physical proximity; therefore, if we increase the diameter of neuron branches, neurons will quickly overlap with synaptic partners (Fig. 3.6).

In the generalized meta-graph $\mathcal{M}_g(\lambda)$ of the fruit fly brain network, vertices represent neurons, and edges indicate conflicts between pairs of neurons – both between pairs that are connected via synapses and pairs that are not. Since synaptic partners necessarily overlap, we expect a positive correlation between the number of synapses a neuron has and the generalized meta-degree of the neuron, this expectation is indeed confirmed by numerical measurements (Fig. 3.7).

On the other hand, edges of the restricted meta-graph $\mathcal{M}_r(\lambda)$ represent physical conflicts only between neuron pairs that are not connected by synapses. In other words, $\mathcal{M}_r(\lambda)$ focuses on conflicts that are not necessitated by the synaptic network. Fig. 3.8 shows that we again find a positive correlation between the number of synapses and the restricted meta-degree of a neuron, indicating that neurons central in the synaptic network are also tightly confined by other neurons. This is non-obvious, as we can construct physical networks that have a negative correlation between the number of synapses and the restricted meta-degree (Fig. 3.5).

One of the potential explanations for the relationships observed in the Figs. 3.6, 3.7 and 3.8 could be the cable length of the neuron. Longer cables provide more spatial opportunities to encounter other neurons, thereby increasing both the chance of forming synapses and the number of potential neighbors. Also, recent studies have shown that in physical networks, a node's degree is often proportional to its size, both in neural networks [126] and other empirical and model networks [9].



Figure 3.6: **Conflicts with synaptic partners.** To form synapses neurons must be in close vicinity of each other; therefore, after thickening the neurons, synaptic partners will be in physical conflict. We show the meta-degree (i.e., the number of conflicts) of the neuron highlighted in Fig. 4 of the main text with non-synaptic (blue) and synaptic (orange) partners as a function of $\Delta\lambda$. Initially, for $\Delta\lambda = 0$ the neuron has no conflicts. After increasing the thickness of the neural branches all 312 synaptic partners become quickly in conflict with the neuron. The number of conflicts with non-synaptic partners outnumbers the conflicts with synaptic partners, for example, at $\Delta\lambda \approx 3.34$ the neuron has 312 conflicts with synaptic partners and 574 conflicts with non-synaptic partners.



Figure 3.7: Generalized meta-graph of the fruit fly brain network. (a) The generalized meta-degree distribution for varying $\Delta \lambda$ values. Physically confined neurons have high meta-degree. (b) Two neurons that are connected by a synapse are necessarily adjacent in physical space, hence are connected in the generalized meta-graph. Hence we expect to find a positive correlation between the generalized meta-degree and number of synapses.



Figure 3.8: **Restricted meta-graph of the fruit fly brain network.** (a) The restricted meta-degree excludes edges between neurons that are synaptic partners, capturing the excess confinement of a neuron that is not necessitated by the synaptic network. For illustration purposes, in the main text we focused on value of $\Delta\lambda$ (blue) that produced a sparse restricted meta-graph. Increasing $\Delta\lambda$ may significantly increase the average meta-degree. (b) We again observe a positive correlation between the restricted meta-degree and the number of synapses for all tested $\Delta\lambda$ values.

3.8.2 Data sets

Fruit fly brain

Relying on automated imaging techniques, a recent project mapped out a large fraction of the brain of the fruit fly *Drosophila melanogaster* containing the three-dimensional map of approximately 25000 neurons and the location 20 million synapses [5]. We downloaded the skeletonized data describing the shape of each neuron through the publicly available NeuPrint API [127].

To reduce the computational complexity, the network had to be sub-sampled, which is a non-trivial task, and we carefully considered different approaches when designing the study. The challenge arises because neurons in the fruit fly brain are not strictly confined to single brain regions, making it difficult to determine their inclusion based on anatomical boundaries alone. However, synapses in the dataset are annotated with precise spatial coordinates and assigned to specific brain regions [5]. This allowed us to select neurons based on their synaptic activity in a region, rather than attempting to assign entire neurons to regions directly. We explored two strategies: (i) extracting a cubic sample independent of functional brain regions, and (ii) selecting neurons based on defined brain regions using synapse location. In both cases, we considered whether to truncate neuron skeletons at specific boundaries or to retain their complete skeletons. Ultimately, we opted to focus on a well-defined region of interest and to keep entire neuronal skeletons intact. This choice was made for two key reasons:

- 1. Ensuring that neurons in the sample are meaningfully connected and functionally relevant within the selected region.
- 2. Ensuring consistency in pairwise relationships in the generalized meta-graph: specifically, if two neurons are included in the sample, whether or not they are connected in the generalized meta-graph remains unchanged, regardless of whether the sample is extended. That is, the meta-graph of the sample forms an induced subgraph of the full meta-graph, preserving all synaptic connections among sampled neurons exactly as they appear in the full network.

While this method provides a practical and functionally motivated approach, we acknowledge that it does not fully resolve the complexities of defining neuron membership in a given region. Future work could avoid sampling issues entirely by constructing the generalized meta-graph of the entire network, enabling a more comprehensive analysis.

Based on this methodology, we analyzed all neurons that had synaptic connections in the

Medula brain region (labeled ME(R), Fig. 3.3a) [128], which contains 2979 neurons and $1.464 \cdot 10^6$ segments, making it a computationally difficult task to identify collisions between neurons exactly. To overcome this difficulty, we substitute each neuron skeleton with a point cloud and use an efficient k-d tree implementation to query minimum distances between them.

In the skeletonized data set, each segment is labeled by the neuron that it belongs to, hence the meta-vertices represent neurons. The skeleton together with the location of the synapse is a physical realization of the synaptic network.

Vascular network

The vascular network data set describes the vasculature found in a $600 \times 600 \times 662 \ \mu m$ sample of a mouse cortex (Fig. 3.3b) [4]. The data is provided as a skeleton including radii at the skeleton vertices. We uniquely label non-branching vessel sections, i.e., each path connecting a pair of skeleton vertices with degree $k \neq 2$ receives a unique identifier. The skeleton is a physical realization of an abstract network, where nodes are vessel segments, and two nodes are connected if the corresponding vessels are bound together at a junction point. We construct the generalized meta-graph such that the meta-vertices represent the labeled vessel segments.

Mitochondrial network

The mitochondrial network data represents the mitochondrial reticulum of yeast cells (Fig. 3.3c) [31]. The data set is available both as a skeleton and as a mesh representing the surface. Radii is not provided with skeleton vertices; therefore we extracted a radius for each skeleton vertex based on the surface mesh using the Skeletor python package [129]. Similarly to the vascular network, we uniquely label non-branching sections of the skeleton, and we construct the generalized meta-graph such that the meta-vertices represent these labeled sections.

Root system

The root network describes the root system of a *Cryptomeria japonica* tree (Fig. 3.3d) [130]. The data is provided as a skeleton including radii at the skeleton vertices. We uniquely label non-branching root sections, i.e., each path connecting a pair of skeleton vertices with degree $k \neq 2$ receives a unique identifier. We construct the generalized meta-graph such that the meta-vertices represent these labeled sections.

Chapter 4

Three-dimensional shape and connectivity of physical networks

4.1 Introduction

Recent physical network research investigated artificial spatial embeddings of complex networks that obey volume exclusion [6], the entanglement of physical links [131], models of physical network growth [8, 9], and the effect of physical shape on the dynamics on networks [9]. However, systematic exploration of the three-dimensional shape, the network properties, and the relationship between them in real networks is still lacking. Such exploration is hampered by the lack of standardized representation. First, there is the technical difficulty that experimental maps of physical networks, like neural or molecular networks, are collected, processed, and analyzed with domain-specific methodology. Therefore, any investigation of physical networks must be preceded by the time-consuming and computationally burdensome task of data pre-processing. Second, even seemingly simple questions like what is a node and a link in a physical network carry a level of ambiguity: a physical network is a continuous object in space; to represent it as a network, we must discretize it into nodes and links. The definition of nodes and links in turn affects, for example, what properties of the network we can study or the right choice of null models.

Here, we compile and standardize 15 data sets from various domains. Each of these phys-

ical networks is composed of tube-like objects bound together at junction points; motivating us to treat the junction points as nodes and the tubes connecting them as physical links. We characterize both the physical shape and the abstract network structure and the correlations between them. For this, we calculate standard descriptors such as the degree distribution of the abstract network or the fractal dimension of the layout. We also introduce a measure of link confinement to understand the role of volume exclusion, which compares the physical links to a null model that randomizes link trajectories. The remainder of the chapter is organized as follows: In the next section, we describe the data sets we collected and their standardization. In sections 4.3-4.5, we analyze the data sets' abstract network properties, their physical shape, and the emergent correlations between network and shape. Finally, Sec. 4.6 provides a brief discussion.



Figure 4.1: **Physical networks. (a)** A physical network composed of three tube-like links bound together at a single junction point. **(b)** The skeleton representation of (a) approximates the original structure as a collection of vertices (black points) and edges (colored segments). **(c)** The combinatorial or abstract network of (a) captures the connectivity of the system without the physical structure: nodes represent junction points and terminal points, with a link between two nodes that are directly connected by a physical link. **(d)** The skeleton representation allows us to approximate the original volume of real physical networks – e.g., vascular network (top) and mitochondrial network (bottom). **(e)** We compiled a set of 15 physical networks from various domains. The size of the networks varies greatly: the number of skeleton segments N_{seg} capturing the shape of each network spans 4 orders of magnitude.

4.2 Data

Our goal is to systematically study the three-dimensional layout of physical networks and to understand the relationship between their physical properties and their network structure. For this, we collected 15 data sets from various domains, including individual neurons [132, 133, 134, 135], biological neural networks [5], plant roots [130], vascular networks [4], a mitochondrial network [31], and the imprint of an anthill (see SI 4.7.1). Before any analysis, however, we must uniformly represent and standardize these data sets. In the following sections, we propose the use of a labeled skeleton representation, which efficiently captures both the physical shape and abstract network of physical networks.

4.2.1 Skeleton representation

Experimental imaging techniques that are used to capture the shape of physical networks, such as scanning electron microscopy or magnetic resonance imaging, typically output a three-dimensional image composed of voxels. Hence, this voxel representation is the most accurate description available of network layouts. A three-dimensional voxel image, however, is difficult to handle both computationally and analytically; therefore a more compact representation of the data is needed.

Physical networks are typically composed of tube-like objects bound together at junction points (Fig. 4.1a), making them suitable to be approximated by a series of straight segments and radii of the network at the endpoints of the segments (Fig. 4.1b). The process of creating these segments from a raw data format is called skeletonization [111], often employed in the fields of computer graphics [136] and neuroscience [137, 138]. Formally, a skeleton representation S of a physical network is a graph whose set of vertices V correspond to points in space and set of edges \mathcal{E} correspond to segments connecting point pairs. Therefore each vertex $i \in V$ has a set of coordinates $\mathbf{r}_i = (x_i, y_i, z_i)$ and a radius ρ_i associated to it. Figure 4.1b shows the skeleton of Fig. 4.1a.

The radius ρ_i captures the thickness of the physical network at each vertex *i*. Therefore, we can approximate the original occupied volume of a segment connecting vertex *i* with radius ρ_i and vertex *j* with ρ_j as a truncated cone, and the full volume of the network is approximated by the sum of these truncated cones. More specifically, for each edge (i, j) in S we add a truncated cone with axis $(\mathbf{r}_i, \mathbf{r}_j)$ and parallel faces with radii ρ_i and ρ_j which has volume:

$$V_{\text{seg}}(i,j) = \frac{1}{3} \cdot \pi \cdot (\rho_i^2 + \rho_j^2 + \rho_i \cdot \rho_j) \cdot |\mathbf{r}_i - \mathbf{r}_j|.$$

$$(4.1)$$

Three-dimensional physical network data obtained from experiments is routinely skeletonized, and the skeleton of the network is published together with the raw data. In fact, all but one of the 15 data sets that we study here was skeletonized by the original authors, the only exception is the anthill imprint provided to us as a surface mesh which we skeletonized using the Tangent-ball [139] algorithm from the Skeleton Python module [138]. The experimental setup and the choices made during the skeletonization may affect our analysis which is performed on the skeleton. For example, increasing the number of skeleton segments N_{seg} increases how well the skeleton approximates the original shape of the network. However, increasing N_{seg} also increases the size of the data set, hence increasing the computational burden of the analysis. To improve the uniformity of the data sets, we perform two pre-processing steps:

- 1. Merging segments: If two consecutive segments $(\mathbf{r}_i, \mathbf{r}_j)$ and $(\mathbf{r}_j, \mathbf{r}_k)$ appear parallel to each other in the data set, we merge them into a single segment $(\mathbf{r}_i, \mathbf{r}_k)$ (see SI 4.7.3).
- 2. Skeleton healing: Due to noisy data, a skeleton may be disconnected even when it represents a single continuous object in reality. For example, a skeleton of a neuron may appear to have multiple components. To remedy this, we add a segment to connect the two nearest skeleton vertices from two disconnected components. We repeat this step until the skeleton becomes connected.

Following these pre-processing steps, the number of segments N_{seg} in a skeleton, as shown in Fig. 4.1e, spans three orders of magnitude from mitochondrial networks, which have approximately 10^3 segments, to fruit fly neural networks which have up to 10^6 segments.

4.2.2 Network structure

A physical network is a continuous object embedded in Euclidean space, to characterize this object as a network we must separate it into discrete nodes and links. For this, first note that all 15 data sets that we collected can be seen as a collection of tube-like objects bound together at junction points. Hence, we define the junction and terminal points of the tubes as physical nodes and the non-branching tubes pairwise connecting these terminal and junction points as physical links. A motivation for this definition is that cutting a physical link (i.e., a tube) at any point along its length causes the same disruption to the connectivity of the network.

More formally, for a skeleton representation S of a physical system, we define each physical node to correspond to a skeleton vertex i with degree $k(i) \neq 2$, and each physical system $k(i) \neq 2$, and each physical system $k(i) \neq 2$.

cal link to correspond to a path in the skeleton given by the ordered set $\mathcal{T}(i_0, i_l) = [(i_0, i_1), (i_1, i_2), \dots, (i_{l-1}, i_l)]$, such that $k(i_0), k(i_l) \neq 2$ and $k(i_j) = 2$ for $j = 1, 2, \dots, l-1$.

With the above definition of nodes and links, we can talk about the abstract or combinatorial network \mathcal{G} of the system which captures its connectivity without the physical structure. The skeleton \mathcal{S} is one possible physical realization of the abstract network \mathcal{G} ; however, there are many possible physical realizations of the same \mathcal{G} . In general, we are interested in understanding the relationship between the physical layout captured by \mathcal{S} and the network structure captured by \mathcal{G} .

As an example consider the physical network shown in Fig. 4.1a which consists of three tubes bound together at a single junction point. Its skeleton representation (Fig. 4.1b), therefore, has three vertices with degree 1 corresponding to the terminal points, one vertex with degree k = 3 corresponding to the junction point, and several vertices with degree k = 2 tracing the trajectory of the tubes. This means that the network consists of four physical nodes and three physical links, and its abstract network is a star (Fig. 4.1c).

Finally, note that for a given skeleton S, the above definition of physical nodes and links is not the only viable definition. For example, in a neural network, it is natural to treat a neuron as a physical node and synapses between them as links, as individual neurons can have complex three-dimensional shapes that can be represented by a skeleton itself. More generally, subgraphs of a large S may represent functional units in a physical network and it can be useful to treat these functional units as physical nodes [9]. Note, however, that our definition of the abstract network G provides the most detailed picture of the system's connectivity, and other definitions can be thought of as coarse-grained versions of G.

With the skeleton representation and the definition of the abstract network at hand, we are in the position to start our analysis. In the following sections, we first explore the structure of the abstract networks of the 15 data sets, then we continue by characterizing their physical properties, and finally, we investigate the relation between the two.

4.3 Abstract network properties

The above definition of physical nodes and links allows us to explore the properties of the abstract networks capturing the connectivity of physical networks without their threedimensional structure; we focus on the degree distribution and motif frequencies.

The nodes in our physical networks are terminal and junction points, meaning that by con-

struction nodes cannot have degree k = 2, only degree k = 1 or k > 2. Figure 4.2a shows the degree distribution p(k) of all 15 networks, and our main observation is that most nodes have degree k = 1 or k = 3, and nodes with a larger degree are exceedingly rare, i.e., $p(1) + p(3) \approx 1$. This means that junctions tend to be bifurcation points along the tube-like physical links making up the network. This is in line with previous empirical observations and theoretical predictions for neurons [140, 141] and transport networks [142, 143]. The observed narrow degree distribution is in contrast with degree-heterogeneous networks typically in the focus of network science and should be accounted for by mathematical models of physical networks [8].

In graph topological terms, 7 out of 15 collected physical networks are trees: the individual neurons, the anthill imprint, and the plant roots. Each bifurcation point with degree k = 3 in a tree creates one new leaf node with degree k = 1; therefore the fact that these networks are trees together with the observation that most junctions are bifurcation points, completely determines their degree distribution as $p(1) \approx p(3) \approx 1/2$. The remainder of the networks contain cycles: The vascular networks have no terminal points, apart from a few appearing due to finite sample size; therefore are almost completely composed of k = 3 nodes. The mitochondrial network representing a network of molecular strands has the highest fraction of k > 3 nodes. Finally, the fruit fly neural networks represent a collection of individual neurons which are trees, bound together by synapses, and their degree distribution closely resembles that of trees.

To explore the local loop structure of the networks, we calculate the abundance of observed 4-node motifs. Namely, we focus on two motifs: the star motif and the 4-cycle. To quantify their abundance, we calculate their Z-score compared to their degree-preserving randomized counterparts:

$$z_{\rm s/c} = \frac{n_{\rm s/c} - \langle n_{\rm s/c} \rangle}{\sigma_{\rm s/c}},\tag{4.2}$$

where $n_{s/c}$ is the number of occurrences of the star and 4-cycle motifs in the original networks, and the expected value $\langle n_{s/c} \rangle$ and standard deviation $\sigma_{s/c}$ is estimated by creating 200 independent randomizations [144], while keeping the degree sequence fixed. Figure 4.2b shows the scatter plot of z_s and z_c for the 15 networks. As expected, in tree networks containing no cycles the star motif is slightly over-represented $z_s > 0$, and the cycle motif is slightly under-represented $z_s < 0$, while for networks containing cycles, we find the opposite. The highest abundance of 4-cycles is observed for the networks representing different brain regions of the fruit fly brain.

Based on the degree distributions and motif profile of the abstract networks, the physical

networks fall into three broad categories: (i) topological trees (the individual neurons, the root systems, and the anthill tunnel imprint), (ii) lattice-like networks that are characterized by a loopy structure and few terminal points (the vascular networks and the mitochondrial network), and (iii) linked trees which are a collection of trees bound together by additional links (the fruit fly brain regions).



Figure 4.2: Abstract network properties. (a) The abstract networks are composed of terminal and bifurcation points; therefore, their degree distribution is mostly concentrated on k = 1 and k = 3. More specifically, lattice-like networks, such as vascular and mitochondrial networks, are mostly made up of branching nodes (degree k = 3). For the rest of the network, nodes with k = 1 and k = 3 are approximately evenly split, as expected for tree networks. (b) We calculate the z-scores of four-node star and cycle motifs of the original networks compared to random networks with the same degree distribution. Markers are the average of $n_t = 200$ independent randomizations, and error bars representing the standard error of the mean are smaller than the marker size. Both axes are symlog axes, i.e., linear from -1 to 1, log otherwise for both positive and negative values. The star motif is slightly over- and the cycle motif is slightly under-represented in tree networks (green markers), as expected. In contrast, stars are under and cycles are overrepresented in both lattices (blue markers) and linked trees (red markers). The overrepresentation of the 4-cycle motif reflects the presence of periodic structures in lattices and highlights the existence of local cycles formed by synaptic connections in the fruit fly brain networks.

4.4 Physical properties

In the previous section, we measured properties of the abstract network capturing the connectivity of the 15 physical networks. We continue our investigation focusing on the physical properties of the system: we characterize the three-dimensional shape of the system without considering the abstract network.

4.4.1 Space filling and fractal dimension

A fundamental property of a physical network is its space-filling, i.e., the amount of volume it occupies from the available space. We expect that networks that are tightly packed in space are strongly affected by physicality [6, 8, 9], although the study of random physical networks built from straight links suggests that volume exclusion can play a significant role even for diminishing small space filling [8]. Many real physical networks have irregular shapes, hence much of their bounding box is unoccupied. Therefore, instead of measuring space-filling globally, we divide the axis-aligned bounding box of each physical network into rectangular boxes. We then measure the local space-filling in each box i as

$$\phi(i) = \frac{V_{\rm occ}(i)}{V_{\rm box}},\tag{4.3}$$

where $V_{\text{occ}}(i)$ is the volume of the intersection of the network and box *i* and V_{box} is the volume of the rectangular box. The distribution of $\phi(i)$ depends on the choice of V_{box} ; therefore, to ensure consistency, we set them separately for each data set such that every bounding box is split into a $10 \times 10 \times 10$ grid of boxes (see SI 4.7.5). Figure 4.3a shows the distribution of ϕ for all 15 physical networks, revealing that the physical networks fill out the space with mostly sparse regions and fewer denser regions. Therefore we expect that physicality will also affect the network structure unevenly: volume exclusion can limit the number and shape of links in dense regions.

To further characterize the shape of the networks, we calculate their box-counting fractal dimension $D_{\rm f}$, which compactly describes the space-filling of a physical object on multiple scales [37, 38, 39] and is widely used to characterize the shape of complex biological systems [39, 145]. Possible values of $D_{\rm f}$ for connected networks range between 1 and the embedding dimension D = 3, Fig. 4.3b shows $D_{\rm f}$ for the 15 networks, we find that both lattices and linked trees have $D_{\rm f} \gtrsim 2$, while trees are typically characterized by $D_{\rm f} \lesssim 2$, except for the anthill imprint. The fractal scaling spans at least two orders of magnitude of length scales (see SI 4.7.5), again pointing towards regions of high and low physical

density at different resolution levels.



Figure 4.3: **Space-filling and fractal dimension.** (a) The boxplots of local space-filling ϕ show the coexistence of mostly sparse and fewer dense regions, where the vertical lines indicate the median, the boxes span the 25th-75th percentile range, and the whiskers extend to 1.5 times the interquartile range. (b) The fractal dimension of physical networks $D_{\rm f}$ ranges between 1 and the embedding dimension D = 3. Linked trees (red) and lattices (blue) have fractal dimension values between $D_{\rm f} \approx 2.0$ and $D_{\rm f} \approx 2.3$, while trees (green) have more variation, ranging from $D_{\rm f} \approx 1.5$ to $D_{\rm f} \approx 2.0$ (except for from the anthill imprint). We estimate $D_{\rm f}$ using the box-counting method, the error bars indicate the standard deviation of the local scaling estimates (see SI 4.7.5).

4.4.2 Link volume and shape

The distribution of space-filling and the fractal dimension characterize the shape of physical networks as a whole. In this section, we continue by quantifying the shape of individual links; we focus on their volume and their straightness.

The skeleton describing the three-dimensional shape of a physical network is composed of straight segments connecting pairs of skeleton vertices and a radius associated to each skeleton vertex, allowing us to approximate the volume belonging to a segment in Eq. (4.1) as a truncated cone. The total volume of a link (i, j) is then:

$$V_{\rm link}(i,j) = \frac{1}{V_{\rm total}} \sum_{(v,w)\in(i,j)} V_{\rm seg}(v,w),$$
(4.4)

where $V_{\text{seg}}(v, w)$ is the volume of each segment tracing the link (i, j). We normalize the link volume by the total volume of the network V_{total} , setting the unit of measurement. We find that linked trees, or the fruit fly neural networks, have consistently high link volume heterogeneity, as their distributions span 6 to 8 orders of magnitude, which is higher compared to most lattices and trees (Fig.4.4a).

We also measure the aspect ratio of physical links $a(i, j) = \rho_{\text{link}}(i, j)/l_{\text{link}}(i, j)$, where ρ_{link} is the average radius and $l_{\text{link}}(i, j)$ is the length of link (i, j). We find the largest average aspect ratios for one of the fruit fly networks and the anthill (med $(a) \approx 0.3$), while med(a) is substantially lower for other data sets (see SI Table 4.1). Overall, this confirms that physical links are elongated tube-like objects.

Since physical links are tube-like objects, we can capture most of their shape by characterizing their one-dimensional trajectory. Here, we calculate the deviation of the link trajectories from a straight line, quantifying how curved a link is. For this, we rely on a measure of straightness introduced originally in the context of geographical networks [146], namely we calculate the complimentary straightness for each link

$$\bar{S}(i,j) = 1 - \frac{|\mathbf{r}_i - \mathbf{r}_j|}{l_{\text{link}}(i,j)},\tag{4.5}$$

where $|\mathbf{r}_i - \mathbf{r}_j|$ is the Euclidean distance between nodes i and j and $l_{\text{link}}(i, j) = \sum_{(v,w)\in(i,j)}|\mathbf{r}_v - \mathbf{r}_w|$ is the length of the physical link (i, j). The complimentary straightness $\bar{S}(i, j)$ is 0 if the physical link is straight and close to 1 if it follows a winding trajectory much longer than the straight path between the two points.

Calculating the median of complimentary link straightness distribution, $\operatorname{med}(\bar{S})$, reveals that links in all of the 15 physical networks tend to follow a trajectory close to a straight line: most networks have $\operatorname{med}(\bar{S}) \approx 0.1$, meaning that the length of links is most often less than 10% longer than the optimal straight trajectory. Similarly to link volume heterogeneity, linked trees tend to cluster together and are among the networks with the straightest links with $\operatorname{med}(\bar{S}) = 0.05$. Reference [21] introduced random linear physical networks, a minimal model that constructs a physical network from straight cylinders. The fact that we observed an abundance of straight or close-to-straight links lends support for using such linear physical network models to understand the role of physicality in real networks. Note, however, that although most links are close to straight, the distribution of \bar{S} is rightskewed as seen in Fig. 4.4, which points to a smaller fraction of links that significantly deviate from a straight trajectory (see SI Table 4.7).

Finally, we computed the correlations between link straightness S(i, j) and the total link length $l_{\text{link}}(i, j)$ and volume $V_{\text{link}}(i, j)$ for each data set using Kendall's rank correlation coefficient τ [147]. Figure 4.4b shows that for all networks, there is a positive rank correlation $\tau > 0$ between $\bar{S}(i, j)$ and $l_{\text{link}}(i, j)$, indicating that longer links tend to follow a more winding path. We also observe a positive correlation $\tau > 0$ between $\bar{S}(i, j)$ and $V_{\text{link}}(i, j)$, since longer links tend to have larger volume. The only exception to this is the fruit fly neural networks, for which $\bar{S}(i, j)$ and $V_{\text{link}}(i, j)$ are negatively correlated $\tau < 0$.

One possible cause contributing to the negative correlation is that fruit fly neural networks are composed of neurons that have large somata, which are represented in the data set as short, yet high-volume segments (see SI 4.7.2).



Figure 4.4: Link shape, length, and volume. (a) Box plots of \overline{S} and V_{link} , where the vertical lines indicate the median, the boxes span the 25th-75th percentile range, and the whiskers extend from the 0.1th to the 99.9th percentile. We find that the bulk of the distributions fall in the range between $\text{med}(\overline{S}) = 0$ and $\text{med}(\overline{S}) = 0.1$, indicating that the networks are mostly composed of close-to-straight links. Link volume V_{link} distributions span a wider range for linked trees and are the most narrow for lattices. (b) By computing Kendall rank correlation τ between link complementary straightness \overline{S} , link volume V_{link} and link trajectory length l_{link} , we observe a consistent trend of $\tau > 0$, meaning that longer and more voluminous links tend to have more winding paths. This trend is only reversed for the fruit fly networks, which have $\tau < 0$ between \overline{S} and V_{link} . This could be explained by neuron somatas, which are represented as high-volume, straight links composed of a small number of skeleton segments.

4.4.3 Link confinement

In the previous sections, we found that space-filling and link properties are heterogeneously distributed: most regions of space are sparse and most links are close-to-straight, yet there exists dense regions of the network and a small fraction of links follow paths that deviate from a straight line significantly. This suggests that volume exclusion or other repulsive physical interactions may also play an uneven role in shaping the network. To further investigate this hypothesis we devise a quantity that captures the confinement of a link by other components of a network.

A link (i, j) following a trajectory $\mathcal{T}(i, j)$ in a real physical network obeys volume exclusion: it does not overlap with other links. Our strategy to quantify the role of repulsive forces that may shape $\mathcal{T}(i, j)$ is to calculate the number of overlaps with other links for a random ensemble of synthetic links that follow similar trajectories to $\mathcal{T}(i, j)$. If the synthetic links typically overlap with many other links, the trajectory $\mathcal{T}(i, j)$ is an outlier and must be shaped by forces not captured by the random ensemble.

The trajectory of a physical link (i, j) in our data sets is given by the ordered set $\mathcal{T}(i, j)$ of oriented three-dimensional segments. To generate the random trajectory $\mathcal{T}_{r}(i, j)$, we shuffle the order of the segments while maintaining their orientation and length, creating a uniform random permutation of $\mathcal{T}(i, j)$. The randomization preserves the endpoints and the total length of the link, but otherwise removes any correlation between subsequent segments (see SI S4.4.); therefore, the possible link trajectories $\mathcal{T}_{r}(i, j)$ have the same complimentary straightness \overline{S} as the original link. Next, we estimate I(i, j; l, k), the expected fraction of intersections between the randomized link $\mathcal{T}_{r}(i, j)$ and a non-randomized link $\mathcal{T}(k, l)$. To quantify the confinement of the link (i, j), we sum up the expected fraction of intersections with other links:

$$C(i,j) = \sum_{k,l \neq i,j} I(i,j;l,k) + I(l,k;i,j),$$
(4.6)

where the first term corresponds to intersections when link (i, j) is randomized, and the second term corresponds to intersections when link (l, k) is randomized. Note that the summation in Eq. (4.6) excludes links that share an endpoint with (i, j). We do this to exclude trivial intersections from the count, since adjacent links (i, j) and (j, k) necessarily overlap at the junction point j even for non-randomized link trajectories.

The procedure of calculating C(i, j) is illustrated by Fig. 4.5a: we start with a link (green) surrounded by two neighboring links (red and blue). The figure shows $n_t = 2$ randomiza-

tion trials of the green link: In trial one, the randomized link intersects the red link, but not the blue. In trial two, the randomization creates an intersection with the blue link; the two links, however, are adjacent (they share a junction point), hence the intersection is not counted. In this particular example, the contribution to the link confinement measure from the randomization of the green link will be:

$$I(\text{green}, \text{red}) = \frac{0+1}{2} = 0.5$$
 (4.7)

$$I(\text{green}, \text{blue}) = \frac{0+0}{2} = 0$$
 (4.8)

To complete the calculation of C(green), we also need to randomize the red link to estimate I(red, green) in the same manner, while I(blue, green) = 0 by definition. Finally, the confinement of the green link is obtained by summing up the contributions, i.e., C(green) = I(green, red) + I(red, green).

Collision detection between link trajectories is a computationally expensive task, in practice we randomize each link $n_t = 20$ times (and $n_t = 5$ for the fruit_fly_1 network) and we rely on an efficient collision detection algorithm leveraging kd-trees [148] (see SI 4.7.5 and SI 4.7.6).

Figure 4.5b shows a large variation in link confinement C. Across all networks, physical links are characterized by $C \approx 0$, indicating that these links are not affected by the physical proximity of other components of the network. However, we also find highly confined links with C > 10 and even C > 100 expected intersections, suggesting again that physicality tends to play a heterogeneous role in forming networks. In particular, the linked tree networks typically have heavy-tailed link confinement distributions (see SI 4.7.7). In terms of absolute counts, the linked trees or the fruit fly neural networks show the highest values of link confinement. This can be explained by the fact that these networks are composed of multiple neurons, hence in these networks, we have more complete information about the physical environment of the links, compared to networks that describe single neurons.



Figure 4.5: Link confinement. (a) To quantify volume exclusion at the link level, we introduce link confinement C, the expected fraction of intersections after randomizing a link's trajectory. To estimate C of the green link, we randomize its trajectory twice. In trial #1, the green link intersects the red link, while in trial #2, it intersects the blue link. The blue link, however, shares an endpoint with the green link; therefore their intersection is not counted. (b) The distribution of C for each physical network. The y-axis is shown on a logarithmic scale, while the x-axis is linear. There are many links with link confinement values close or equal to C = 0, and typical values of link confinement are around $C \sim 10$, and only for the fruit fly networks, there are links with link confinement values C > 100, indicating highly confined links for the linked tree networks.

4.5 Link confinement correlation profiles

In the previous section, we defined the link confinement C as the expected fraction of intersections if a link would follow a random trajectory, allowing us to identify links whose trajectory is most affected by repulsive forces in the network. Here, we characterize the properties of such confined links by calculating the Kendall rank correlation τ between the link confinement C and other link properties. Specifically, we focus on the (i) physical properties, complementary straightness \bar{S} and link volume V_{link} (ii) abstract network properties link betweenness B_{link} and link degree $k_{\text{link}}(i, j)$, where the latter is defined as the sum of the degrees of the endpoints of link (i, j).

Figure 4.6 shows the correlation profiles of all 15 networks. A persistent pattern we observe is the positive correlation between link confinement C and link volume V_{link} . This is expected since larger links have more opportunities to intersect or be intersected by neighboring links. On the other hand, correlations between link confinement and straightness show a more curious pattern: we observe that most networks tend to have positive and significant correlations τ between the link confinement C and link complementary straightness \overline{S} , as expected, indicating that more winding links are also more confined. However, for linked trees (fruit fly neural networks) we find a negative τ between C and \overline{S} . To explain this, recall that in the fruit fly neural networks, we found a negative correlation between \overline{S} and V_{link} , and a positive correlation between \overline{S} and l_{link} (Sec. 4.4.2). This means that short links tend to be more confined due to their large volume, while also following a straighter path.

For correlations between link confinement C and the abstract network properties, such as link betweenness B_{link} and degree k_{link} , we find consistent and significant positive correlations for fruit fly neural networks. This indicates emergent correlations between the three-dimensional layout and abstract network properties of physical networks: more central links in the abstract network tend to be more confined in physical space. For lattice-like networks and trees, we find less consistent and weaker positive correlations. Overall, we are able to show that the abstract network structure and physical layout are intertwined for networks where we have sufficient information about the surrounding environment of the physical links, such as the fruit fly neural networks, which contain multiple neurons in close proximity with each other.

vascular_1 -	0.095***	0.205***	-0.028	-0.013	
vascular_2 -	0.132***	0.268***	0.056**	0.035*	<u>a</u>
vascular_3 -	0.108***	0.191***	0.043*	-0.004	E.
mitochon -	0.348***	0.269***	-0.086	-0.031	ces
h_neuron -	0.092***	0.290***	0.047	0.039	
r_neuron -	0.013	0.288***	0.046	0.099*	
m_neuron -	-0.063	0.115*	0.002	0.058	
z_neuron -	0.126***	0.111**	0.069	0.022	tre
root_1 -	0.100***	0.245***	-0.024	0.001	ŝ
root_2 -	0.074**	0.168***	0.028	0.056	
anthill -	0.118***	0.043***	0.052***	0.103***	
fruit_fly_1 -	-0.146***	0.278***	0.155***	0.119***	1
fruit_fly_2 -	-0.157***	0.299***	0.140***	0.091***	द ≕
fruit_fly_3 -	-0.164***	0.345***	0.131***	0.130***	R K
fruit_fly_4 -	-0.116***	0.222***	0.251***	0.091***	0, Q
-	Ŝ	V _{link}	k _{link}	B _{link}	
	Sig. levels: 0.10 0.05 0.01 < p ***	–0.1 0.0 Ker	0.1 0 ndall rank correlation	τ 0.3	

Figure 4.6: Link confinement correlations. We compute the Kendall rank correlation τ between the link confinement C and the physical and abstract network properties of links, obtaining a correlation profile for each physical network. Across all datasets, except some trees, link volume V_{link} and link confinement C have a statistically significant (p < 0.01) moderate positive relationship. We also find a significant association with complementary straightness \bar{S} , which is positive for lattices and trees, and negative for linked trees, consistent with the correlations between V_{link} and \bar{S} (Fig. 4.4). For the linked trees, which are the data sets with the most complete information about the environment of the physical links, we find a significant positive association between the centrality of the links in the abstract network (link degree k_{link} and link betweenness B_{link}) and their link confinement C.

4.6 Discussion

Experimental data describing the three-dimensional shape of physical networks is increasingly becoming available, and the growth in the number and size of these data sets is expected to continue: connectome of the human brain consists of $\approx 10^{11}$ [50] neurons and fungal mycorrhizal networks are estimated to span $\approx 10^{17}$ km in Earth's soil [149]. The new data calls for extending the toolset of network science to analyze, model, and understand how the three-dimensional layout and physical interactions shape the structure and function of physical networks. Here, we contributed to this effort in three distinct ways: (i) We collected and standardized 15 data sets describing the three-dimensional layout of physical networks from diverse domains. (ii) We characterized the structure of both the abstract network and physical layout of the 15 systems using descriptors such as the degree distribution and fractal dimension. (iii) We introduced link confinement as a method to quantify how physical interactions shape link trajectories in physical networks, allowing us to investigate emergent correlations between physical and abstract network properties.

Our work may support future research on physical networks in several ways. First, we promote the use of labeled skeleton graphs to represent both the layout and the connectivity of physical networks. The skeleton captures the shape of the network, while the labeling identifies the physical objects corresponding the the nodes and links of the abstract network. Here, we focused on treating junction points in the skeleton as nodes and sequences of segments connecting them as links; however, the labeled skeletons are not limited to such interpretation. For example, sub-graphs representing larger functional units, such as neurons in the brain, can be identified as physical nodes.

Second, our results also inform theoretical models of physical network growth. Recent work that modeled physical nodes as spheres and links between them as tubes [6, 8]. We found that most physical links follow close to straight trajectories, suggesting that linear physical network models where links are straight cylinders are indeed a useful class of models to understand physicality in networks. On the other hand, these physical network models generalize the classic Erdős-Rényi and Barabási-Albert models to physical space and thus do not restrict the node degree. We, however, found that junction points in real physical networks almost exclusively have degree three, a fact that must be accounted for by future models. Note that to obtain real physical networks with non-trivial degree distributions one must abandon identifying junction points as nodes, instead we must identify larger sub-graphs of the skeleton as physical nodes. In more formal terms, these networks can be modeled as a network-of-networks: we represent each physical node as a skeleton that has junction points with degree 3, and these physical sub-networks are bound together

to form a network-of-networks with no restriction on the number of connections a subnetwork can make with other sub-networks [9]. Future work may explore the relationship between the network-of-networks representation and the more fine-grained junction network representation.

Finally, we quantified the physical confinement of individual links by comparing the path that links follow to randomized trajectories, allowing us to identify correlations between physical and abstract network properties. In general, understanding the relationship between physical shape and abstract network structure is one of the key challenges of physical network research [8, 9, 150]. Future work may rely on other spatially randomized null models and abstract network measures to probe the relation between the two.

Our work is limited by the scope of the available data sets and computational constraints. First, our data sets do not contain information about the environment the networks are embedded in; therefore, we can only investigate interactions between the components of the network and not interactions between the networks and their surroundings. For example, we found the strongest relationship between link confinement and abstract network structure for the fruit fly neural network data sets and we found a weaker or no relationship for individual neurons. This is likely due to the fact that the fruit fly data sets contain multiple neurons, thus capturing more of the environment of individual physical links. Future work may consider more complete data sets as they become available or theoretical models of network growth could incorporate non-trivial environments.

4.7 Supplementary Information

4.7.1 Data sets

In this section, we provide a summary table of data sets, along with a subsection providing more details about every data source.

4.7.2 Data sets Summary

Data set	N_{link}	$N_{\rm node}$	$N_{\rm seg}$	l_{seg}	$ ho_{\mathrm{seg}}$	a_{seg}	Category	Source
h_neuron	631	632	38340	$1.16 \pm$	$0.11 \pm$	$0.1 \pm$	tree	[134]
				0.07	0.00	0.01		
r_neuron	185	186	4536	$2.21 \pm$	$0.46 \pm$	$0.22 \pm$	tree	[133]
				1.98	0.19	0.27		
m_neuron	154	155	16814	$0.36~\pm$	$0.23 \pm$	$0.62 \pm$	tree	[132]
				0.28	0.15	0.3		
z_neuron	307	308	2867	$1.51 \pm$	$0.34 \pm$	$0.22 \pm$	tree	[135]
				1.24	0.12	0.19		
anthill	15240	15241	29387	$16.4 \pm$	$9.61 \pm$	$0.59~\pm$	tree	[151]
				8.38	3.17	0.3		
root_1	975	976	5621	$25.66 \pm$	$4.69 \pm$	$0.18~\pm$	tree	[130]
				0.61	5.11	0.2		
root_2	410	411	2132	$38.49\pm$	$7.2 \pm$	$0.18~\pm$	tree	[130]
				12.56	7.47	0.2		
fruit_fly_1	100388	97588	535611	$48.5~\pm$	$19.8~\pm$	$0.41 \pm$	linked	[127]
				49.2	17.38	0.19	tree	
fruit_fly_2	32121	31408	181068	$48.99 \pm$	$20.0 \pm$	$0.41 \pm$	linked	[127]
				46.06	15.86	0.2	tree	
fruit_fly_3	49599	49233	121318	$39.6 \pm$	$18.38 \pm$	$0.49 \pm$	linked	[127]
				41.97	20.2	0.27	tree	
fruit_fly_4	34987	32749	138488	$41.57\pm$	$16.97\pm$	$0.41 \pm$	linked	[127]
				41.57	17.85	0.19	tree	
vascular_1	2359	1558	17935	$4.69~\pm$	$3.0 \pm$	$0.62 \pm$	lattice	[4]
				1.62	1.22	0.33		
vascular_2	1300	862	16078	$3.91 \pm$	$3.17 \pm$	$0.83 \pm$	lattice	[4]
				1.11	1.41	0.45		
vascular_3	1181	789	12487	5.1 \pm	$2.96 \pm$	$0.61 \pm$	lattice	[4]
				1.95	0.97	0.31		
mitochon	73	59	847	$0.09 \pm$	$0.11 \pm$	$1.17 \pm$	lattice	[31]
				0.06	0.02	0.67		

Table 4.1: **Data sets summary.** For each data set, we provide the total number of physical nodes N_{node} (i.e., junction and terminal points in the skeletonized representation), physical links N_{link} and skeleton segments N_{seg} . We also provide the segment statistics - segment length l_{seg} , segment radius ρ_{seg} , and segment aspect ratio a_{seg} , along with the abstract network categories and sources. For quantities with \pm , we used the median and interquartile range (difference between the 75th and 25th percentile) to quantify their variation.

Anthill imprint

The anthill imprint (named **anthill**) was created as an art project by casting a fire ant colony with molten aluminum, the resulting cast was then scanned by the artist and provided to us as a surface mesh [151]. We skeletonized the mesh using the maximal tangent ball method implemented by the Skeletor Python package [129]. The anthill imprint network is a tree (i.e. it does not contain cycles) with a single exception where two branches of the tree became connected; this single cycle, however, is ignored by the skeletonization algorithm.

There are several potential explanations for the tree structure of the anthill imprint, based on the available studies, which are not directly related to this dataset:

- 1. Energy efficiency—a tree minimizes tunnel length, saving time and labor, especially in small colonies, where loops rarely appear [152].
- 2. Digging behavior—ants follow local excavation rules, extending tunnels step by step. Forming a loop would require two digging fronts to meet underground, which is unlikely without centralized planning [153].
- 3. Structural stability—a tree-like layout provides strong load support, with branched tunnels acting as pillars and arches that resist collapse [153, 154].

These factors could potentially explain why the original nest, and thus its imprint, lacks cycles.

Vascular networks

Each vascular network data sets (named vascular_1, vascular_2 and vascular_3) describes the vessels in a $600 \times 600 \times 662 \ \mu m$ sample of mouse cortex [4]. The data is provided by the authors as a skeleton including radii at the skeleton vertices.

Mitochondrial network

The mitochondrial network (named **mitochon**) represents the mitochondrial reticulum in a yeast cell [31]. The data set was published by the authors both as a skeleton and as a mesh representing the surface. The authors did not provide the radii at the skeleton vertices; therefore, we extracted a radius for each skeleton vertex based on the surface mesh using the Skeletor Python package [129].
Root systems

The root networks (**root_1** and **root_2**) describe the root system of a *Cryptomeria japonica* tree [130]. The data is originally shared as a skeleton including radii at the skeleton vertices.

Individual neurons

In total, four neurons were obtained from *NeuroMorpho.Org* [155] a centrally curated database of digitally reconstructed neurons associated with peer-reviewed publications. Specifically, we characteize neuron of a rhesus monkey [132], a rat [133], a human [134] and a zebrafish [135] (named **m_neuron**, **r_neuron**, **h_neuron** and **z_neuron**, respectively).

Fruit fly brain regions

The Hemibrain project mapped a large portion of the fruit fly *Drosophila melanogaster* brain, providing a three-dimensional reconstruction of approximately 25,000 neurons and 20 million synapses [5]. We obtained the skeletonized neuron morphology and synapse data via the publicly available NeuPrint API [127].

To manage computational complexity, we focused on four anatomically defined brain regions (neuropils): *POC* (Posterior Optic Commissure), GF(R) (Giant Fiber Right), mALT(L)(Median Antennal Lobe Tract, Left), and *GC* (Great Commissure). These regions were selected for their high density of reconstructed neurons, well-documented connectivity, and practical dataset size, offering a balance between analytical relevance and computational tractability.

Each synapse in the dataset is annotated with precise spatial coordinates and assigned to a specific brain region [5]. We used this to define neuron inclusion: neurons were selected based on their synaptic activity in a given region rather than their entire morphology. Using the same methodology as in Sec. 3.8.2, we retained entire neuron skeletons without truncation to preserve the physical structure. Initially, we applied a 1-synapse threshold, including any neuron with at least one synapse in the region, which led to excessive dataset size. To reduce the resulting network size, we adopted a 10-synapse threshold (10 input and 10 output synapses), which helped filter out weakly connected or incomplete neurons and kept only those with meaningful connections. Moreover, since branching points were treated as physical nodes, this resulted in networks with around $\sim 10^4$ nodes, which were large enough for detailed analysis, but still computationally manageable.

We performed two additional data processing steps:

- Due to noise, the skeleton of a neuron may appear disconnected in the data set. To ensure that each neuron is a connected subgraph of the network, we heal each neuron individually: We iteratively merge disconnected components of the neuron, by adding a new segment between their closest points, until a single network component remains.
- 2. In the original data set the shape of each neuron is provided by a separate skeleton, these individual skeletons are disjoint. The location of each synapse is provided by two coordinates: the location of the presynaptic site and the postsynaptic site, the former belonging to the neuron sending the signal, the latter to the neuron receiving the signal. In the data set, the synaptic sites do not correspond to skeleton vertices. To form one connected physical network, we bound together neuron pairs that share a synapse by adding three new skeleton segments: one segment for each neuron that connects the closest vertex of the skeleton to the presynaptic or postsynaptic site, and one segment that bridges the two synaptic sites. The radii of the segments are chosen as the minimum radius of the segment for each neuron. Note that two neurons typically connect through more than one synapse and that the resulting network will be fully connected, with no isolated neurons.

Table 4.2 summarizes the number of neurons, number of synapses, links, and nodes retained for each network in each region, following these data processing steps.

Data set	Region	N _{neuron}	N _{synapse}	N _{link}	N _{node}
fruit_fly_1	POC	96	6249	100388	97588
fruit_fly_2	GF(R)	10	1947	32121	31408
fruit_fly_3	mALT(L)	20	429	49599	49233
fruit_fly_4	GC	28	13079	34987	32749

Table 4.2: Fruit fly neural network data sets. We chose 4 regions of interest in the *Drosophila melanogaster* brain, which had a specific number of neurons N_{neuron} associated with them and total number of synapses N_{synapse} , given our criteria of connectivity (at least 10 in-going and 10 out-going synaptic connections). Additionally, we provide the total number of abstract network links N_{link} and the total number of abstract network nodes N_{node} .



Figure 4.7: Link volume-length correlations. In Fig.4.4 of the main text, we show that there is a negative rank correlation between link volume and length. To better understand this counter-intuitive finding, we show here the number of segments used to represent physical approximately follows an exponential distribution (upper row). Links represented with $\gtrsim 5$ segments have a higher volume as the number of segments increases. For links with $\lesssim 5$ segments, the trend is reversed. This at least is partially explained by the presence of the neurons somata, represented in the skeleton as short segments with a large radius.

4.7.3 Data processing

In this section, we provide details about the skeletonization algorithms and data preprocessing steps that we take to increase the uniformity of the empirical data sets and to allow efficient collision detection.

Skeletonization

The three-dimensional shape of physical networks can be represented using different data structures, such as point clouds, 2D and 3D meshes [156, 157], and volumetric images (voxels) [158], which are often transformed into a more computationally efficient format via skeletonization algorithms [111]. Skeletonization aims to represent the shape of a 3D object using a collection of straight segments, making it particularly useful for describing elongated objects, such as physical links. Although there are many skeletonization methods that vary in details and how their quality is assessed, a typical skeletal representation aims to trace the medial axis of a 3D object, i.e., the locus of the centers of all inscribed spheres of maximal radius [111, 137]. Skeletal representations of physical networks are routinely published together with 3D imaging data. In fact, all but one of the 15 data set were skeletonized by the original authors. The only exception was the anthill imprint, which we skeletonized using the Skeletor Python package [138].

Merging paralleled skeleton segment pairs

Since some data sets contained sequentially connected, parallel skeleton segments, this wouldn't accurately represent the separate components of the links, and would therefore influence the computation of the link confinement C. To address this issue, we perform the following steps on an example link (k, l):

- 1. We compute path length l_{link} of the (k, l) link, as a sum of all segment lengths l_{seg} that compose that link.
- For each consecutive pairs of segments of [(i₀, i₁), (i₁, i₂)...(i_{n-1}, i_n)] that compose a link (k, l) the cosine of the angle between them is computed. For example, we can have subsequent segment pairs (i₀, i₁) and (i₁, i₂), with their respective direction vectors n and m. We calculate cos(θ)_{m,n} = m·n / |m||n|, where m · n is the dot product between their direction vectors and |m| and |n| are their lengths.
- 3. All segment pairs are ranked based on the cosine of the angle between them in descending order. The top-ranked (highest value) pair of segments are merged into a

single segment. For example, merging segments (i_0, i_1) and (i_1, i_2) results in segment (i_0, i_2) , and now link (k, l) is composed of segments $[(i_0, i_2)...(i_{n-1}, i_n)]$.

4. Steps 2. and 3. are repeated until the total path length l_{link} of the link (k, l) would decrease after the next merge.

Note that using the above stopping criteria only merges completely parallel consecutive skeleton segments; therefore it does not result in any loss of information.

A more relaxed stopping criteria would reduce the size of the skeleton at the price of decreasing how well the skeleton approximates the original neuron volume. Merging skeleton segments is related to the concept of persistence length from polymer physics [159], which roughly quantifies how long a segment can be before we can stop treating it as a stiff rod.

Labeled Point Clouds and KD-Trees

The computation of space-filling ϕ , fractal dimension D_f , and link confinement C require identifying physical intersections (collisions) that might occur between two physical links or a physical link and the side of a cube. We relied on collision detection methods utilized in computer graphics to identify physically intersecting objects [160]. More specifically, we developed a custom algorithm that utilizes kd-trees to efficiently detect overlapping physical objects [148]. A kd-tree is a data structure that partitions space and allows to query points that are in the physical proximity of each other. Hence to detect overlaps, we transform physical links into point clouds, arrange the points in a kd-tree, and if the points representing two distinct links are closer to each other than a threshold, we conclude that the links overlap.

Segment to point cloud transformation

To transform the skeleton segments to a point cloud, we perform three following steps:

- 1. First, for each segment starting at the \mathbf{r}_i and ending at \mathbf{r}_j with radii ρ_i and ρ_j at the endpoints, a line of points is created in the direction $\mathbf{r}_j \mathbf{r}_i$, with the distance between the points is l_{res} . We choose l_{res} as the average skeleton vertex radius $\langle \rho \rangle$.
- 2. Second, we account for local thickness by generating points on circles perpendicular to the line segment at each point, interpolating radii linearly from ρ_i to ρ_j . The number of points on each circle is chosen as min $\left(3, \left\lceil \frac{2\pi\rho}{l_{res}} \right\rceil\right)$ to accurately represent the surface of the truncated cone segment.

3. Finally, for segments where the endpoint diameters $2 \cdot \rho$ exceed l_{res} , additional points are generated on concentric inner circles to fill these larger gaps in the bases of the segments, ensuring that all segments are enclosed (contrary to being hollow),

By controlling the resolution l_{res} of the point cloud, we ensure that our representation of volumetric data matches the resolution of the original data while remaining computationally efficient.

Detecting intersections using kd-trees

Once the point cloud is created, a single kd-tree is constructed that stores all points. To test whether a point \mathbf{r} (e.g., belonging to a new physical link) intersects any of the existing physical links, we query the kd-tree the point \mathbf{r} at distance l_{res} , which provides all points whose distance from \mathbf{r} is less than l_{res} . The labels of these points provide the physical links that intersect \mathbf{r} .

Data set	D _{net}	k_{link}	B_{link}
root_1	87	5.0 ± 2.0	$[2.05 \pm 16.24] \times 10^{-3}$
root_2	34	5.0 ± 2.0	$[4.87 \pm 28.7] \times 10^{-3}$
h_neuron	49	4.0 ± 2.0	$[3.16 \pm 18.78] \times 10^{-3}$
z_neuron	46	4.0 ± 2.0	$[6.49 \pm 62.61] \times 10^{-3}$
m_neuron	20	4.0 ± 2.0	$[12.9 \pm 49.94] \times 10^{-3}$
r_neuron	21	4.0 ± 2.0	$[10.75 \pm 41.85] \times 10^{-3}$
anthill	343	5.0 ± 2.0	$[0.13 \pm 1.05] \times 10^{-3}$
vascular_1	27	6.0 ± 0.0	$[3.78 \pm 4.34] \times 10^{-3}$
vascular_2	22	6.0 ± 0.0	$[6.43 \pm 7.06] \times 10^{-3}$
vascular_3	22	6.0 ± 0.0	$[7.04 \pm 7.27] \times 10^{-3}$
mitochon	11	6.0 ± 0.0	$[57.62 \pm 70.81] \times 10^{-3}$
fruit_fly_1	602	6.0 ± 2.0	$[0.06 \pm 0.25] \times 10^{-3}$
fruit_fly_2	289	6.0 ± 2.0	$[0.19 \pm 0.76] \times 10^{-3}$
fruit_fly_3	479	6.0 ± 2.0	$[0.04 \pm 0.49] \times 10^{-3}$
fruit_fly_4	254	6.0 ± 2.0	$[0.18 \pm 0.61] \times 10^{-3}$

4.7.4 Abstract network properties

Table 4.3: Summary of abstract network properties. Having defined links and nodes in our skeleton data, we provide the abstract network properties, where k_{link} is link degree, D_{net} is the network diameter and B_{link} is the link betweenness centrality. For quantities with \pm , we used the median and interquartile range to quantify their variation (difference between the 75th and 25th percentile).



Figure 4.8: Abstract network degree distribution. Node degree k has a very sharp distribution centered around k = 1 and k = 3 with higher degree nodes being increasingly rare. The nodes with degree > 3 in fruit fly networks are mostly junction points that correspond to synaptic connections between two neurons and not internal branching points of dendrites. Degree k = 2 nodes are not present by the definition of the abstract network.

Data set	n_s	n_c	$\langle n_s \rangle$	$\langle n_c \rangle$	σ_s	σ_c	Z_s	Z_c
z_neuron	185	0	179.60	0.70	5.85	0.86	0.92	-0.78
h_neuron	395	0	388.65	0.60	9.30	0.72	0.68	-0.83
m_neuron	129	0	117.94	0.70	12.39	0.93	0.89	-0.76
r_neuron	92	0	88.47	0.60	2.84	0.80	1.24	-0.73
anthill	10488	0	10481.94	0.70	4.44	0.85	1.36	-0.85
root_1	623	0	617.71	0.70	4.69	0.80	1.13	-0.88
root_2	333	0	320.81	0.90	14.98	0.88	0.81	-1.02
fruit_fly_1	57169	222	60354.6	0.76	6.50	0.83	-490.17	265.39
fruit_fly_2	18017	77	19658.4	0.81	6.93	0.82	-236.83	93.30
fruit_fly_3	27785	33	27959.8	0.64	3.62	0.76	-48.32	42.80
fruit_fly_4	23722	286	30522.1	1.04	21.70	0.97	-313.36	294.16
vascular_1	1613	58	1726.0	2.30	4.83	1.61	-23.41	34.61
vascular_2	853	29	930.8	2.06	4.74	1.39	-16.42	19.41
vascular_3	709	21	786.9	2.02	4.06	1.36	-19.19	13.92
mitochon	36	1	44.3	1.39	4.37	1.07	-1.90	-0.36

Table 4.4: Four node motifs. To understand which motifs are over- or under-represented in the empirical data, we compared the abstract network structure with the configuration model (which is not affected by physicality) allowing multi-links. The table shows the motif count of the original network $n_{s/c}$, as well as the expected value $\langle n_s/c \rangle$ and standard deviation $\sigma s/c$ of the motif counts in the configuration model and the corresponding zscores $Z_{s/c}$. We generated $n_t = 200$ independent randomizations for each network.

4.7.5 Physical properties

In this section, we provide details about how space-filling ϕ and fractal dimension $D_{\rm f}$ are computed.

Space-filling

To compute the space-filling ϕ of physical networks, we perform the following steps:

- 1. We determine the axis-aligned bounding box of the network (the smallest box that fully contains the network), which we further partition into equally sized rectangular boxes, by splitting the bounding box into 10 equal segments along each dimension in space, leading to a grid of 1000 rectangular boxes. Note the rectangular box sides do not need to be equal.
- 2. For each rectangular box i in the grid, we determine the number of segments that have both endpoints inside.
- 3. The space-filling ϕ is calculated as the ratio of the sum of all segment volumes and the volume of the rectangular box.

One possible issue with this method is that even though both endpoints of the segments are inside the rectangular box, the segment might be thick enough to be physically larger than the rectangular box. To avoid this, we have chosen rectangular box sizes large enough so that the number of these cases is below 1%.

Fractal dimension

We use the box-counting method to compute the fractal dimension $D_{\rm f}$ of the physical networks [161], by performing the following steps:

- 1. The physical network is transformed into a point cloud of minimum resolution l_{res} (Sec. 4.7.3).
- 2. We determine the axis-aligned bounding box (the smallest box that fully contains the network), which we further split into equally sized cubes of side l_b , thus forming a grid. To account for the fact that our cubes might not perfectly align with the bounding box, we add one extra cube along each dimension to fully cover the original bounding box.

- 3. For all cubes, we check if at least 1 point from the point cloud is inside it, thus accounting for the total number of occupied boxes $n_b(l_b)$.
- 4. This procedure is repeated for a range of cube side lengths l_b spanning at least two orders of magnitude.

In the log-log plots of n_b and l_b , we extract the negative slope (with two different methods), as shown in Fig. 4.9 to obtain the fractal dimension

$$D_{\rm f} = -\frac{\log n_{\rm b}}{\log l_{\rm b}} \tag{4.9}$$

We performed linear ordinary least squares regression (OLS) to estimate $\bar{D}_{f,OLS}$ as the slope of $n_b(l_b)$ on the log-log plot. Since the OLS requires independent data points, which is not satisfied, the standard error of $\bar{D}_{f,OLS}$ is underestimated. To remedy this, we also estimate the slope in this plot as the average local slope. Specifically, we compute the slope for every consecutive data point pair, thus obtaining a distribution of slopes $\bar{D}_f(1), \bar{D}_f(2), \ldots, \bar{D}_f(n-1)$. We estimate the fractal dimension as the mean of these slopes, i.e., $\bar{D}_{f,local} = 1/(n-1) \sum_i D_f(i)$, while our error estimate is the standard deviation of this local slope distribution σ_{local} .



Figure 4.9: Estimating the fractal dimension. To compute the fractal D_f we find the line of best fit for the log-log scatter plots of the number of filled boxes $\log(n_b)$ and $\log(l_b)$. Ordinary least squares (OLS) linear regression line is displayed, along with the local slopes, that connect consecutive points.

Data set	$\bar{D}_{\rm f,OLS}$	R^2	$\sigma_{\rm OLS}$	$\bar{D}_{\rm f,local}$	$\sigma_{ m local}$	$\min(D_{\mathrm{f}}(i))$	$\max(D_{\mathrm{f}}(i))$
root_1	-1.69	1.00	0.02	-1.73	0.15	-2.05	-1.62
root_2	-1.63	1.00	0.02	-1.62	0.08	-1.76	-1.54
h_neuron	-1.25	1.00	0.03	-1.34	0.16	-1.59	-1.13
z_neuron	-1.37	1.00	0.04	-1.30	0.18	-1.52	-1.03
m_neuron	-1.32	1.00	0.02	-1.29	0.16	-1.44	-0.98
rat_neuron	-1.46	1.00	0.03	-1.54	0.19	-1.91	-1.36
anthill	-2.51	1.00	0.02	-2.53	0.07	-2.58	-2.37
vascular_1	-1.94	1.00	0.06	-2.12	0.35	-2.75	-1.78
vascular_2	-1.94	1.00	0.05	-2.10	0.33	-2.73	-1.76
vascular_3	-1.88	1.00	0.04	-2.01	0.26	-2.42	-1.74
mitochon	-1.73	1.00	0.02	-1.76	0.10	-1.91	-1.61
fruit_fly_1	-2.25	1.00	0.03	-2.31	0.15	-2.58	-2.10
fruit_fly_2	-2.01	1.00	0.01	-1.99	0.12	-2.15	-1.75
fruit_fly_3	-1.88	1.00	0.02	-1.84	0.12	-2.00	-1.69
fruit_fly_4	-2.05	1.00	0.02	-2.06	0.07	-2.14	-1.95

Table 4.5: **Fractal dimension analysis.** Summary of the OLS linear regression (fractal dimension $\bar{D}_{f,OLS}$, coefficient of determination R^2 and standard error σ_{OLS}) and the local slope estimation (fractal dimension $\bar{D}_{f,Iocal}$, local slope standard deviation σ_{Iocal} , minimum and maximum values of the local slope min $(D_f(i))$ and max $(D_f(i))$.

Kendal- τ correlation

Kendall's τ coefficient measures the association between the ranks of two quantities [162]. The coefficient τ is useful to measure correlations between non-normally distributed quantities as it does not make assumptions about their distributions. We use the tau-b version of Kendall's τ which accounts for ties:

$$\tau(x,y) = \frac{(P-Q)}{\sqrt{(P+Q+T) \cdot (P+Q+U)}}$$
(4.10)

where x and y are the two quantities we compare, P is the number of concordant pairs, Q is the number of discordant pairs, T is the number of ties only in x, and U is the number of ties only in y. If a tie occurs for the same pair in both x and y, it is not added to either T or U. Accounting for ties is necessary, since link properties often have identical values, for example, all straight links have $\bar{S} = 0$ and link degrees $k_{\text{link}} = 4$ or $k_{\text{link}} = 6$ are abundant in physical networks.

Data set	$\tau(\bar{S}, V_{\text{link}})$	p-val	$\tau(\bar{S}, l_{\text{link}})$	p-val
		$\tau(\bar{S}, V_{\text{link}})$		$\tau(\bar{S}, l_{\text{link}})$
root_1	0.094	$< 10^{-3}$	0.462	$< 10^{-3}$
root_2	0.134	$< 10^{-3}$	0.457	$< 10^{-3}$
h_neuron	0.305	$< 10^{-3}$	0.369	$< 10^{-3}$
z_neuron	0.388	$< 10^{-3}$	0.504	$< 10^{-3}$
m_neuron	0.048	0.375	0.328	$< 10^{-3}$
r_neuron	0.276	$< 10^{-3}$	0.456	$< 10^{-3}$
anthill	0.455	$< 10^{-3}$	0.609	$< 10^{-3}$
vascular_1	0.312	$< 10^{-3}$	0.482	$< 10^{-3}$
vascular_2	0.366	$< 10^{-3}$	0.589	$< 10^{-3}$
vascular_3	0.412	$< 10^{-3}$	0.556	$< 10^{-3}$
mitochon	0.363	$< 10^{-3}$	0.437	$< 10^{-3}$
fruit_fly_1	-0.061	$< 10^{-3}$	0.413	$< 10^{-3}$
fruit_fly_2	-0.065	$< 10^{-3}$	0.407	$< 10^{-3}$
fruit_fly_3	-0.136	$< 10^{-3}$	0.463	$< 10^{-3}$
fruit_fly_4	-0.109	$< 10^{-3}$	0.353	$< 10^{-3}$

Table 4.6: Correlations summary between shape, volume and length. Kendall- τ correlations and their corresponding *p*-values between link complementary straightness \bar{S} and link volume V_{link} and l_{link} .

Generating randomized trajectories

Each link trajectory is composed of a series of segments $\mathcal{T}(i_0, i_l) = [(i_0, i_1), (i_1, i_2), \dots, i_l)$ (i_{l-1}, i_l)], where each segment (i_k, i_{k+1}) is characterized by an offset vector and has two radii at its endpoints. For example, the first segment in the $\mathcal{T}(i_0, i_l)$ trajectory, (i_0, i_1) , has an offset vector $\mathbf{o}_1 = \mathbf{r}_{i_1} - \mathbf{r}_{i_0}$ (where \mathbf{r}_{i_k} is the location of point i_k) starting at the point i_0 with radius ρ_{i_0} and ending at the point i_1 with radius ρ_{i_1} . This means that we can attribute to each link $\mathcal{T}(i_0, i_l)$, an ordered set of vectors $[\mathbf{o}_1, \mathbf{o}_2, \dots, \mathbf{o}_l]$ and ordered set of radii at points where segments are connected $[\rho_0, \rho_1, \dots, \rho_l]$. To generate a randomized trajectory, we randomly shuffle the ordered sets of offset vectors and base radii (independently of each other), thus obtaining new randomized ordered set with the same number of elements of direction vectors $[\mathbf{o}_{j_1}, \mathbf{o}_{j_2}, \dots, \mathbf{o}_{j_l}]$ and radii pairs $[\rho_{k_0}, \rho_{k_1}, \dots, \rho_{k_l}]$. For example, o_{j_1} will correspond to the truncated base radii of ρ_{k_0} and ρ_{k_1} after the shuffling. Note that the radii list has one more element than the direction vector list (as each subsequent pair corresponds to a direction vector.) and that both randomizations are done independently (with different sets of indices). The new randomized trajectory is constructed by sequentially adding the offset vectors together starting from the original starting location \mathbf{r}_{i_0} . For example, the first segment of the randomized trajectory starts from \mathbf{r}_{i_0} and ends at $\mathbf{r}_{i_0} + \mathbf{o}_{i_1}$, the radii at its endpoints are ρ_{k_0} and ρ_{k_1} . This construction ensures that the randomized link trajectory has the same starting and ending locations as the original trajectory.

4.7.6 Collisions and link confinement

To calculate link confinement C, we need to count the number of links that randomized trajectories intersect. For this task, we developed a collision detection algorithm that utilizes labeled point clouds and kd-trees [160, 148]. By using labeled point clouds, this data can be sparsely, but accurately represented, and an intersection can be quickly found by using the spatial search capabilities of kd-trees. More specifically, we identify collisions through the following steps:

- 1. All links of the original physical network are transformed to labeled point clouds with the distance between the points l_{res} (Sec. 4.7.3), which are then stored in a kd-tree.
- 2. When a single link is randomized, it is also transformed to a point cloud of a minimum resolution l_{res} and then stored to a link-specific kd-tree.
- 3. By using query_ball_tree() method of the scipy.spatial kd-tree containing all the original links, we can query it using the kd-tree of a single randomized

link, with a threshold distance l_{res} , which provides us with all the points that the randomized link intersects. The original physical links corresponding to the intersecting points are the links that the randomized trajectory overlaps with.

Each link is randomized for n_t trials, hence the average fraction of intersections between a link (i, j) and a link (k, l) is:

$$I(i,j;k,l) = \frac{1}{n_t} \sum_{n} I_n(i,j;k,l),$$
(4.11)

where $I_n(i, j; k, l)$ is an indicator function which is 1 if the *n*th randomization for the link (i, j) intersects the original link (k, l), and is otherwise 0.

It's important to recognize that two long links may intersect at multiple points, and in principle, a single link could fully constrain another, leading to numerous intersections between just one pair of links. However, in practice, links are continuous objects, while our analysis relies on discrete representations. This makes it inherently ambiguous to distinguish between one or multiple intersections, as the classification depends on discretization (i.e skeletonization). To ensure consistency and comparability across datasets, we adopt a simplified approach: rather than counting each individual intersection, we record only whether a link is intersected at least once. This provides a conservative yet robust lower-bound estimate of confinement effects. Apart from allowing for multiple intersections, one potential avenue for extending this methodology is to measure the volume of overlap between intersecting links.

Also, note that I(i, j; k, l) is not symmetric, i.e., $I(i, j; k, l) \neq I(k, l; i, j)$. For example, a longer link (i, j) might often collide with a smaller link (k, l) after randomization, while a smaller (k, l) link might not collide with (i, j) at all.

Data set	S	n_{seg}	a_{link}	V_{link}
root_1	0.03414 ± 0.1012	5 ± 6	0.045 ± 0.079	$[2.76 \pm 0.67] \times 10^{-4}$
root_2	0.02326 ± 0.0967	4 ± 5	0.054 ± 0.103	$[4.54 \pm 1.34] \times 10^{-4}$
h_neuron	0.06744 ± 0.1298	40 ± 66	0.002 ± 0.003	$[3.32 \pm 0.51] \times 10^{-4}$
z_neuron	0.07432 ± 0.1877	5 ± 8	0.053 ± 0.107	$[0.51 \pm 1.30] \times 10^{-3}$
m_neuron	0.0892 ± 0.0812	62 ± 163	0.008 ± 0.04	$[2.42 \pm 2.78] \times 10^{-3}$
r_neuron	0.19821 ± 0.1654	18 ± 37	0.011 ± 0.069	$[3.1 \pm 4.21] \times 10^{-3}$
anthill	0.000 ± 0.1934	1 ± 1	0.374 ± 0.376	$[4.7 \pm 5.9] \times 10^{-5}$
vascular_1	0.06068 ± 0.1038	6 ± 7	0.109 ± 0.17	$[0.20 \pm 0.25] \times 10^{-3}$
vascular_2	0.03443 ± 0.1063	9 ± 12	0.100 ± 0.166	$[0.400 \pm 0.56] \times 10^{-3}$
vascular_3	0.10353 ± 0.1978	7 ± 10	0.083 ± 0.151	$[0.42 \pm 0.60] \times 10^{-3}$
mitochon	0.06387 ± 0.0921	9 ± 9	0.107 ± 0.107	$[9.58 \pm 11.62] \times 10^{-3}$
fruit_fly_1	0.0532 ± 0.1115	3 ± 5	0.144 ± 0.288	$[1.0 \pm 4.0] \times 10^{-6}$
fruit_fly_2	0.05698 ± 0.1096	3 ± 5	0.132 ± 0.258	$[3.0 \pm 8.0] \times 10^{-6}$
fruit_fly_3	0.0 ± 0.0738	1 ± 2	0.324 ± 0.508	$[6.0 \pm 13.0] \times 10^{-6}$
fruit_fly_4	0.05053 ± 0.1042	3 ± 4	0.154 ± 0.251	$[5.0 \pm 14.0] \times 10^{-6}$

Physical link properties

Table 4.7: **Summary of physical link properties.** With a definition of a link as a series of physical segments joining two junction points, we calculate the number of segments composing a link n_{seg} , the aspect ratio of the link $a_{\text{link}} = l_{\text{link}} / \langle \rho_{\text{link}} \rangle$ (where l_{link} is the link length and $\langle \rho_{\text{link}} \rangle$ is the average radius of the link) and link volume V_{link} . For quantities with \pm , we used the median and interquartile range to quantify their variation (difference between the 75th and 25th percentile).



4.7.7 Link confinement distributions

Figure 4.10: **Difference between confined and non-confined links.** We split the links into two groups: confined C > 0 and non-confined C = 0 links. Then, we compared the two groups across different properties: complimentary straightness \overline{S} , the volume V_{link} , the link degree k_{link} and the link betweenness B_{link} , by performing Kolmogorov-Smirnov (KS) and Mann Whitney (MW) tests. We find that for linked trees (fruit fly networks) and anthill imprint network, confined C > 0 and non-confined C = 0 links differ in both physical and network properties, while for most of the other data sets, we were able to detect significant differences in the physical properties.

We examine the statistical significance of the fit between the observed data and several theoretical distributions. The table 4.8 summarizes the p-values obtained from comparing the fit of an exponential distribution to a stretched exponential, truncated power law, lognormal, and power law distributions for different types of neuronal data and other structures:

Data gat	Stretched	Truncated	Lognomial	Power
Data set	Exponential	Power Law	Lognormai	Law
human_neuron	0.139	0.311	0.314	0.317
rat_neuron	0.119	0.092	0.884	0.004
monkey_neuron	0.169	0.170	0.062	0.170
zebrafish_neuron	$< 10^{-3}$	0.029	0.076	0.201
vascular_2	0.186	0.357	0.443	0.564
vascular_3	0.816	0.697	$< 10^{-3}$	0.024
vascular_1	0.140	0.383	0.795	0.180
mitochondrial	$< 10^{-3}$	0.046	0.098	0.103
root_1	0.369	0.311	0.807	0.080
root_2	0.760	0.830	0.730	0.461
anthill	0.314	0.545	0.642	0.951
fruit_fly_1	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$
fruit_fly_2	0.055	0.182	0.425	0.780
fruit_fly_3	$< 10^{-3}$	$< 10^{-3}$	$< 10^{-3}$	0.002
fruit_fly_4	$< 10^{-3}$	0.006	0.595	$< 10^{-3}$

Table 4.8: Link confinement distributions. Using powerlaw Python package [163], we compare how well the exponential distribution describes the tail of the link confinement distribution against several candidate distributions: stretched exponential, truncated power law, lognormal, and power law distributions. Our results indicate that the link confinement distributions of the most linked trees (fruit fly networks) follow a heavy-tailed distribution.

Chapter 5

Physical network robustness

5.1 Introduction

From the earliest days of complex network research, percolation processes were used to study the robustness of networks against external perturbations [104, 105, 164]. Since then, various variants have been introduced, including percolation on spatially embedded networks [165, 90, 166, 167], interdependent percolation [168, 169, 170], explosive percolation [171, 172], and many others [173, 174]. Here, we explore the robustness of spatial networks against physical damage. By physical damage, we mean the random or targeted removal of entire regions of the space where the network is embedded, such that all links and nodes passing through are disrupted. Note that recent literature defined physical networks as networks where volume exclusion plays an important role, i.e., the network is composed of tightly packed nodes and links [6, 8, 9]. Here, we model a broader class of systems that include networks such as the air traffic network, where volume exclusion is irrelevant, nonetheless, links can be disrupted by physical perturbations such as storms, volcano eruptions, or military conflicts.

To study the robustness of such physically embedded networks, we introduce and analyze a percolation process, where in each step we damage not single links, but a region of the embedding space, removing any links that pass through. Motivating examples of spatially correlated disruption include damage to the brain through injury or diseases [175, 176],

natural disasters, such as floods or storms, affecting critical infrastructure [177, 178, 92, 91], or even the effect of traffic on road networks [179].

To formally set up the problem, we represent a physically embedded network by a combinatorial network \mathcal{G} and a physical layout \mathcal{P} , the latter provides the location and shape of the physical nodes and links. Here, we focus on physical nodes represented by a point in space connected by straight or curved lines; however, our framework easily extends to alternative physical network representations, including nodes and links that occupy a positive volume [6, 8] or network-of-networks representations [180, 181, 9].

To capture spatially correlated damage, we first tile the *D*-dimensional space occupied by a physical network \mathcal{P} with *D*-dimensional cubes of side length *b* (Fig. 5.1a). We then damage tiles sequentially, and when a tile *t* is damaged, we remove from \mathcal{G} each link *e* intersected by *t*. As the tiles are removed, the combinatorial network \mathcal{G} undergoes a continuous percolation transition, which is a mixture site and bond percolation: If a node is inside a tile being damaged, all of its links are removed simultaneously, in effect removing the node. On the other hand, if a link is traversing a tile that is being damaged, the link is removed, but its endpoints are not. In this paper, we aim to understand how the physical layout \mathcal{P} and the structure of the combinatorial network \mathcal{G} jointly affect this critical transition.

The remainder of the chapter is organized as follows. In the next section, we introduce the intersection graph, an auxiliary graph that captures how tile damage translates to link removal. The intersection graph and its randomizations serve as our main tool to numerically and analytically study the percolation transition. In Secs. 5.3 and 5.4, we use randomly embedded model networks to analytically and numerically investigate the robustness of networks against random damage and targeted attacks. Finally, in Sec. 5.5, we use randomizations of the intersection graph to probe how physical layout affects the critical transition in several empirical networks.

5.2 Intersection graph

We start by introducing the intersection graph \mathcal{I} to represent concisely how tile damage translates to link removal. First, we identify which physical link e intersects which tile t and we summarize these intersections as a bipartite graph \mathcal{I} : on one side of \mathcal{I} each vertex represents a tile t, on the other side each vertex represents a physical link e; a tile t and a link e is connected in \mathcal{I} if they intersect in physical space (Fig. 5.1b).

The intersection graph \mathcal{I} encodes potential sources of heterogeneity of the physical layout that affect link removal. Fig. 5.1c illustrates this using a single randomly embedded Erdős-Rényi (ER) network with $N = 10^5$ nodes, an average degree of c = 4, and a tile density $\rho = 4$ (nodes per tile): (i) long links intersect more tiles than short links, captured by the degree distribution $P_1(k)$ of the vertices which represent physical links in \mathcal{I} (Fig. 5.1c); (ii) in absence of periodic boundary conditions, centrally located tiles are expected to intersect more links than peripheral tiles, captured by the degree distribution $P_t(k)$ of the vertices which represent tiles (Fig. 5.1c); and (iii) spatial organization of \mathcal{P} is captured by structural correlations of \mathcal{I} , for example, two physical links running approximately parallel to each other tend to intersect the same tiles, leading to an abundance of length-4 cycles in \mathcal{I} .

Beyond its structure, an additional way \mathcal{I} carries information relevant to the percolation process is through its link-side vertex labels which connect \mathcal{I} and \mathcal{G} . For example, physical links attached to the same node v must all intersect the tile t that contains v, therefore, if t is damaged, all links incident on v are removed together from \mathcal{G} . Furthermore, because long links intersect many tiles, making them vulnerable to tile damage, and if such links tend to be important in \mathcal{G} , the combinatorial network inherits this vulnerability.



Figure 5.1: Spatially correlated damage and the intersection graph. (a) We tile a physical network with D-dimensional square tiles. Damaging a tile t removes all links e intersecting t, for example, damaging tile (3,3) (light blue) removes blue and red links from \mathcal{G} . (b) The bipartite intersection graph \mathcal{I} captures how tile damage of \mathcal{P} translates to link removal in \mathcal{G} . Vertices on the left represent tiles and vertices on the right represent links; a tile and a link are connected, if they intersect in the layout. (c) The tile-side and link-side degree distribution of I for a single randomly embedded ER network ($N = 10^5, c = 4, \rho = 4$). In random embeddings, links typically span the entire system, hence \mathcal{I} becomes dense. (d) We increasing the network size N while keeping the expected number of nodes per tile ρ constant. Both the tile-side average degree c_t and link-side average degree c_1 scale as $\sim N^{-1/D}$. Networks are generated using parameters c = 4 and $\rho = 4$; each marker represents an average of 20 independent runs and the error bars represent the standard error of the mean.

To understand how the above heterogeneities and correlations of \mathcal{I} affect the robustness of physical networks, we randomize \mathcal{I} and compare the percolation transition guided by the original \mathcal{I} and its randomized version \mathcal{I}_r . Different randomizations allow us to probe the role of different features of the physical embedding. For instance, substituting \mathcal{I} with a bipartite configuration model with the same degree distributions $P_1(k)$ and $P_t(k)$, preserves link and tile heterogeneity but removes any additional structure (e.g., structure originating from parallel links or links sharing an endpoint) from \mathcal{I} . To remove link heterogeneity, we homogenize \mathcal{I} by setting the vertices representing links to have approximately the same degree equal to the average c_1 . In practice, this means that in the randomized \mathcal{I}_r the linkside vertices are a mixture of vertices with degree $[c_1]$ and $|c_1|$ in a way that ensures that the overall average degree remains c_1 . Applying the same degree-homogenization to the tile vertices leads to four possible degree-preserving (DP) or homogenized (H) randomization protocols of \mathcal{I} : (i) tile and link degree-preserved (tDP-lDP), (ii) tile degree-preserved and link homogenized (tDP-lH), (iii) tile homogenized and link degree-preserved (tH-IDP), and (iv) tile and link homogenized (tH-lH). Note that the randomized intersection graphs do not correspond to valid physical layouts because a link in \mathcal{I}_r generally intersects non-adjacent tiles.

The randomizations that preserve link-side degree in \mathcal{I} (tDP-lDP and tH-lDP) do not remove correlations between \mathcal{G} and \mathcal{I} : if long links are important in \mathcal{G} , then important links in \mathcal{G} tend to have high degree in \mathcal{I} . To study the effect of this correlation we introduce an additional randomization procedure called "label shuffle" (LS): we shuffle the vertex labels in \mathcal{I} and create a randomized \mathcal{I}_{LS} that is uncorrelated with \mathcal{G} but otherwise has the same structure as \mathcal{I} . This means that dismantling \mathcal{G} using \mathcal{I}_{LS} removes, on average, the same number of links as \mathcal{I} , but the links are chosen randomly in \mathcal{G} independent of the original layout. We summarize in Table 5.1 the main features of the randomization protocols introduced above.

	tDP-	tDP-1H	tH-1DP	tH-lH	LS
	1DP				
$P_{t}(k)$	1	1	X	X	 ✓
$P_1(k)$	1	X	1	X	 ✓
$k(e)$ - \mathcal{G}	1	X	1	X	X
correla-					
tion					
Shared	X	X	X	X	X
endpoint					

Table 5.1: **Randomizations of the intersection graph.** Brief summary of properties preseved by each randomization; shared endpoint means that all links connected to a node vintersect the tile that contains v.

5.2.1 Link-side degree

The degree k(e) of a link e in the intersection graph \mathcal{I} determines the vulnerability of e to tile damage: the more tiles e intersects, the more likely e is removed. In this section, we describe the relation between the length of e and k(e). We consider a physical network with N nodes and M links embedded in the unit D-dimensional cube such that the links are straight segments. We tile the network with cubes of side length b, hence the intersection graph \mathcal{I} contains $n_t = b^{-D}$ vertices representing tiles and $n_1 = M$ vertices representing links. A link e with endpoints $\mathbf{r} = (r_1, r_2, \ldots, r_D)$ and $\mathbf{s} = (s_1, s_2, \ldots, s_D)$ following a straight trajectory intersects a sequence of tiles $(t_1, t_2, \ldots, t_{k(e)})$. Whenever e crosses from a tile t_i to the next t_{i+1} , it punctures the shared face of t_i and t_{i+1} , the probability of crossing at an edge or a corner is zero. Therefore, link e must cross at least $|s_i - r_i|/b$ tiles along each axis i, hence the approximate number of tiles intersected by e, i.e., its degree in \mathcal{I} , is

$$k(e) = 1 + \sum_{i} \frac{|s_i - r_i|}{b},$$
(5.1)

where the plus one corresponds to the starting tile. Note that it is not the Euclidean but the Manhattan distance of the endpoints of e that determines k(e). For example, in a randomly embedded network the typical link length ℓ is on the order of the system size, $\ell \sim 1$, meaning that a typical link intersects $c_{\rm l} \sim Db^{-1}$ tiles and a typical tile is intersected by $c_{\rm t} \sim MDb^{D-1}$ links. Therefore, in the $N \to \infty$ large network limit, if we fix the average degree of \mathcal{G} as $\langle d \rangle = 2M/N$ and the tile density as $\rho = N/b^{-D}$, the intersection graph has diverging average degrees $c_{\rm l} \sim N^{1/D}$ and $c_{\rm t} \sim N^{1/D}$ (Fig. 5.1d). On the other extreme, if the physical network is lattice-like, i.e., nodes connect to their immediate spatial neighborhood and $\ell \sim b$, the average degrees $c_{\rm l}$ and $c_{\rm t}$ remain constant. The diverging average degree $c_{\rm t}$ indicates that randomly embedded networks are more susceptible to physical damage than lattice-like networks. In the following, we systematically investigate the role of physicality in random and targeted damage by relying on \mathcal{I} both numerically and analytically.

5.3 Random damage

In this section, we explore the effect of the combinatorial network \mathcal{G} and the layout \mathcal{P} on the physical percolation of randomly embedded networks. Fig. 5.2 shows the relative size S of the largest component during random tile removal for randomly embedded Erdős-Rényi (ER) networks and scale-free (SF) networks generated by the static model [182,

183]. We recall that the static model generates networks by fixing the expected degree of each node and allows controlling both the degree exponent γ and the average degree of the network c. We compare S of the original \mathcal{I} to the five randomized null models: protocols tDP-lDP, tH-lDP, and LS that preserve $P_1(k)$ follow the original percolation transition $(S \approx S_{tDP-IDP} = S_{tH-IDP} = S_{LS})$, while link-homogenized randomizations tDP-lH and tH-lH accelerate the transition, shifting f_t^* to the left $(S_{tDP-IH} = S_{tH-IH} < S)$. This means that when tiles are damaged independently, only the heterogeneity of the link lengths affects robustness, while tile heterogeneity and correlations between adjacent tiles have negligible effects. To explain these observations and to systematically investigate random damage, we first develop an analytical solution for the relative size of the giant component. Then, we use this analytical characterization together with the numerical randomizations of the intersection graph to explore the role of the degree distribution in randomly embedded networks.



Figure 5.2: **Random tile damage in randomly embedded networks.** We show the relative size S of the largest connected component as a function of the fraction of tiles removed for randomly embedded (a) Erdős-Rényi (ER) networks in D = 2, (b) ER networks in D = 3, (c) scale-free (SF) networks in D = 2, and (d) SF networks in D = 3 dimensions. The dashed line represents the theoretical prediction obtained solving Eqs. (5.6) and (5.7). Networks were generated with $N = 10^5$ nodes and average degree c = 4; for SF networks the degree exponent is $\gamma = 2.5$, and the tile density is set to $\rho = 4$. Each curve is an average of 10 independent realizations.

5.3.1 Analytical characterization

We start by calculating S for the case when \mathcal{G} is generated using the configuration model and tiles are removed in random order. We rely on the standard generating function formalism with the addition that link removal depends on the intersection graph \mathcal{I} , leading to an analytical characterization similar to the so-called feature-enriched percolation [184]. In our solution, we assume no correlations between the removed links, an assumption in general only valid for the randomized versions of the intersection graph. We focus on the sparse large network limit $N \to \infty$, where the average degree of the combinatorial network c remains constant, and we also fix the tile density $\rho = N/b^{-D}$, i.e., the expected number of physical nodes contained in a tile. This means that the total number of tiles scales as

$$n_{\rm t} \sim N,$$
 (5.2)

and the tile size scales as

$$b \sim n_{\rm t}^{-1/D} \sim N^{-1/D}.$$
 (5.3)

Link e is removed if we damage any of its neighbors in \mathcal{I} ; therefore, the probability that e is removed after independently damaging K random tiles is

$$f(k(e)) = 1 - \left(1 - \frac{K}{n_{\rm t}}\right)^{k(e)} = 1 - (1 - f_{\rm t})^{k(e)} \approx 1 - e^{-k(e)f_{\rm t}},\tag{5.4}$$

where $f_t = K/n_t$ is the fraction of tiles removed, and the exponential approximation assumes large k(e). For straight links, Eq. (5.1) connects the degree of links with its length as $k(e) = 1 + b^{-1}l$, which means that the survival probability of a link drops exponentially with l, making long links extremely vulnerable to random tile damage.

Let s(k) denote the probability that a random link with link-side degree k leads to the giant component in \mathcal{G} . Assuming no correlation between the degree of a link in \mathcal{I} and its position in \mathcal{G} , we write the self-consistent equation for s(k)

$$1 - s(k) = f(k) + (1 - f(k)) \sum_{d} q(d) \left(\sum_{k_i} P_1(k_i) \left(1 - s(k_i) \right) \right)^d,$$
(5.5)

where q(d) = (d+1)/cp(d+1) is the excess degree distribution of \mathcal{G} . Averaging Eq. (5.5) over k, we obtain

$$s = G_{\rm l} \left(1 - f_{\rm t} \right) \left[1 - H \left(1 - s \right) \right], \tag{5.6}$$

where $H(z) = \sum_{d} q(d) z^{d}$ is the generating function of q(d), and $G_{l}(z) = \sum_{k} P_{l}(k) z^{k}$ is the moment generating function of the link-side degree distribution of \mathcal{I} . Similarly, we can obtain the relative size of the giant component S as

$$S = 1 - G(1 - s), (5.7)$$

where $G(z) = \sum_{d} p(d) z^{d}$ is the generating function of the degree distribution p(d) of \mathcal{G} .

A crucial quantity in Eq. (5.6) is $1 - G_1(1 - f_t) \equiv f$ providing the probability that a random link is removed, which we calculate by averaging Eq. (5.4) over $P_1(k)$. Equivalently, for straight links, we can leverage Eq. (5.1) connecting the degree of a link in \mathcal{I} to its length to obtain f by averaging over the link lengths, i.e.,

$$1 - f = \int dl p(l) \left(1 - f_{t}\right)^{1 + l/b} \approx \int dl p(l) e^{-(1 + l/b)f_{t}},$$
(5.8)

where l is the link length measured by its Manhattan distance and p(l) is the link length distribution. Equation (5.8) is valid for the original \mathcal{I} and the randomizations that do not modify the link-side degree (tDP-lDP and tH-lDP). On the other hand, randomizations tDP-lH and tH-lH homogenize the link degree in \mathcal{I} , i.e., $k = 1 + b^{-1} \langle l \rangle$ for all links in \mathcal{I}_r , where $\langle l \rangle$ is the average Manhattan link length. Therefore, tDP-lH and tH-lH also modify the link removal probability as

$$1 - f_{\rm IH} = e^{-(1 + \langle l \rangle/b)f_{\rm t}}.$$
(5.9)

Invoking Jensen's inequality, we find that

$$f(f_{\rm t}) \le f_{\rm IH}(f_{\rm t}),\tag{5.10}$$

for any p(l), meaning that link length heterogeneity always decreases the number of links removed for a given f_t (for example, see Fig. 5.2).

Note that Eqs. (5.6) and (5.7) are exactly the equations describing bond percolation in the configuration model with link removal probability $f = 1 - G_1 (1 - f_t)$. When Eqs. (5.6) and (5.7) hold, the only relevant feature of the layout is the link-side degree distribution $P_1(k)$ of \mathcal{I} , which affects the percolation transition only through a number of links removed.

The main assumptions we made when deriving these equations are that (i) G is generated by the configuration model, allowing the use of generating functions based solely

on degree distributions; (ii) the links removed from \mathcal{G} are uncorrelated, enabling a bond percolation framework; and (iii) there are no correlations between a link's degree in \mathcal{I} and its importance in \mathcal{G} , which allows us to treat link removal as independent from the network's topological structure. While these assumptions hold in randomly embedded or randomized networks, they are generally violated in empirical systems (for more details, see SI Sec. 5.7.1). Consequently, in Sec. 5.5, we extend beyond this minimal model to quantify the effects of such correlations using simulations on real networks.

5.3.2 Effect of degree distribution

To investigate the role of the degree distribution of the combinatorial network \mathcal{G} , we focus on purely random embeddings. We select the position of physical nodes uniformly at random from the *D*-dimensional unit cube, $\mathcal{B}_D = [0,1]^{\times D}$, and connect pairs of nodes with straight links. The Manhattan length of a link *e* is $l(e) = \sum |r_i - s_i|$, where $\mathbf{r} \in \mathcal{B}_D$ and $\mathbf{s} \in \mathcal{B}_D$ are the endpoints of *e*, since r_i and s_i are chosen uniformly from the unit interval, their difference $x = |r_i - s_i|$ follows the distribution p(x) = 2(1 - x). Hence, following Eq. (5.8), we get that the average link removal probability is

$$f = 1 - (1 - f_{t}) \left(2 \int_{0}^{1} dx (1 - x) (1 - f_{t})^{x/b} \right)^{D} \approx$$

$$\approx 1 - e^{-f_{t}} \left(2 \int_{0}^{1} dx (1 - x) e^{-xf_{t}/b} \right)^{D} =$$

$$= 1 - e^{-f_{t}} \left(2 \frac{e^{-b^{-1}f_{t}} - 1 + b^{-1}f_{t}}{b^{-2}f_{t}^{2}} \right)^{D},$$
(5.11)

which is valid for the original \mathcal{I} and the randomizations that do not modify the link-side degree (tDP-lDP and tH-lDP). For randomizations tDP-lH and tH-lH that homogenize the link degree, the link removal probability is obtained using Eq. (5.9), providing

$$f_{\rm IH} \approx e^{-(1+\langle l \rangle/b)f_{\rm t}} = e^{-f_{\rm t}} e^{-\left(1+\frac{Df_{\rm t}}{3b}\right)}.$$
(5.12)

In the $N \to \infty$ large network limit, keeping the tile density $\rho = N/b^{-D}$ constant makes the side length of the tiles scale as $b \sim n_t^{-1/D} \to 0$. Hence, the majority of links are removed after damaging only a vanishing fraction of the tiles for both the original and the homogenized distributions $P_1(k)$. Notice, in fact, that the second term of both Eqs. (5.11) and (5.12) indicates that almost all links are removed on the scale $f_t \sim n_t^{-1/D}$, while the first term for vanishing f_t is $e^{-f_t} \approx 1$. This means that the number of tiles to destroy a positive fraction of links in a randomly embedded network scales as $\sim n_t^{(D-1)/D}$, i.e., it is on the order of the number of tiles needed to be damaged to cut the network into two parts.

Fig. 5.2 compares numerical simulations with the analytical estimate of S obtained by inserting Eqs. (5.11) and (5.12) into Eq. (5.7). We find that the analytical solutions align perfectly with the randomizations and also closely follow the simulations using the original \mathcal{I} . We observe small deviations between the predicted S and the original simulated S, particularly for ER networks in D = 2. To explain this, recall that our calculations assumed that the links are removed from \mathcal{G} in an uncorrelated fashion. This assumption only holds approximately for the original \mathcal{I} : links connected to the same node v tend to intersect the same tiles near the vicinity of v, hence having a higher chance of getting removed together. The effect of such correlations depends on the typical link length ℓ and tile size b, if $\ell \gg b$ the likelihood of removing a link near its endpoint diminishes. In the limit $N \to \infty$ with fixed tile density ρ , the relevant length scales are $\ell \sim 1$ and $b \sim N^{-1/D}$; therefore, we expect that the above analytical solution correctly captures Sfor large networks.



Figure 5.3: The scaling of the critical point for scale-free networks. We simulate random tile damage on randomly embedded SF networks with increasing size N and fixed tile density ρ , and we measure the location of the critical point f_t^* by finding the maximum of the second largest component. We show the scaling of f_t^* with N for (a) D = 2 and (b) D = 3 dimensions: markers represent numerical simulations, dashed lines represent the scaling $\sim N^{-(\tau-1)/D}$ predicted by Eq. (5.17) for networks with diverging $\langle d^2 \rangle$, and the dotted lines represent the scaling $N^{-1/D}$ predicted for networks with finite $\langle d^2 \rangle$. We generated networks using c = 4 and $\rho = 4$, the markers represent the average of 50 independent runs, and the error bars represent their standard deviation.

The location of the critical point where the giant component is destroyed is often used to quantify the robustness of networks. For a network with average degree $\langle d \rangle$ and degree second moment $\langle d^2 \rangle$, this critical point f_t^* can be determined using the percolation-based Molloy–Reed criterion [185, 186], given by

$$f_t^* = 1 - \frac{1}{\left(\frac{\langle d^2 \rangle}{\langle d \rangle} - 1\right)}.$$
(5.13)

To determine the critical point f_t^* in our setup, we insert Eq. (5.11) into the Eq. (5.13)

$$\left(2\frac{e^{-b^{-1}f_{t}^{*}}-1+b^{-1}f_{t}^{*}}{\left(b^{-1}f_{t}^{*}\right)^{2}}\right)^{D} = \frac{1}{\left\langle d^{2}\right\rangle / \left\langle d\right\rangle - 1},$$
(5.14)

where the left-hand side only depends on the physical layout, while the right-hand side only depends on the abstract network structure. For combinatorial networks with finite second moment $\langle d^2 \rangle$, the right-hand side does not depend on N and hence on b, while the left-hand side only depends on $b^{-1}f_t = Nt^{1/D}f_t$. Therefore, the critical point vanishes as

$$f_{\rm t}^* \sim N^{-1/D}$$
 (5.15)

in the large network limit.

Scale-free combinatorial networks with $\gamma < 3$ have diverging second moments, hence, almost all links need to be removed to destroy the giant component in random fashion in the $N \to \infty$ large network limit, i.e., $f^* \approx 1$. For traditional random percolation, the finite size scaling of the critical point is characterized by the scaling $1 - f^* \sim N^{-\tau}$, where the exact value of the critical exponent τ depends on the subtleties of how the scale-free networks are generated [187, 188, 189]. Inserting the scaling relation into Eq. (5.14) and keeping only leading terms in $b^{-1}f_t$ yields

$$(b^{-1}f_t)^{-D} \sim N^{-\tau}.$$
 (5.16)

This leads to the finite-size scaling

$$f_t^*(\gamma) \sim N^{-\frac{\tau-1}{D}},\tag{5.17}$$

for $3 < \gamma < 2$. To test the above relation, we first numerically estimate the critical expo-

nent τ by simulating traditional bond percolation on SF combinatorial networks and insert these numerical estimates into Eq. (5.17). Fig. 5.3 compares the theoretically obtained scaling relation to numerical simulations of f_t^* for physically embedded SF networks, finding a good agreement for large N.

Overall, we demonstrated that randomly removing a vanishingly small fraction of tiles is sufficient to dismantle randomly embedded networks and that higher dimensional embeddings increase their vulnerability. The reason for this is the presence of long links that do not scale with the network size N, causing them to intersect a number of tiles that diverge as $\sim b^{-1} \sim N^{1/D}$, thus making them extremely vulnerable to physical damage. We also found that the analytical solution, which in general is valid for the randomized versions of the intersection graph, well describes the percolation transition for the original \mathcal{I} in large networks, revealing that random tile damage is equivalent to a random bond percolation, where the number of links we remove is determined by the layout \mathcal{P} . In the next section, we study networks where we restrict the typical link length ℓ to study the effect of more realistic layouts.

5.4 Targeted damage

We now turn our attention to targeted physical attacks, where we iteratively damage a fraction f_t of the tiles having the highest degree in \mathcal{I} . More formally, given a tiling described by the intersection graph \mathcal{I} :

- 1. We find tile t with the highest degree in \mathcal{I} ;
- 2. We remove t from \mathcal{I} together with each of its neighbors, i.e., with each link e that intersects t;
- 3. We repeat steps 1 and 2 until all links are removed.

In the following, we investigate targeted attacks in detail: first, we explore the effect of the degree distribution for randomly embedded networks, then the effect of restricting the link length.



Figure 5.4: Targeted attack of randomly embedded networks. We show the relative size S of the largest connected component as a function of the fraction of tiles removed for randomly embedded (a) Erdős-Rényi (ER) networks in D = 2, (b) ER networks in D = 3, (c) scale-free (SF) networks in D = 2, and (d) SF networks in D = 3 dimensions. Networks were generated with $N = 10^5$ and c = 4, for SF networks, the degree exponent is $\gamma = 2.5$, and the tile density is set to $\rho = 4$. Each curve is an average of 10 independent realizations.
5.4.1 Effect of degree distribution

As before, to investigate the role of the degree distribution of \mathcal{G} , we focus on randomly embedded networks. Figs. 5.4a, b show the size of the largest component of a randomly embedded Erdős-Rényi (ER) network in D = 2 and D = 3 dimensions under targeted attack. In Sec. 5.3, we found that the only relevant property affecting S during random tile removal is the link-side degree distribution of \mathcal{I} . In the case of targeted physical attacks, a richer picture emerges. By comparing the original \mathcal{I} to its randomized versions, we find that $S_{tDP-IH} < S_{tDP-IDP} < S \approx S_{LS} < S_{tH-IH} < S_{tH-IDP}$ for the entire range of f_t . This means that (i) tile heterogeneity increases the vulnerability of the network, (ii) correlations in \mathcal{I} (such as short loops caused by neighboring links intersecting the same tiles), and link heterogeneity makes the network more robust against targeted attacks. Finally, we find that S for the original \mathcal{I} is identical to the case where we randomly remove the same number of links (LS randomization), meaning that for the ER network, targeted attack dismantles the network faster than random tile removal because it damages more links per tile, but does target links that are important for the cohesion of the network.

Figs. 5.4c, d show instead the relative size of the giant component, S, for SF networks with degree exponent $\gamma = 2.5$, thus having a divergent second moment. The portrait, in this case, is analogous to the one observed in ER networks, with one key exception: while initially $S \approx S_{\text{LS}}$, near the critical point the original network falls apart faster than the LS and even the tDP-IDP version, i.e., $f_t^* < f_{t, \text{tDP-IDP}}^* < f_{t, \text{LS}}^*$. This means that correlations between \mathcal{I} and \mathcal{G} accelerate the targeted disruption of the network.

To clarify the role of degree heterogeneity in \mathcal{G} , we plotted the location of the initial 50 tiles removed for a D = 2 SF network with $\gamma = 5$ and with $\gamma = 2.1$, for both the original network (Fig. 5.5a and d) and the tDP-lDP randomization (Fig. 5.5b and e). For the original homogeneous network ($\gamma = 5$), the initial removal of the tiles concentrates in the center of the embedding square, forming a neat spatial structure that cuts through the network along a straight line (for D = 3, such a structure is less apparent). In contrast, for the heterogeneous network ($\gamma = 2.1$), the removed tiles are randomly scattered in space.



Figure 5.5: Example targeted tile removal. (a) The location of the first 50 tiles removed from a SF network with degree exponent $\gamma = 5$. The removed tiles (b) The tDP-lDP randomization of the network removes the overlap between the links intersected by neighboring tiles, therefore, the attack targets the center tiles. (c) The spatial distribution of the tile-degree shows that the center tiles intersect the most links and monotonically drops towards the edges of the square. (d) The first 50 tiles removed from a SF network with degree exponent $\gamma = 2.1$ target the hubs in \mathcal{G} . (e) In the case of the tDP-lDP randomization, tile removal targets the tiles surrounding the highest degree nodes. (f) The spatial distribution of the tile-degree has peaks at tiles that contain hubs of \mathcal{G} . Figure shows single networks with N = 50,000, c = 4, and $\rho = 4$, the color of the tiles in (a), (b), (d), and (e) indicates the order of the tile removal.

To understand this pattern, consider that the spatial distribution of links in homogeneous networks is approximately the same as picking uniformly random segments from the unit square. As a result, the expected tile degree k_t is the highest in the center of the embedding square and monotonically decreases toward the edges (Fig. 5.5c), explaining why the center tiles are picked initially. However, the highest-degree center tiles are redundant: they are intersected by the same links, i.e., they share many neighbors in the intersection graph \mathcal{I} . The one-dimensional structure of the removed tiles emerges as a result of the targeted attack greedily minimizing the redundancy between the removed tiles. Indeed, the tDP-IDP randomization keeps the degree of the tiles but removes correlations between them, hence, the initially removed tiles concentrate at the center of the embedding square, forming a two-dimensional patch (Fig. 5.5b). This also means that the total number of links removed by the original \mathcal{I} , explaining the observation $S_{\text{tDP-IDP}} < S$.

For heterogeneous networks, on the other hand, links are not uniformly distributed: tiles that contain the hubs of \mathcal{G} intersect an out-sized number of links, resulting in an uneven spatial distribution of the tile-degree (Fig. 5.5f). The random distribution of the initially removed tiles is a result of the target attack selecting tiles that contain the hubs of \mathcal{G} . The tDP-lDP randomization removes redundancy between the tiles surrounding the hubs, hence tile removal is concentrated on the few largest hubs of the network, explaining $S_{\text{tDP-IDP}} < S$ in the early stages of the targeted attack. The LS and tDP-lDP randomizations remove links in an uncorrelated way from \mathcal{G} , this means that hubs are not removed in a single step, but lose links continuously (for more details, see SI Sec. 5.7.2). The fact that tile removal for LS and tDP-lDP does not eliminate hubs entirely, delays the critical point of the transition, explaining the observed $f_t^* < f_{t,tDP-lDP}^* < f_{t,tS}^*$.

In the above, we have shown that, for homogeneous networks, tiles with the most links passing through get targeted first, while, for heterogeneous networks, the location of the hubs of \mathcal{G} determines which tiles get removed. To explore when node degree dominates tile removal, with divide degree k(t) of tile t in \mathcal{I} into two contributions:

$$k(t) = k_{\text{pass}}(t) + k_{\text{nodes}}(t), \qquad (5.18)$$

where $k_{\text{pass}}(t)$ is the number of links that pass through t, i.e., links that intersect t, but have endpoints outside t, and $k(t)_{\text{nodes}}$ is the number of links that have at least one endpoint in t. We estimate the maximum of the two contributions in the $N \to \infty$ large network limit with fixed tile density $\rho = Nb^D$. First, note that the tile t_0 at the center of the unit square or cube has the highest expected number of links passing through, i.e., links that intersect t_0 but have endpoints outside of t_0 . The probability that a randomly placed segment e intersects t_0 is proportional to the cross section of t_0 perpendicular to e which is $\sim b^{D-1} \sim N^{-\frac{D-1}{D}}$. The number of links in the network is $\sim N$; therefore, the total number of links passing through t_0 scales as

$$\max[k(t)_{\text{pass}}] \sim N \cdot N^{-\frac{D-1}{D}} = N^{\frac{1}{D}}.$$
(5.19)

The scaling of the maximum contribution of $k_{\text{nodes}}(t)$ is provided by scaling the largest degree node in \mathcal{G} , hence, it depends on the topology of the network. For heterogeneous networks generated in the static model [190], this is given by $k_{max} \propto N^{\theta}$ with $\theta = 1/(\gamma - 1)$, so that

$$\max[k_{\text{nodes}}(t)] \sim N^{\frac{1}{\gamma-1}}.$$
 (5.20)

The above two scaling relations determine whether the center tile or the tile containing the largest hub of the network gets removed in the first step of the targeted tile removal: for $\gamma < D + 1$, the value of max $[k_{nodes}]$ outgrows max $[k_{pass}]$ and initially the hubs get removed, otherwise the targeted attack removes the tiles close to the center. Fig. 5.6 illustrates the scaling of the maximum tile degree. For $\gamma = 2.1$, the contribution of hubs max $[k_{nodes}]$ dominates both in D = 2 and D = 3 dimensions. In contrast, for $\gamma = 3.5$, the contribution max $[k_{pass}]$ dominates for D = 2, while for D = 3, hubs eventually outgrow the effect of links passing through. Note, however, that the latter only happens for very large networks outside of the regime of most real networks.



Figure 5.6: Scaling of the maximum tile-degree. We measured the maximum tile degree (circles) for increasing size N for SF networks embedded in D = 2 and D = 3 dimensions and with $\gamma = 2.1$ and $\gamma = 3.5$ degree exponents and average degree c = 4. We randomly placed cN/2 segments in the unit square and measured the maximum number of segments intersecting a tile (circles), and we also measured the maximum degree of the combinatorial networks (triangles). The dashed lines represent the scaling predicted by Eqs. (5.19) and (5.20). (a,b) For $\gamma = 2.1$, the contribution of the hubs dominates the maximum tile degree for both D = 2 and D = 3. (c) For $\gamma = 3.5$ and D = 2 dimensions, $\gamma > D + 1$, hence the contribution of max k_{pass} dominates. (d) In contrast, for $\gamma = 3.5$ and D = 3, we predict that max k_{nodes} dominate. However, extrapolating the simulations shows that max k_{nodes} only outgrows max k_{pass} for extremely large networks. Circle markers represent the average of 20 independent physically embedded networks, while triangles and squares represent the average of 100 runs.

5.5 Empirical networks

In this section, we analyze the robustness of three empirical networks using the intersection graph: an airline network, a vascular network, and a neural network. For each case study, we tile the network and calculate the intersection graph. We then perform both random and targeted tile removal, and we compare the percolation transition obtained for the original layout against the randomized null models. Finally, we test the robustness of our results by systematically changing the size of the tile.

A difference between model networks and empirical data is that we embedded model networks in the unit square or cube. Real networks, on the other hand, typically have a less regular shape, hence, their bounding box may contain large empty regions. Therefore, to tile an empirical network, we identify its axis-aligned bounding box, we tile this bounding box with cubic boxes, and, crucially, we leave out the empty tiles from our analysis. In other words, we remove isolated vertices from the intersection graph \mathcal{I} before simulating tile removal. In the following, we discuss each case study separately.

5.5.1 Airline network

Our first case study is a network representing air traffic in the contiguous US, which we constructed using data available from the Bureau of Transportation Statistics for the year 2023 [191]. The network contains N = 419 nodes representing cities, and we added a link between two cities if the total number of passengers on direct flights between the pair exceeded 1000, resulting in an average degree of $c \approx 16.7$. We obtain the coordinates of the cities from OpenStreetMap, and we transform the longitude and latitude pairs to Euclidean space using the Albers equal area projection. We consider flight paths to be straight lines between cities.

Fig. 5.7a shows the degree distribution p(d) of the combinatorial network \mathcal{G} . We find that p(d) is highly heterogeneous: the median degree is 4, while the largest hub is connected to 194 nodes, representing close to half of the cities. To construct the intersection graph \mathcal{I} , we tile the network such that we place 40 square tiles along the longest axis of its bounding box, resulting in $n_t = 743$ non-empty square tiles and tile density $\rho \approx 0.56$. Flights often traverse the US, hence the longest links in the network are comparable to the size of the bounding box. As a consequence, the tile-side degree distribution $P_t(k)$ and the link-side degree distribution $P_e(k)$ of \mathcal{I} resemble the degree distributions observed in randomly embedded networks (Fig. 5.7b), where there is also no constraint on the maximum link length.

Fig. 5.7c shows the size of the largest component S as a function of the tiles removed. Due to the high average degree $c \approx 16.7$, a large fraction of the links need to be removed to dismantle the network: for traditional bond percolation, we must remove approximately $f \approx 0.97$ fraction of the links from \mathcal{G} to reduce its largest component to S = 0.1. In stark contrast, the same reduction in S is achieved by randomly removing only $f_t \approx 0.24$ fraction of the tiles. Comparing the original intersection graph \mathcal{I} to its randomizations, we find that tile-degree heterogeneity by itself has little effect and that the link-side degree heterogeneity delays the percolation ($S_{tDP-IH} \approx S_{tH-IH} < S_{tDP-IDP} \approx S_{tH-IDP}$), similarly to randomly embedded model networks (Fig. 5.2). However, in contrast to randomly embedded networks, we find that the LS randomization initially reduces S faster than the original \mathcal{I} (S > S_{LS}), but eventually, LS delays the percolation transition (S < S_{LS}). Recall that LS randomization removes the same number of links from \mathcal{G} , but randomly; therefore, the above observations suggest that there is a correlation between a link's degree in \mathcal{I} and its importance in \mathcal{G} . Indeed, calculating the Pearson correlation between link-degree and the product of the degree of a link's endpoints in \mathcal{G} , we find a positive correlation of $r \approx 0.26$. This means that the original tile removal tends to remove links connecting hubs faster than the LS randomization, which explains the observed pattern: removing links between hubs in the network with high c initially does not reduce S, but in the long run accelerates the destruction of the largest component.

For targeted tile removal, in Sec. 5.4, we found that tiles containing the largest hubs are removed first from degree heterogeneous networks, hence, we expect a similar pattern for the airline network. Indeed, the first five tiles removed, for example, all contain major airline hubs, such as Denver, Dallas, or Atalanta. Fig. 5.7d compares the original S to its randomized counterparts, and we find a similar pattern to randomly embedded networks: $S \approx S_{\text{LS}} < S_{\text{tDP-IH}} < S_{\text{tDP-IDP}} < S_{\text{tH-IH}} < S_{\text{tH-IDP}}$, meaning that tile-degree heterogeneity accelerates, while link-degree heterogeneity slows down the percolation process. A key difference compared to model networks is that the original removal decays even faster than the tDP-IH and tDP-IDP randomizations. To explain this observation, note that the links intersecting tiles that contain hubs in \mathcal{I} have less overlap than in the randomized versions. For example, in our network Dallas has 194 and Denver has 182 connections, but only one of these connections, namely flights between Dallas and Denver, overlap. The expected overlap between random sets of links of the same size is $194 \cdot 182/3500 \approx 10$, hence, when removing the tiles containing Dallas and Denver, more unique links are damaged by the original process than by the randomized variants. For the visual representation of targeted damage on the airline network, see SI Sec. 5.10.

Finally, to test the effect of tile size, we measure the fraction of tiles $f_{t,10\%}$ needed to be

removed to reduce the largest component to S = 0.1 for tilings of various sizes. Fig. 5.7e and f show that the order of the randomizations does not change in the entire range of tiles that we tested both for random and targeted percolation.



Figure 5.7: Airline network robustness. (a) The degree distribution p(d) of the combinatorial network. The largest hub is connected to 194 of the N = 419 nodes of the network. (b) The tile-side degree distribution $P_t(k)$ and the link-side degree distribution $P_e(k)$ of the intersection graph \mathcal{I} . (c,d) The size of the largest component S during random and targeted tile removal. (e,f) The fraction of tiles $f_{t,10\%}$ needed to be removed to reduce the largest component to S = 0.1 for random and targeted tile removal as a function of the number of non-empty tiles n_t used to cover the network. The order of the randomized variants is insensitive to the choice of tile size. In panels (c-f), lines and markers represent an average of 20 independent randomizations, and the error bars indicate the standard deviation.

5.5.2 Vascular network

Our second case study is a network representing the vasculature in a sample of the brain of a mouse [4]. In the network, nodes represent branching points of the vessels or terminal points at the edge of the sample, while links represent vessels in between branching points, overall resulting in N = 1558 nodes and M = 2359 links. Note that links are not straight lines, but follow a winding trajectory. Fig. 5.8a shows that the degree distribution p(d) is highly homogeneous, largely concentrated on d = 3, which indicates that most branching points split vessels into two new branches. For more details about the properties of the network see Ref. [17].

We tile the network with cubes such that 20 tiles are placed along the longest axis of the network's bounding box. After dropping the empty tiles, the network is covered by $n_t = 3276$ boxes, resulting in a tile density of $\rho \approx 0.48$. In contrast to the airline network, Fig. 5.8b shows that the link-side degree distribution $P_1(k)$ is peaked at k = 1, meaning that typical links are short compared to tile size b. As a consequence, the average tile-side degree is also much lower compared to the airline network. The low link-side degrees of \mathcal{I} together with the homogeneous degree distribution of \mathcal{G} make the vascular network lattice-like, counter to the airline network and the randomly embedded model networks.

For random tile removal, Fig. 5.8c shows that the randomizations overlap, especially in the later stages of the percolation process $(S_{tDP-IDP} \approx S_{tDP-IH} \approx S_{tH-IDP} \approx S_{tH-IH})$. This is explained by the fact that $P_1(k)$ follows an exponential distribution; therefore, further homogenizing it has little effect on random removal. A curious pattern is that the original process is slower at dismantling the largest component than randomly removing the same number of links ($S < S_{LS}$). To understand this, notice that the majority of links intersect only a few tiles; therefore, a link e is likely to be removed at its endpoint node v, together with other links adjacent to v. Links connected to the same node v play a redundant role in the connectivity of the network, hence, removing them together reduces S slower than removing the same number of random links.

For targeted removal, Fig. 5.8d shows that tile-side degree heterogeneity matters ($S_{tDP-IDP} \approx S_{LS} \approx S_{tDP-IH} < S < S_{tH-IDP} < S_{tH-IH}$), meaning that although $P_t(k)$ is exponentially distributed, targeting its tail still gives an advantage. Similarly to random removal, we observe that $S < S_{LS}$, which is again explained by removing links at their endpoint and the fact that p(d) lacks hubs that would need to be removed.

Overall, tH null models are more robust than the original layout, which would make sense as for homogenized tiles, each one would be equally likely, thus resembling the random attack scenario. On the other hand, all other null models are less robust and break down quicker than the original layout. One potential explanation is that even though some regions contain many dense tiles, which might cause redundant removals that effectively just prune the network, instead of severing it into larger disconnected components.

Finally, to test the effect of tile size, we measure the fraction of tiles $f_{t,10\%}$ needed to be removed to reduce S to 0.1. Similarly to the airline network, Fig. 5.8 and f show that the order of the randomizations does not change in the entire range of tiles that we tested both for random and targeted percolation.



Figure 5.8: Vascular network robustness. (a) The degree distribution p(d) of the combinatorial network. The majority of nodes are bifurcation points with degree d = 3. (b) The tile-side degree distribution $P_t(k)$ and the link-side degree distribution $P_e(k)$ of the intersection graph \mathcal{I} . (c,d) The size of the largest component S during random and targeted tile removal. (e,f) The fraction of tiles $f_{t,10\%}$ needed to be removed to reduce the largest component to S = 0.1 for random and targeted tile removal as a function of the number of non-empty tiles n_t used to cover the network. The order of the randomized variants is insensitive to the choice of tile size. In panels (c-f), lines and markers represent an average of 20 independent randomizations, and the error bars indicate the standard deviation.

5.5.3 Neural network

As the final case study, we analyze a network of neurons comprising a region of the central nervous systems of a fruit fly [127]. The network is composed of 96 neurons and 6249 synaptic connections. Each neuron in the data set is represented as a spatially embedded tree and these embedded trees are bound together through synapses. Here, we focus on a microscopic representation of this network: we treat the branching points and terminal points of the linked trees as nodes, and we treat the connections between them as links. This way our network contains N = 97,588 nodes and M = 100,388 links, making it our largest example. Fig. 5.9a shows that the degree distribution p(d) of \mathcal{G} is concentrated on d = 1 and d = 3, indicating that most nodes are terminal or bifurcation points of the neurons. For more details about the properties of this network, see Ref. [17].

We tile the network with cubes such that 40 tiles are placed along the longest axis of the network's bounding box. After dropping the empty tiles, the network is covered by $n_t = 11,389$ boxes, resulting in a tile density of $\rho \approx 8.6$. Fig. 5.9b shows that the linkside degree distribution $P_1(k)$ is sharply peaked at k = 1, meaning that typical links are shorter than b and are contained inside a single tile. Note, however, that despite the peak at k = 1 there are still a few links that span the bounding box. We observe a high maximum tile-side degree, this is due to tiles that contain many nodes. Although there are some key differences, the high peak of $P_1(k)$ at k = 1 and the homogeneous p(d) make the fruit fly neural network similar to the vascular network.

For random tile removal, Fig. 5.9c shows a very similar pattern to the vascular network, with the difference that link-degree does have an effect. For targeted removal, shown in Fig. 5.9d, the ordering of the randomizations is identical to that of the vascular network.

Finally, as in both cases before, Fig. 5.9e and f show that the order of the randomizations is not sensitive to the choice of tile size in the ranges that we tested.



Figure 5.9: Fruit fly neural network robustness. (a) The degree distribution p(d) of the combinatorial network. The majority of nodes are terminal or bifurcation points with degree d = 1 or d = 3, respectively. The average degree of the network $c \approx 2.06$ is close to two, which would correspond to a tree. (b) The tile-side degree distribution $P_t(k)$ and the link-side degree distribution $P_e(k)$ of the intersection graph \mathcal{I} . (c,d) The size of the largest component S during random and targeted tile removal. (e,f) The fraction of tiles $f_{t,10\%}$ needed to be removed to reduce the largest component to S = 0.1 for random and targeted tile removal as a function of the number of non-empty tiles n_t used to cover the network. The order of the randomized variants is insensitive to the choice of tile size. In panels (c-f), lines and markers represent an average of 20 independent randomizations, and the error bars indicate the standard deviation.

5.6 Discussion

In this chapter, we provide a framework to study the robustness of spatially embedded networks against physical damage. The setup aims to model spatially localized damage, and it takes into account the routing of links. Our key observation is that long links are necessarily susceptible to physical damage, hence, their presence can make networks vulnerable to localized attacks. Traditional network science focuses solely on combinatorial networks, while spatial network theory also takes into account the coordinates of nodes but for most cases, ignores link routing. Our results highlight that incorporating the physical shape of links and nodes can reveal properties of networks that are otherwise missed by more traditional approaches.

The central tool of our analysis is the intersection graph, which concisely captures how the physical layout affects the percolation transition. Faithfully representing the shape of physical links and nodes requires large amounts of data; therefore, directly working with such representations is computationally expensive and makes analytical description difficult. Calculating the intersection graph provides a way to extract the relevant properties of the physical layout of a network, thus simplifying numerical exploration and enabling us to adapt the analytical tools of network science to characterize the percolation transition. The intersection graph and the conceptually similar meta-graph of Ref. [8] or contactome of Ref. [192] may provide a blueprint for tackling the complexity of physical layouts.

Our work raises several new questions. For example, we studied randomly embedded model networks, which allowed simple analytical characterization. Future work may extend this to more realistic models that take into account distance when creating links [88] or other physical constraints [8, 9], or may explore the role of the spatial organization of links, such as bundling [10] and entanglement [7, 29]. Also, throughout this chapter, we focused on network embeddings where nodes are point-like and links are extended objects connecting them. Many physically embedded networks, however, are better characterized by extended nodes with point-like connect to each other via point-like synapses. Such physical networks are better represented as spatially embedded network-of-networks, future work may extend the tile removal percolation to such representations [9].

5.7 Supplementary Information

5.7.1 Analytical characterization assumptions

In Chapter 5, I began with randomly embedded configuration models to construct a minimal, analytically tractable framework, which would allow us to fully understand basic underlying mechanisms. The three assumptions below, which are justified in detail, were necessary to derive closed-form results:

(i) \mathcal{G} is generated by the configuration model

This choice concerning the abstract network allows us to use the standard generating function formalism to calculate the size of the giant component. It also allows us to systematically investigate the role of the degree distribution, arguably the most important structural feature affecting percolation on complex networks.

From an analytical standpoint, Eqs. (5.6) and (5.7) rely on configuration model properties for generating function calculations.

This assumption holds in large, sparse networks where degree distribution dominates connectivity, but real networks often violate this (e.g., due to spatial constraints, clustering, or modularity). For example, in transportation networks, biological neural networks, or infrastructure systems, link formation is often dictated by physical space and not purely by node degree.

(ii) Links are removed independently

This simplifies the analysis to a bond percolation problem. The assumption is used for Eq. (5.4), where the link removal probability depends only on its degree in

The assumption formally holds for randomized versions of \mathcal{I} , where the correlation of the links inside tiles is removed. For example, if a hub v is contained in tile t, then damaging t removes all links attached to v, hence, the link removal is not independent. On the other hand, randomizing \mathcal{I} , randomizes the links in t, and link removal becomes independent. Additionally, in large, randomly embedded networks, most links are long and are typically removed due to intersections with damaged tiles along their length, not at their endpoints. Hence, links removed together typically have endpoints far away from each other and can be considered independent. As shown in Figs. 5.1 and 5.2, numerical simulations confirm that link removal behaves approximately independently, supporting this assumption empirically. This assumption might fail in some real systems, for example, when links are short or, damaging a tile removes multiple links simultaneously.

(iii) No correlation between a link's degree in ${\cal I}$ and its importance in ${\cal G}$

This assumption naturally holds for random embeddings; however, it is often violated by real networks (e.g., the size of neurons is correlated with their synapse count and confinement). The random embedding allowed us (i) to explicitly calculate the probability of link removal and (ii) ensure that links are removed approximately independently. This is a limitation of the minimal model, and to go beyond it we study empirical networks in Sec. 5.5 using simulations and randomizations of \mathcal{I} , while the minimal model served as a starting point to understand the patterns numerically observed for real networks.

This assumption enters directly in Eq. (5.5), where s(k), the probability that a link with degree k in \mathcal{I} (i.e., it intersects k tiles) connects to the giant component in \mathcal{G} , is treated as a function of k only.

Without this assumption, we could not decouple link confinement from the topological position, and Eq. (5.5) would require modeling the joint distribution of confinement and importance—rendering the analysis intractable.

5.7.2 tDP-IDP randomization

The two mechanisms of the tile removal process in the tDP-IDP randomization discussed in Sec. 5.4.1, at first glance, seem contradictory, yet both can hold simultaneously.

To illustrate, consider a scenario of targeted damage on a large embedded network of size $N \sim 10^5$, featuring one large hub with degree $k \sim 1000$, one smaller hub with $k \sim 10$, and the remaining nodes having low degree on the order of $k \sim 1$, all uniformly embedded in a square, partitioned into $n \sim 10^5$ tiles.

In the original embedding, the tile containing the largest hub and its adjacent tiles exhibit significant link overlap, as the hub's outgoing links traverse neighboring tiles. When the tile containing the largest hub is attacked, all links within it are removed, and adjacent tiles lose a substantial portion of their links. Consequently, the second attack targets an unrelated tile containing the second-largest hub. The first attack removes approximately ~ 1000 links, while the second removes only ~ 10 links. The immediate removal of hubs, which are important for maintaining global connectivity, accelerates the percolation process.

With the tDP-IDP randomization, tiles that previously contained the largest hub and tiles adjacent to it, will not have the membership overlap, as the links contained in them are now randomly selected. Once the tile with the highest number of links is attacked (which before the randomization contained the largest hub), the number of links passing through it drops to 0, but unlike in the original scenario, this will have a reduced impact on the adjacent tiles. Therefore, the adjacent tiles retain their original number of links, but now tiles are populated with random links from \mathcal{G} . Compared to the original embedding, in the scenario of having a single high-degree node, the number of links removed in the subsequent attacks would be higher. The initial attack will, similarly as for the original embedding, remove ~ 1000 links, but, the second attack will remove ~ 1000 links as well (depending on the number of links in the adjacent tile), which accelerates the percolation process. It's important to note that although the second attack removes more links, they are randomly selected, which slows down the dismantling process as the second largest hub is more likely to remain intact.

Under the tDP-IDP randomization, the tiles that originally contained the largest hub and its neighbors no longer have overlapping links, as their link content is now randomly assigned. Attacking the tile with the most links (previously hosting the largest hub) still removes ~ 1000 links, but the adjacent tiles are largely unaffected, retaining their original link count. Now, the links within tiles are randomly chosen from \mathcal{G} . As a result, the second attack removes approximately ~ 1000 links as well, thereby accelerating link removal compared to the original embedding. However, although more links are removed, they are randomly selected. This slows down network dismantling because the second-largest hub remains intact.

To summarize, there are two competing effects at play with the tDP-IDP randomization, whose balance depends on the network's size and structure:

- 1. By eliminating link redundancy between neighboring tiles, each targeted tile removal results in more links being removed, thus accelerating the dismantling process.
- 2. However, since link selection becomes random, hubs are not directly targeted. This can slow down dismantling, especially if hubs are critical for global connectivity.

5.7.3 Targeted damage on the airline network



Figure 5.10: **Visualization of targeted damage on the airline network.** Selected snapshots from a targeted tile removal process on the U.S. airline network, visualizing which links are removed during attacks. Each panel (a–d) highlights the edges removed at specific stages of the 52-step attack, color-coded by the attack index (see color bar). Panel (a) corresponds to the first attack, which removes tiles containing major hubs, resulting in 13.5% of links being removed. In later steps, such as (b) and (c), progressively fewer links are removed due to decreased tile connectivity. By panel (d), only 0.1% of links are affected. The spatial pattern shows that early attacks disproportionately target central long-range connections.

Chapter 6

Conclusions

6.1 Summary

The findings of this thesis advance our understanding of physical networks through a combination of theoretical development, empirical network analysis, and methodological innovation. Each chapter has contributed to this overarching goal, as summarized below:

I performed a comprehensive literature review in Chapter 2, tracing the chronological development of the relevant fields, ending with the emerging domain of physical network research, which is the topic of study of this thesis. This chapter provides the context for the thesis, emphasizing how disciplines such as graph theory, polymer physics, neuroscience, transportation networks, spatial networks, and networks-of-networks contribute tools and principles to understand real-world physical networks. By integrating insights from these fields, this chapter also highlights the interdisciplinary nature of physical network research and sets the stage for investigating how spatial embedding and physical constraints influence physical network structure and robustness, the key themes explored in the subsequent chapters.

I introduced the generalized meta-graph formalism in Chapter 3, a framework that extends the original meta-graph concept to study real-world physical networks with complex structures. This approach allowed for the quantification of spatial proximity and physical confinement in systems with curved links and heterogeneous geometries. The generalized meta-graph was adapted and applied to datasets like the fruit fly neural and vascular networks, therefore revealing how physical constraints shape network properties and predict functional features, such as synapse formation or structural organization. Overall, this chapter established a computationally efficient and versatile tool for analyzing physical networks, providing insights into their structure and function.

In Chapter 4, I systematically processed and analyzed 15 empirical physical network data sets from diverse domains, uncovering the relationships between their network structure and physical properties. I adapted metrics previously used in other fields, to quantitatively describe the shape of the network and the individual links. Also, I introduced a novel descriptor called link confinement, which captures the spatial constraints of individual links. My results have revealed correlations between physical layout and network topology, revealing general and domain-specific traits, such as how physical constraints influence abstract network connectivity and link trajectories. These findings demonstrate that network properties cannot be fully understood without considering their spatial embedding.

Finally, in Chapter 5, I explored the robustness of physical networks when subjected to spatially correlated damage, modeled as a percolation process. This study showed the importance of physical link length, and the network layout in general in determining the vulnerability of embedded networks. By systematically investigating random and targeted spatially correlated damage, I demonstrated that network robustness depends not only on the properties of the abstract networks but also on the interplay between physical layout and combinatorial network structure. This duality offers a new perspective on understanding how real-world physical networks might fail under localized or global disruptions.

Overall, with this thesis, I provided insights, data sets, methods, and results that deepen our understanding of physical networks and provide a foundation for future work in this interdisciplinary field.

6.2 Limitations and future extensions

The development of the theory of physical networks within network science is still in its nascence. In this final section, I summarize the limitations of my thesis and the challenges that physical network research faces in general. I also point out areas of potential future research addressing these issues.

6.2.1 Computational resources

The sheer amount of data needed to represent the detailed three-dimensional shape of physical networks makes analyzing them computationally expensive and often requires specialized knowledge. For example, one of the most comprehensive physical network maps available during my research was the Hemibrain data set, which represents a portion of a fruit fly's central nervous system. The available data mapped $25 \cdot 10^3$ neurons and $20 \cdot 10^6$ synapse locations, using $117 \cdot 10^6$ straight segments. Indeed, I resorted to only using a sub-sample of the available data for this thesis. Furthermore, the types of data representing three-dimensional objects and the computational geometry algorithms needed to analyze them are outside of the scope of typical research within network science, which may discourage researchers from joining the field and hinder the development of physical network research. One general solution is to provide easy access to the software and computational resources that would allow for the processing of these large data sets. A solution perhaps more aligned with the approach of network science, is to identify what aspects of the physical layout are relevant to specific research questions, allowing for more tractable representations. An example of such an approach from my thesis is the intersection graph (introduced in Chapter 5). Once calculated it allows us to efficiently analyze the robustness of physical networks using tools of traditional network science and relying upon fewer computational resources.

6.2.2 Data standardization

Each experiment providing physical network data has its standards and idiosyncrasies which makes cross-comparison difficult. To perform research that would encompass data originating from different experiments or even different domains, a standardized processing and representation framework is needed. In this thesis, I compiled 15 new datasets and developed my own data standardization protocols, although, limited in their size and scope. Furthermore, I worked with skeletonized data published by the original authors, therefore, all previous data collection and processing steps, like imaging or choosing parameters for skeletonization algorithms, affected the data I used and potentially the results. Therefore, a collective community effort is necessary to define and test the data collection and processing standards and to build databases that would allow easier access to all future network scientists venturing into this field.

6.2.3 Incomplete data

To empirically understand how physical interaction influences the evolution of a physical network, the mapping of the network needs to be both exhaustive and detailed, as every unmapped part decreases the accuracy of the results. In this thesis, I included complete or as large as possible data sets, to minimize the effect of incomplete data. Nevertheless, all data sources contained data about only the network itself, almost always assumed to be made of homogenous material, while the surrounding non-network material, which interacts physically with the network, was not included. Additionally, even though these networks grow or sustain damage, thus changing their structure in a time-dependent manner, only static data was available. For example, during the development of a brain, neurons grow, rewire, and die. Incorporating data describing the physical environment or temporal evolution would inspire new theoretical research and provide a more complete understanding of the role of physicality.

6.2.4 Additional applications

The data sources used in this thesis have mostly been from the biological domain, with the most prominent field being neuroscience. However, extending physical network research to other disciplines, such as engineering and materials science, presents significant opportunities for interdisciplinary developments:

- 1. Three-dimensional metamaterials [116, 1, 117] made of specifically designed physical structures offer up new electromagnetic and acoustic properties and they can be represented as physical networks. Closely related field of network materials research [193] examines networks from the perspective of materials science, and offers a complementary avenue of exploration.
- 2. All real computational systems have hardware components, which have to be designed and manufactured. The field of neuromorphic engineering [194, 195] aims to physically design and create artificial systems that exhibit similar computational capabilities as biological neural networks. The adjacent field of wetware computing [196, 197] investigates how to utilize real biological neurons to perform computation. All these networked systems have to be physically realized, which means that research on how to realize or grow physical networks might provide principles or results that could aid in developing a general theory of physical networks.
- 3. The function of many physical networks is to transfer flow, which has been explored in microfluid network [198, 199, 200] and pore network [201, 202, 203] research.

The field of microfluid networks mainly focuses on the design and functions of the systems of transport and delivery of chemicals, while the study of pore networks focuses on the flow of materials through porous media - like heavy oil passing through the pores of the soil [204]. Understanding how physical flow fluids pass throughout the tubular structures of a physical network can be simulated or analyzed using methods of these fields, and may provide general insights into the dynamics on physical networks.

6.2.5 Outlook

The success of network science lies in its ability to unify diverse systems under a single framework, revealing universal patterns and principles that govern complexity across scales and domains. In the emerging field of physical networks, this mission is extended to spatially embedded systems, where physical constraints such as geometry, material properties, and spatial embedding influence network behavior. By bridging the connective and the physical properties, physical network research not only deepens our understanding of real-world systems but also potentially equips us with tools to design and optimize systems in engineered and natural contexts.

The broader vision for the future of physical network research is to provide a unifying framework that is versatile enough to encompass disciplines as diverse as neuroscience and materials science, while remaining robust and generalizable. This interdisciplinary approach advances scientific knowledge and paves the way for practical innovations in fields like neuromorphic computing, bio-inspired design, and materials engineering.

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