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Adaptive Networks

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Abstract. The investigation of complex networks has received a rapidly increasing amount of attention in recent years, with many applications in social, biological and technical systems. In particular, most research proceeded in two distinct directions. On the one hand, attention has been paid to the structure of the networks, revealing that simple dynamical rules, such as preferential attachment, can be used to generate complex topologies. Many of these rules are not only a useful tool for the generation of model graphs, but are also believed to shape real-world networks. On the other hand, research has focused on large ensembles of dynamical systems, where the interaction between individual units is described by a complex graph. These studies have shown that the network topology can have a strong impact on the dynamics of the nodes, e.g., the absence of epidemic thresholds on scale free networks. This lecture will review recent progress in the field of complex networks. We will introduce adaptive networks which combine topological evolution of the network with dynamics in the network nodes and discuss several applications from biology and epidemiology.

Contents

1 Introduction

Complex networks are ubiquitous in nature and are gaining increasing attention in the nonlinear sciences. They occur in a large variety of real-world systems ranging from ecology and epidemiology to neuroscience, socio-economics and computer science [1, 2, 3]. Important examples include ecological food webs, the network of social contacts, the internet, the road network and the neuron network in our brain. While physics has for a long time been concerned with well-mixed systems, lattices and spatially explicit models, the investigation of complex networks has in the recent years received a rapidly increasing amount of attention. In particular, the need to protect or optimize natural networks as well as the quest for creating robust and efficient technical nets that exploit similar organizing principles prove to be strong incentives for research.

Beside the identification and characterization of network structure in real natural systems, most recent studies revolve around two key questions: what are the topological properties of a network that is evolving in time and, secondly, how does the functioning of the network depend on these properties? These questions have given rise to two distinct lines of research. The first of these is concerned with the *dynamics of networks*. Here, emphasis is put on the structure of the network, which itself is regarded as a dynamical system that grows or changes over time according to specific, often local, rules. Notable examples include the investigation of the small-world property of social networks [4] and the formation of a scale free topology in growing networks, like citation networks [5] or the internet [6]. These and a large number of subsequent works have revealed that simple evolution rules, such as preferential attachment or selective rewiring, can be used to generate complex network topologies. Many of these rules are not just useful theoretical algorithms, but mimic natural processes of network formation.

The second major line of network research has focused on the *dynamics on networks*. Here, the network represents an ensemble of dynamical systems, where each node is attributed a dynamic state and the interaction between individual units is described by the adjacency matrix of the network. Thus, the topology of the network remains static but the states of the nodes change according to local evolution rules. Important processes that are studied within this framework include synchronization in ensembles of coupled oscillators [7] or contact processes, such as opinion formation and epidemic spreading [8, 12, 9, 10, 11]. These studies have made it clear that the network topology can have a strong impact on the dynamics of the nodes. For instance it was shown that vaccination of a fraction of the nodes can not stop epidemics on a scale free network [8, 12].

Until recently, the two lines of network research described above were pursued almost independently in the physics literature. While there was certainly a strong interaction and cross-fertilization, a given model would either describe the dynamics *of* a certain network or the dynamics *on* a certain network. Nevertheless, it is clear that in most real world networks the evolution of the topology is invariably linked to the state of the network and vice versa. Consider for instance a road network.

The topology of the network, that is the pattern of roads, influences the dynamic state, i.e. the flow and density of traffic. But, if traffic congestions are common on a given road, it is likely that new roads will be build in order to decrease the load on the congested one. In this way a feedback loop is formed in which the topology of the network affects the dynamics on the network, while the dynamics on the network has an influence on the time evolution of the topology. This feedback loop can give rise to a complicated mutual interaction between a time varying network topology and the nodes' dynamics. Networks which exhibit such a feedback loop are called *coevolutionary* or *adaptive* networks [13]. More examples of this class of networks are discussed below.

Based on the successes of the two lines of research mentioned earlier, it is the next logical step to bring these strands back together and to investigate the dynamics of adaptive networks which combine the time evolution of the topology with that of the state of the nodes. Indeed, a number of papers on the dynamics of adaptive networks have recently appeared. Since adaptive networks occur over a large variety of scientific disciplines they are currently investigated from many different directions. While present studies can only be considered as a first step toward a general theory of adaptive networks, they already crystallize certain general insights. Especially these studies show that the interplay of network state and topology leads to interesting new physical phenomena. Despite the thematic diversification, the reported results, considered together, show that certain dynamical phenomena repeatedly appear in adaptive networks: the formation of complex topologies, robust dynamical self-organization, spontaneous emergence of different classes of nodes from an initially inhomogeneous population, and complex mutual dynamics in state and topology [13].

In this lecture we review the present state of research in the dynamics of adaptive networks. The text is strongly guided by a previous comparative study of adaptive networks across disciplines [13, 14]. We start in Sec. 2 by giving essential definitions from graph theory. We provide a basic overview of the central properties of adaptive networks and discuss several examples that illustrate the abundance of adaptive networks in the real world and also in certain classes of applied models. In Sec. 3 we study the spread of diseases on adaptive social networks, which will illustrate the rich dynamics that can arise in dynamic networks. We conclude in Sec. 4 with a short summary and outlook.

2 Adaptive networks: a definition

2.1 Basic definitions of graph theory

Any treatment of complex networks resides on the terminology of graph theory. Here we just present some basic definitions and the most commonly used terminology to provide some basic knowledge. For a more thorough introduction we refer the reader to one of the excellent review articles (see e.g., [1, 2, 3, 15]). As usual we define a network as an ensemble of N *nodes* (also called *vertices*) which are connected by K (directed or undirected) *links* (or *edges*). The nodes form the principal elements of

the network and may represent the basic units of the system under investigation. The total number of nodes is called the *size* of the network and here denoted as N.

The edges of a network usually represent some kind of interaction or relation between the nodes. Together all edges define the network's *topology*, which denotes a specific pattern of connections between the network nodes. Two nodes are said to be *neighbors* or *adjacent* if they have a common link. The *neighborhood* of a node corresponds to the set of all adjacent nodes in the graph. The topology can be described by the *adjacency matrix* a_{ij} $(i, j = 0 \dots N)$, where each element is taken from $\{0, 1\}$. If two nodes i and j are adjacent, one has $a_{ij} \neq 0$. Depending on the network under consideration the links can be *directed* or *undirected*. The adjacency matrix of an undirected matrix is symmetric $a_{ij} = a_{ji}$. In general, the links may be of different nature (e.g., inhibiting or activating) and can have different *weights* (interaction strength). This is accordingly described by the weight matrix w_{ij}, where each element is a real number.

The *degree*, k_i, of a node i is the number of nearest neighbors to which it is connected. In a directed network one has to distinguish between the *in-degree*, k_i^{in}, and the *out-degree*, k_i^{out}, corresponding to the number of edges entering or leaving the node. The total degree, then, is the sum $k_i = k_i^{in} + k_i^{out}$. The *mean degree* or *connectivity*, $\langle k \rangle = \frac{1}{N} \sum_i k_i$, is defined as the mean of the individual degrees of all nodes in the network.

An important quantity to characterize a network's topology is its *degree distribution* $P(k)$ which describes the probability that a randomly selected node has a certain number of links. Important examples are the Poisson degree distribution, $P(k) = e^{-\langle k \rangle} k^k / k!$, which is formed by a network in which a fixed number of nodes are randomly connected (*Erdös-Rényi random graph*). The Poisson degree distribution is characterized by a modal hump at the mean degree and exponentially decreasing tails. In contrast, several real-world networks are rather described by power-law degree distributions of the form $P(k) \sim k^{-\alpha}$. Such networks are called *scale-free* and arise for example in a growing network in which new nodes are preferentially connected to nodes which have already many connections (*preferential attachment*). In scale free networks some vertices, the so-called *hubs*, have a degree that is orders of magnitude larger than the average.

Another useful measure to describe the structural and dynamical properties of a network are degree-degree correlations, i.e., correlations between the degrees of different nodes on the network. A very natural approach would be to consider the correlations between two adjacent nodes which may be expressed, for example, by the conditional probability $P(k|k')$ that an arbitrary neighbor of a node of degree k has degree k'. Usually, however, it will be more easy to compute the average degree $k_{\rm nn}$ of the nearest neighbor of a node of degree k, which is described as $k_{\rm nn} = \sum_{k'} k' P(k|k')$. In the special case that there are no degree correlations, the average degree of the nearest neighbors of a node is independent of its degree k, and $k_{\rm nn}$ is given by $k_{\rm nn} = \langle k^2 \rangle / \langle k \rangle$.

If k_{nn} is an increasing function of the degree k then nodes with a large degree tend to connect to nodes of a large degree. In this case the network is called *assortative*.

In the opposite case, if k_{nn} is a decreasing function of the degree k, nodes with a large degree tend to connect to nodes of a small degree and the network is called *disassortative* [11]. In undirected networks the degree correlation can be computed as the cross correlation $r_{\mathrm{corr}} = \sigma_q^{-2} \sum_{ab} ab(e_{ab} - q_a q_b)$ where $q_a = (a+1)\rho_{a+1} / \sum_k k\rho_k$, e_{ab} is the probability that a randomly chosen link connects nodes with the degrees $a+1$ and $b+1$, and σ_q^2 is the variance of the distribution q_a [11].

Usually, most of the networks of interest are sparse, meaning that only a small fraction of all possible links are present. As a consequence, two randomly chosen nodes i and j of a network will in general not be connected by a direct link. However, it may still be possible that the two non-adjacent nodes are connected through a sequence of l intermediate links. Such a set of links is called a *walk* between nodes i and j of length l [15]. Two nodes are *connected* if there is at least one walk connecting them. A *path* is defined as a walk in which all nodes and links are distinct. Finally, a *loop* or *cycle* is defined as a path starting and terminating in the same node. A path of length three is called a *triple* and a loop of length three is called a *triangle*.

The property of connectedness between two nodes is transitive. If two nodes i and j are connected and the nodes j and k are connected, too, then i and k will also be connected. This property can be used to partition a network into non-overlapping equivalence classes of connected nodes, which define the *network components*. Another measure for network transitivity is the clustering, which measures the probability that if node A is adjacent to node B and node B to node C, then also A is adjacent to C, or, in the terminology of social networks, wheter the friend of your friend is also your friend. More formally the *clustering coefficient* C is defined as $C = 3N_\Delta / N_3$, where N_Δ is the number of triangles and N_3 the number of triples in the network.

Based on the notion of a path one can define several measures of distance on a network. The *shortest path* between two nodes is the path that traverses the minimal number of links between the two nodes. The *closeness* of a node is the length of the mean shortest path to all other nodes in the network. The *diameter* of a graph is the average shortest path length between all nodes in the network. The *betweenness* of a node is the number of shortest paths that go through the node. Finally, a network is said to have the *small-world* property if it has a large clustering coefficient, but still most nodes can be reached from the others through a small number of connections, so that the diameter of the network is relatively small.

The term *complex network* refers to a graph that has certain non-trivial topological features that do not occur in simple networks. Such non-trivial features include a heavy-tail in the degree distribution, a high clustering coefficient, assortativity or disassortativity among vertices, community or hierarchical structure. In contrast, simple networks have none of these properties, and are typically represented by graphs such as a lattice or a random graph, which exhibit a high similarity no matter what part is examined.

2.2 Dynamic and evolving networks

In most cases of interest the nodes of a network have a *dynamic state*. This may be a discrete variable characterizing the node (occupied/non-occupied, infected/suscep-

tible, spin up/down, active/inactive), a scalar variable (such as a density, concentration, flow etc.), or a more complicated construct like, e.g., a lookup table describing a strategy in a game. Collectively, we refer to the state of all nodes as the *state of the network*. Note that depending on the context in the literature the state of a network is used either to describe the state of the network nodes or the state of the whole network including the states and the topology. Here, we use the term state to refer exclusively to the collective state of the nodes. Thus, the state is a priori independent of the network topology.

All models considered in this review are *dynamic networks*, in the sense that the state of the nodes changes dynamically in time. These changes can generally be described by a, possibly stochastic, mathematical function, which depends on the current state of the nodes, external parameters and the network topology. In other words, a dynamic network is an ensemble of interacting dynamical systems, where the network connections define the strength and direction of the interactions.

We distinguish between *static networks*, in which the connections remain fixed in time and *evolving networks*, where the network topology is allowed to change as a function of time. Again, depending on the context, the terms 'dynamics' and 'evolution' are used in the literature to refer to a temporal change of either the state or the topology of a network. In this review we use '*dynamics*' exclusively to refer to a temporal change in the state of a node, while the term '*evolution*' describes temporal changes in the topology.

Depending on the model under consideration, in evolving networks the change of the topology can consist of several possibilities. These are listed in increasing order of complexity (clearly, the later changes give rise to a larger class of topological dynamics than the former):

- Changes in connection weights or the nature of links.
  This is the weakest form of network evolution. The principal network topology (who connects to whom) remains conserved and only the nature of the links is modified. Such changes include evolutions in the connection weights, i.e., changes from from strong to weak links, but could also involve other changes in the nature of links, such as switches from activating to inhibiting links or in the directionality of the connection.

- Rewiring of links.
  Here the network topology is changed by rewiring of links. There are two possibilities in which a certain link may be reconnected. Either the link is totally removed and replaced by another one, or the link remains attached to one node, but only the second node is changed. Rewiring keeps the total number of nodes, N, and of links, K, constant.
  A famous example of a network that is evolving via rewiring of connections is given by the small-world model from Watts-Strogatz [4]. Here, starting from a regular lattice (the pristine world), a certain fraction q of links are randomly rewired. Even if the fraction q is very small, which means that only a small perturbation in the topology has been done and the network locally remains

unchanged, it was shown that the global properties, such as mean distances between two nodes, are strongly changed.

- Creation and deletion of links.
  Links are created or removed (deleted) from the network. This results in a temporal evolution of the topology, but is more general than rewiring. While the (number of) nodes of the network remains unchanged, the number of links K will change over time.

- Creation and deletion of nodes.
  Nodes are created and removed from the network. This is the most drastic form of network evolution. If a node is deleted, some rule is needed that determines the fate of the links that used to connect to the node. Frequently, all the in- and out-going connections of the node are destroyed as well. Or, if a new node is inserted into the network, for this new node, new connections must be substituted. Obviously creation of deletion of nodes goes together with a change of both N and K.
  A famous model for an evolving network with increasing number of nodes was presented by Barabàsi and Albert [16]. In their model, starting from a small initial network, successively new nodes are inserted. Each new node has m connections, which are attached preferentially to the other nodes j in dependence of their degree k_j. This means that nodes with a large degree have a higher chance to receive additional new links. As was shown in [16], such a rich-get-richer mechanism leads to scale free networks, which are characterized by a power-law degree distribution $P(k) \sim d^{-\alpha}$.

2.3 Adaptive networks

With these definitions we are able to describe what we understand as an adaptive network [13]. *Adaptive* networks are evolving, dynamic networks, in which the topology changes in dependence of the dynamic state of the nodes, while the dynamics of the state depends on the topology (see Fig. 1). Note that this definition excludes skew-product networks: dynamic networks in which network evolution takes place independently of the state of the nodes or in which the dynamics of the state are independent of the topology.

In almost all real world networks there is some feedback loop that connects the dynamics of the nodes to the network evolution. In this sense almost all real world networks can be considered to be adaptive. However, this does not imply that the adaptive nature of these networks necessarily plays a dominant role in the overall dynamics. This can be understood by considering the involved time scales. For most networks there is a typical dynamic timescale, characterizing the time in which the state of the nodes can change, and a typical evolution time scale over which the network topology changes. If the dynamic timescale is much larger than the evolution time scale, we have the classic evolving network and the dynamic state can be neglected. On the other hand, if the evolution time scale is much larger

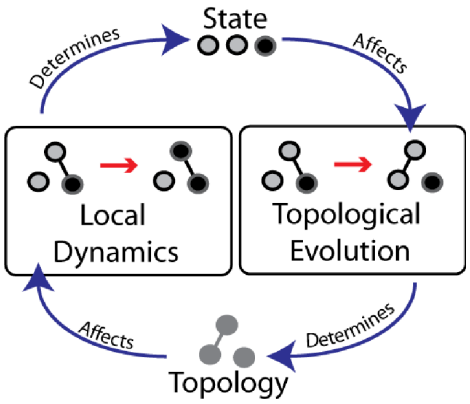

Figure 1: In adaptive networks the local dynamics in the state of the nodes is interwoven with the topological evolution in the network structure. Thus, the temporal evolution of the topology depends on the dynamics of the nodes, while the dynamics of the nodes is affected by the topology. In this way a feedback loop is created in which a dynamical exchange of information is possible.

than the dynamic timescale, then we have practically a fixed network. In contrast to truly adaptive networks, in which the dynamics of topology and state happen approximately on the same timescale, we can expect that the dynamical interplay between state and topology in scale-separated networks is often weak. Therefore, we can define adaptive networks in a strong sense as networks for which these two time scales are close, so that the interaction between these different types of dynamics must be taken into account. However, in the following it will become apparent that in certain scale-separated adaptive networks a dynamical interplay between network state and topology takes place nevertheless.

Finally, frequently an adaptive dynamical interplay can only be observed transiently. In such cases the system typically approaches an attractor on which the network topology stops to evolve in time, while the dynamics of the states can continue. In other systems the dynamical interplay between topology and state continues on the attractor of the system. Note that, although this means that the topology and state never settles down to a static pattern, emergent properties (e.g., mean degree of nodes, degree correlations, number of nodes in a certain state) can approach a steady state. It is therefore useful to distinguish between long-term adaptive networks in which an adaptive interplay persists on the attractor and transient adaptive networks in which an adaptive interplay is only transiently observed.

2.4 Ubiquity of adaptive networks across disciplines

Adaptive networks arise naturally in many different applications. Although studies that target the interplay between network state and topology have only recently

begun to appear, models containing adaptive networks have a long tradition in several scientific disciplines. In the introduction we have already mentioned the example of a road network that can be considered as a prototypical adaptive network. Certainly, the same holds for many other technical distribution networks such as power grids [17], the mail network, the internet or wireless communication networks [18, 19]. In all these systems a high load on a given component can cause component failures, e.g. traffic jams or electrical line failures, with the potential to cut links or to remove nodes from the network. On a longer timescale, high load will be an incentive for the installation of additional connections to relieve this load – thereby giving rise to the above described adaptive interplay, where the state of the network effects the topology, which in turn affects the state.

Essentially the same mechanisms are known to arise in natural and biological distribution networks. Take for example, the vascular system. While the topology in the network of blood vessels directly controls the dynamics of blood flow, the blood flow also exhibits a dynamic feedback on the topology. One such process is arteriogenesis, where new arteries are formed to prevent a dangerous restriction in blood supply (ischemia) in neighboring tissues. This adaptive response in the topology of blood vessels is triggered by a steep pressure gradient that develops along the shortest path within the interconnecting network [20].

More examples of adaptive networks are found in information networks like neural or genetic networks (cf. the contribution by A. Engel in this volume [21]). The functioning of these networks puts relatively tight constraints on the dynamics and topology of the network. In the training of an artificial neuronal network for example it is obvious that the the strength of connections and therefore the topology has to be modified depending on the state of the nodes. The changed topology then determines the dynamics of the state in the next trial. Also in biological neural and genetic networks some evidence suggests that the evolution of the topology depends on the dynamics of the nodes [22].

In the social sciences networks of relationships between individuals or groups of individuals have been studied for decades. On the one hand, important processes like the spreading of rumors, opinions and ideas take place on social networks – and are influenced by the topological properties. On the other hand, it is obvious that, say, political opinions or religious beliefs, can in turn have an impact on the topology, when for instance conflicting views lead to the breakup of social contacts, while new links are formed preferentially between the likeminded.

In game theory there is a long tradition to study the evolution of cooperation in simple agent based models. In recent years spatial games that are played on a social network have become very popular. While most studies in this area so far focused on static networks, one can easily imagine that the willingness of an agent to cooperate has an impact on his social contacts or business relations. To our knowledge the huge potential of games on adaptive networks and the absence of previous investigations in this area was first pointed out by Skyrms and Pemantle [23].

Games on adaptive network have recently become a hot topic in the engineering literature where they are called network creation games. These are currently investi-

gated in the context of evolutionary engineering [24, and references therein].

Further examples of adaptive networks are found in chemistry and biology. One paradigmatic example is provided by the immune system, in particular the vertebrate immune system, which constitutes a highly parallel, distributed dynamical system and involves large, diverse populations of migratory cells (the human immune network contains about 10 trillion cells). These immune cells are able to communicate in a networked interaction, with the ability for a rapid adaptive response to external stimuli. Thus, more appropriately the immune system is described as an immune network as proposed by N. K. Jerne [25]. The immune network is highly adaptive. It uses learning, memory, and associative retrieval to solve recognition and classification tasks. In particular, it learns to recognize relevant patterns and remember patterns that have been seen previously, for example upon vaccination. Models for the immune network have been prosposed already for some time [25, 26].

A model of an adaptive chemical network, originally proposed by Jain and Krishna, is studied in [27, 28]. In the model the nodes of the networks are chemical species which interact through catalytic reactions. Once the population dynamics has reached an attractor the species with the lowest concentration is replaced by a new species with randomly generated interactions. Although the topology of the evolving network is not studied in great detail, this model shows that the appearance of a topological feature – an autocatalytic loop–has a strong impact on the dynamics of both state and topology of the network.

While Jain and Krishna focus on the evolution of chemical species, their work is clearly inspired by models of biological evolution. In ecological research models involving adaptive networks have a long tradition. A prominent area in which adaptive networks appear is food web evolution. Food webs describe communities of different populations that interact by predation. A food web can be represented by a directed graph in which the nodes correspond to populations while the edges correspond to predator-prey interactions. In general the state of a node consists at least of the population size, but – depending on the model – may contain additional information about evolutionary traits of the species. In almost all models the abundance of a species, i.e. the dynamic state, depends on the available prey as well as on the predation pressure, both of which depend in turn on the topology of the network. It is very reasonable to assume that Nature does not choose randomly from all possible ecologies, but that instead individual species adapt to their environment so as to enhance their own survival. Many models have attempted to include such adaptation [29, 30, 31, 32]. These models often assume that the population goes extinct if its abundance drops below a critical threshold. In such a case the node is removed from the network, and consequently the dynamics of the topology depends on the state of the network.

The examples discussed above show that adaptive networks appear in a large variety of different contexts. However, the nature and dynamics of the adaptive feedback as such has to-date only been investigated in a relatively small number of studies. In the following sections we focus on papers that specifically investigate the adaptive interplay of state and topology and illustrate the implications this interplay

can have.

3 Adaptive networks in epidemic dynamics

3.1 Epidemiological models

A simple framework for investigating epidemics spread is offered by contact processes, which describe the transmission of some property, such as information, political opinion, religious belief or epidemic infection along the network connections. One of the simplest models in this class is the epidemiological SIS model. This model describes a population of N individuals forming a social network with K bidirectional links. Each individual is either susceptible (S) to the disease under consideration or infected (I). A susceptible individual in contact with an infected individual becomes infected with a fixed probability p per unit time. Infected individuals recover at a rate r immediately becoming susceptible again. If considered on a static network the SIS model has at most one dynamical transition. Below the transition only the disease-free state is stable, while above the transition the disease can invade the network and approaches an endemic state.

The spatial SIS model can be turned into an adaptive network if an additional process is taken into account: susceptible individuals are allowed to protect themselves by rewiring their links [33]. This takes into consideration that humans tend to respond to the emergence of an epidemic by avoiding contacts with infected individuals. By changing their local contact structure individuals can cause changes in the topology of the network as a whole. Such structural changes can have a strong effect on the dynamics of the disease, which in turn influences the rewiring process; finally resulting in the typical complicated mutual interaction between a time varying network topology and the dynamics of the nodes.

Such a scenario was studied by Gross *et al.* [33]. In their model with probability w a given susceptible breaks the link to an infected neighbor and forms a new link to another randomly chosen susceptible (Fig. 2). Double- and self-connections are not allowed to form in this way. As was shown in Gross *et al.* [33] this simple intuitive rewiring rule for the network connections has a profound impact on the emerging network. Even for moderate rewiring probabilities it is able to change the dynamics of the system qualitatively and generates specific network properties such as a wide degree distribution, assortative degree correlations and the formation of two loosely connected sub-compartments. The dynamical consequences are the emergence of new epidemic thresholds (corresponding to first order transitions), the coexistence of multiple stable equilibria (leading to hysteresis), and the appearance of an oscillatory regime, all of which are absent on static SIS networks.

A first measure for the effect of adaptive rewiring is given by the threshold infection probability p^* that is necessary to maintain a stable epidemic. On a random graph without rewiring ($w = 0$) the basic reproductive number, which denotes the secondary infections caused by a single infected node on an otherwise susceptible network is $R_0 = p\langle k\rangle/r$, where $\langle k\rangle = 2K/N$ is the mean degree of the nodes. Demanding that

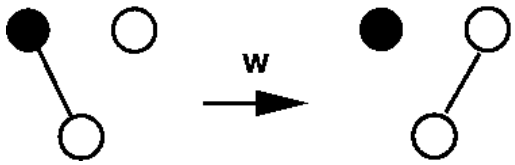

Figure 2: Adaptive rewiring in an epidemic network. Nodes can be either susceptible (open circle) or infected (filled circle). With a certain probability w per unit time, susceptibles break their link to the infected individuals and form a new connection to another randomly selected susceptible.

exactly one secondary infection is caused yields $p^* = r/\langle k\rangle$. If rewiring is taken into account a single infected node will on average loose a constant fraction w of its links. Therefore the degree of such a node can be written as $k(t) = \langle k\rangle \exp(-wt)$, where t is the time since infection. By averaging over the typical lifetime $1/r$ of an infected node, we obtain the effective number of links $\langle k\rangle(1-\exp(-w/r))\, r/w$ and therefore the threshold infection rate

$$p^* = \frac{w}{\langle k\rangle(1-\exp(-w/r))}. \tag{1}$$

Note that this corresponds to $p^* = r/\langle k\rangle$ for $w = 0$, but $p^* = w/\langle k\rangle$ for $w \gg r$. In this sense a high rewiring rate can act as a very efficient protection and can significantly increase the epidemic threshold and thereby reduce the prevalence of the epidemics (see also Fig. 3 left). In comparison, the effect of adaptive rewiring on the topology is more subtle. Even if a component of the network manages to disconnect itself from all infected, it will generally not stay disease free since rewiring introduces an ongoing mixing in the network that can re-establish bridges to the disconnected component (see Fig. 3 right). In this sense in the adaptive social network there are no "safe havens".

However there are further topological effects. Consider first the trivial case in which rewiring is independent of the state of the nodes. In this case the degree distribution becomes Poissonian and the average degree $k_{\rm nn}$ of the next neighbors of a given node is independent of the degree k, as one would expect in a static random graph. Now, assume that the adaptive rewiring rule described above is used, but the local dynamics is switched off, $r = p = 0$. In this case the density of infected, i, and susceptibles, $s = 1 - i$, stays constant. However, the number of SI-links is reduced systematically over time until the network has split into two disconnected clusters, one of which is occupied by infected while the other is occupied by susceptibles. Assuming that we start with a random graph, the per-capita densities of SS-, II- and SI-links are initially $l_{\rm SS} = s^2\langle k\rangle/2$, $l_{\rm II} = i^2\langle k\rangle/2$ and $l_{\rm SI} = \langle k\rangle/2 - l_{\rm SS} - l_{\rm II} = si\langle k\rangle$, respectively. With adaptive rewiring, in the stationary state all SI links have been converted into SS links so that $l_{\rm SS} = (1-i^2)\langle k\rangle/2$ and $l_{\rm SI} = 0$. Consequently, susceptibles and infected assume different degree distributions ρ_k, in which the mean degree of a susceptible

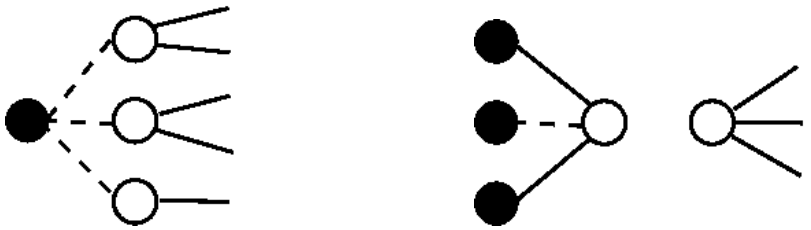

Figure 3: Two main effects of adaptive rewiring. Similar to Fig. 2 nodes can be either susceptible (open circles) or infected (filled circles). Edges that will be reconnected in the next time step are indicated as dashed lines. Left (isolation): due to rewiring infected nodes become isolated, which results in an effective reduction of transmission. Right (mixing): the susceptible to the right is not connected to the herd of infection and therefore without rewiring would be safe. Rewiring, however, can connect previously non-connected or isolated compartments of the network, and so allows for a transmission of the disease into the previously safe component.

node is $\langle k_{\mathrm{S}} \rangle = (1+i)\langle k \rangle$ and the mean degree of an infected node is $\langle k_{\mathrm{I}} \rangle = i\langle k \rangle$. While both clusters are still individually Poissonian, the susceptible cluster has a higher connectivity. Since k_{nn} is independent of k in each of the two clusters, the degree correlation within each cluster vanishes. However a considerable net degree correlation $r_{\mathrm{corr}} > 0$ (see section 2.1) can arise if both clusters are considered together because k_{nn} is larger for the susceptible cluster.

Finally, consider the case with both adaptive rewiring and epidemic dynamics (Fig. 4). Even though rewiring is not fast enough to separate infected and susceptibles completely, it still structures the system into two loosely connected clusters of susceptibles and infected (e.g., $l_{\mathrm{SI}} \approx 0.01\langle k \rangle$ in the figure). While inter-cluster connections are continuously removed by rewiring, new ones are formed by recoveries in the infected cluster and infections in the susceptible cluster. With increasing rewiring rate w the degree correlation grows rapidly. Moreover, the mean degree of the susceptibles increases while the degree of the infected decreases slightly. Even more pronounced is the increase in the variance of the degree distribution of susceptibles [33]. This indicates the formation of strongly connected hubs and temporarily isolated nodes, which are rapidly reconnected due to rewiring.

Thus, adaptive rewiring has different antagonistic effects on the spreading of the disease. Locally, rewiring promotes the isolation of infected individuals, which can significantly increase the epidemic threshold. However, in doing so rewiring introduces a mixing of connections in the population so that every herd of infection has the potential to jump into previously unconnected compartments of the network. Finally, over a longer timescale rewiring leads to a build up of links in the susceptible population. In this way a highly connected cluster of susceptibles is formed in which the epidemic rapidly propagates once it manages to invade. Therefore the local effect of rewiring tends to suppress the epidemic while the topological effect promotes it.

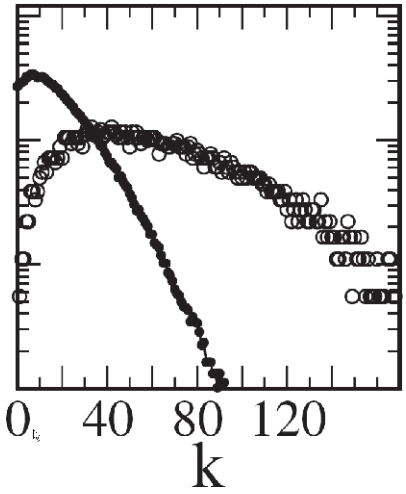

Figure 4: Spontaneous 'division of labour' in the model of Gross *et al.* [33]. Plotted is the degree distribution ρ_k for susceptibles (circles) and infected (dots). Two topologically distinct populations of nodes emerge and are characterized by low and high degree k respectively. Parameters are $N = 10^5$, $K = 10^6$, $w = 0.3$, $r = 0.002$, $p = 0.008$.

The adaptive rewiring of the topology leads to large temporal fluctuations in the degree $k_i(t)$ of a node (see Fig. 5). The picture reveals three characteristic phases:

i: *jump upwards*
As long as an individual is susceptible, it rapidly obtains new links due to the rewiring activity of the other susceptibles. This results in a fast increase in the degree of the node which is approximately linear in time, $\dot{k}(t) = wl_{SI}$.

ii: *jump downwards*
Once a susceptible has become infected, very rapidly all susceptible neighbors rewire and cut the connection. This results in an even faster reduction in the degree directly after infection, until the infected has only infected neighbors.

iii: *decay*
Eventually the infected neighbors of the node under consideration recover and immediately rewire to new susceptible neighbors. This results in the third phase, characterized by a slow exponential decay in the degree, $\dot{k}(t) \sim -wk$. This phase continues until the infected node itself recovers and phase (i) is reinitialized.

Note that the fast phases (i) and (ii) give rise to the characteristic spikes in the temporal dynamics $k_i(t)$ of the degree of a single node, while the slow phase (iii) accounts for the long exponentially decaying segments (see Fig. 5). In this way, by ongoing changes in the local degree of each node, a complicated dynamical equilibrium

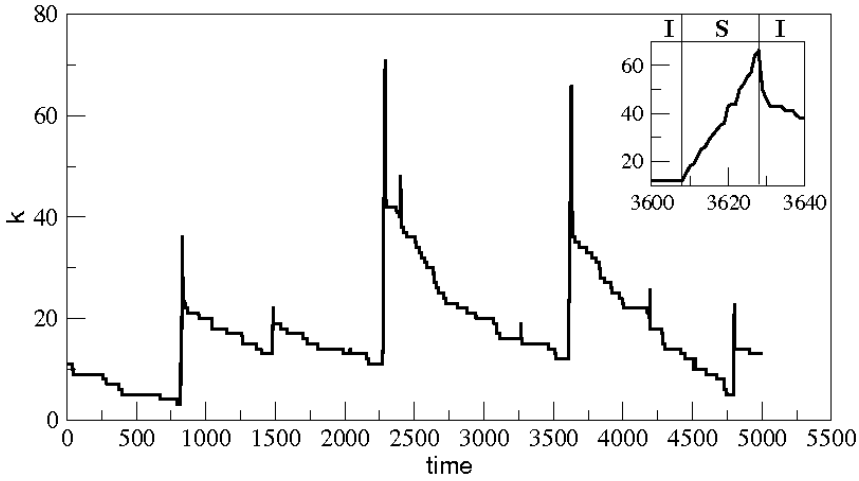

Figure 5: Dynamics of a single node in the fixed point regime. Plotted is the local degree $k(t)$ of a single node as a function of time. Obviously, even in the steady state there are locally strong fluctuations in the topology. The picture reveals three characteristic phases in the dynamics of the degree of a single node (see text). The inset shows an enlarged view of the fast temporal spikes when the node under consideration has recovered and is in the state S. Parameters are $N = 10^5, L = 10^6, w = 0.4, p = 0.008, r = 0.002$.

can form in which the average number of inter- and intra-cluster links as well as the density of susceptibles and infected stays constant.

In order to capture the dynamics of the adaptive network it is useful to consider a low dimensional model. From the discussion above both the dynamic state and the topological structure of the network can be characterized in terms of the density of infected i and the second network moments: the density of links between susceptibles l_{SS} and the density of links between susceptibles and infected l_{SI}. To describe the time evolution of these variables Gross *et al.* [33] and subsequently also Zanette [34] apply the moment closure approximation proposed in [35]. In this pair approximation the density of all triples l_{abc} in the network with the respective states $a, b, c \in \{S, I\}$ are approximated by $l_{abc} = l_{ab} l_{bc}/b$, i.e., as the product of the number of ab-links l_{ab} with the probability l_{bc}/b that a given node of type b has a bc-link. This yields for instance for the density of S-S-I chains

$$l_{\mathrm{SSI}} \approx \frac{2 l_{\mathrm{SS}}\, l_{\mathrm{SI}}}{s}, \tag{2}$$

where $s = 1 - i$ is the density of susceptibles.

Using this approximation, straightforward calculation leads to a system of three

coupled ordinary differential equations

$$\frac{\mathrm{d}}{\mathrm{dt}} i = p\, l_{\mathrm{SI}} - r\, i \tag{3}$$

$$\frac{\mathrm{d}}{\mathrm{dt}} l_{\mathrm{II}} = p\, l_{\mathrm{SI}} \left(\frac{l_{\mathrm{SI}}}{s} + 1 \right) - 2r\, l_{\mathrm{II}} \tag{4}$$

$$\frac{\mathrm{d}}{\mathrm{dt}} l_{\mathrm{SS}} = (r + w)\, l_{\mathrm{SI}} - \frac{2p\, l_{\mathrm{SI}}\, l_{\mathrm{SS}}}{s}. \tag{5}$$

The first term in Eq. (3) describes the infection of susceptible individuals, while the second term describes recovery. These two processes also effect the dynamics of the links. The first term in Eq. (4) corresponds to the conversion of SI links into II links as a result of new infections while the second term represents the conversion of II links into SI links as a result of recovery. Equation (5) is analogous except for the fact that the conversion of SI links into SS links by rewiring has been taken into account. Note that in Eqs. (3 - 5) three dynamical variables are necessary, while the system-level dynamics of the standard (non-adaptive) SIS model can be captured by only one variable. This illustrates that in the adaptive model two topological degrees of freedom communicate with the dynamics of the nodes.

Investigation of the low dimensional model reveals a complex bifurcation structure (for some background knowledge on Nonlinear Dynamical Systems and bifurcation theory, see the contribution by U. Feudel in this volume [36]). Without rewiring, there is only a single, continuous dynamical transition, which occurs at the well known epidemic threshold, p^*. As the rewiring is switched on, this threshold increases in perfect agreement with Eq. (1). While the epidemic threshold still marks the critical parameter value for the invasion of new diseases another, lower threshold, corresponding to a saddle-node bifurcation, appears. Above this threshold an already established epidemic can persist (endemic state). In contrast to the case without rewiring the two thresholds correspond to discontinuous (1st order) transitions. Between them a region of bistability is located, in which the healthy and endemic state are both stable. Thus, a hysteresis loop is formed.

By numerical simulations Gross *et al.* show that the presence of a hysteresis loop and first order transitions is a generic feature of the adaptive model and can be observed at all finite rewiring rates (see Fig. 6). While increasing the rewiring rate hardly reduces the size of the epidemic in the endemic state, the nature of the persistence threshold changes at higher rewiring rates. First, a subcritical Hopf bifurcation, which gives rise to an unstable limit cycle replaces the saddle-node bifurcation. At even higher rewiring rates this Hopf bifurcation becomes supercritical. Since the emerging limit cycle is now stable, the Hopf bifurcation marks a third threshold at which a continuous transition to oscillatory dynamics occurs.

Thus, at high rewiring rates the adaptive SIS model in [33] can approach an oscillatory state in which the prevalence of the epidemic changes periodically. The oscillations are driven by the two antagonistic effects of rewiring mentioned above. On the one hand, rewiring isolates the infected and thereby reduces the prevalence of the disease. On the other hand, the rewiring leads to an accumulation of links between

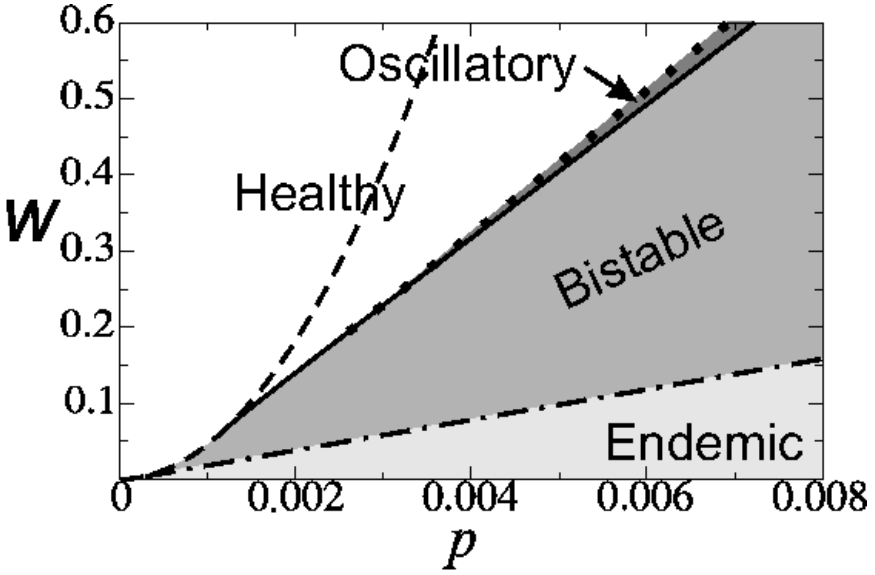

Figure 6: Two parameter bifurcation of the adaptive epidemiological network studied by Gross *et al.*, Phys. Rev. Lett. **96**, 208701 (2006), Fig. 4 [33]. Bifurcations divide the parameter space into regions of qualitatively different dynamics, depending on the infection probability p and the rewiring rate w. In the white and light grey regions there is only a single attractor, which is a healthy state in the white region and an endemic state in the light grey region. In the medium grey region both of these states are stable. Another smaller region of bistability is shown in dark grey. Here, a stable healthy state coexists with a stable epidemic cycle. The transition lines between these regions correspond to bifurcations. The dash-dotted line marks a transcritical bifurcation that corresponds to the threshold at which the epidemic can invade the disease-free system. The region in which an established epidemic can remain in the system is bounded by a saddle-node bifurcation (dashed), a Hopf bifurcation (continuous), and a fold bifurcation of cycles (dotted). The saddle-node and transcritical bifurcation lines emerge from a cusp bifurcation at $p = 0.0001$, $w = 0$.

susceptibles and thereby forms a tightly connected cluster. At first the isolating effect dominates and the density of infected decreases. However, as the cluster of susceptibles becomes larger and stronger connected a threshold is crossed at which the epidemic can spread through the cluster. This leads to a collapse of the susceptible cluster and an increased prevalence which completes the cycle. While this cycle exists only in a narrow region (Fig. 6) in the model described above, the parameter region in which the oscillations occur and the amplitude of the oscillations are enlarged if one takes into account that the rewiring rate can depend on the awareness of the population and therefore on the prevalence of the epidemic [37].

For the control of real world diseases the mechanism of adaptive rewiring is beneficial since it increases the invasion threshold and also the persistence threshold for epidemics. However, the topological changes that are inevitably induced as a natural response to an emerging disease are a cause for concern. Vaccination policies depend on a precise knowledge about important network properties. However, as we have shown, the network structure can rapidly change in response to the onset of an epidemic. Thus, the topology at the peak of a major epidemic can be very different from that in the disease-free state. In particular, adaptive rewiring can lead to the formation of a highly volatile cluster of susceptibles which enables the persistence of epidemics even below the epidemic threshold. Further, it can rapidly introduce positive degree correlations with a strong detrimental effect on the effectiveness of targeted vaccination. As a consequence of the natural reaction of the network topology, a disease which seems to be a minor problem while it is rare can be very difficult to combat once it has reached an endemic state. Vaccination levels that may seem sufficient in the healthy state may therefore be insufficient to stop epidemics of major diseases.

4 Summary and Outlook

The four hallmarks of adaptive networks

Adaptive networks arise in a large number of different areas including ecological and epidemiological systems; genetic, neuronal, and immune networks; distribution and communication nets, and social models. The functioning of adaptive networks is currently studied from very different perspectives including nonlinear dynamics, statistical physics, game theory and computer science. Despite the diverse range of applications from which adaptive networks emerge, there are a number of hallmarks of adaptive behaviour that recurrently appear [13, 14]:

- *Robust topological self-organization.*
  The adaptive feedback provides a robust mechanism for global self organization based on local rules. It enables the agents that form the network to robustly organize into a state with special topological or dynamical properties.
- *Spontaneous emergence of hierarchies and division of labour.*
  The self-organizing properties of adaptive networks may explain many of the peculiar topological properties that we observe in the real world. One of these

properties is the existence of different classes of nodes. In adaptive networks classes of topologically and functionally distinct nodes can arise from an initially homogeneous population. In certain models a 'de-mixing' of these classes is observed, so that nodes that are in a given class generally remain in this class.

- *Additional local degrees of freedom.*
  A genuine adaptive network effect which is not related to global topological organization is the increased number of local degrees of freedom. Agents which form an adaptive network can affect their local topological environment. Properties of the local topology can therefore be regarded as additional local degrees of freedom.
- *Complex system-level dynamics.*
  Since information can be stored and read from the topology, the dynamics of adaptive networks involves local as well as topological degrees of freedom. Therefore, the dynamics of adaptive networks can be more complex than that of similar non-adaptive models. In particular adaptive networks can give rise to new continuous and discontinuous phase transitions. Furthermore, even very basic models of adaptive networks that are based on simple local rules can give rise to complex global topologies.

Adaptive networks: future impacts

Adaptive networks could hold the key for addressing several current questions in many areas of research, but in particular in biology [13]. Adaptive self-organization could explain how neural and genetic networks manage to remain in a dynamically critical state. Spontaneous division of labor could be important for many social phenomena, such as leadership in simple societies, but also for developmental problems such as cell differentiation in multicellular organisms. The capability of adaptive networks to form complex topologies has not been studied in much detail, but it seems to offer a highly elegant way to build up large-scale structures from simple building blocks. A biological example where this certainly plays a role is for instance the growth of vascular networks.

Many important processes have so far mainly been studied only on static networks. However, by doing so important aspects of such systems may be overseen or neglected. Take, for example, the spread of infectious diseases. Currently huge efforts are made to determine the structure of real world social networks. These are then used as input into complicated prediction models, which help to forecast the spread and dynamics of future epidemics (e.g. influenza). However, the most involved model or the best survey of the actual social network is in vain if it is not considered that people may radically change their behaviour and social contacts during a major epidemic.

We want to stress that answers to the questions outlined above would not only enhance our understanding of real world systems comprised of adaptive networks, but could also be exploited in bio-inspired technical applications that self-assemble or self-organize many subunits towards desired configurations. Such strategies are much sought for because many of these artificial systems will soon be too complicated to

be easily designed by hand. Thus adaptive network structures may hold the key to provide novel, much-needed design principles and could well radically change the way in which future electrical circuits, production systems or interacting swarms of robots are operating.

Future challenges: towards a unifying theory of adaptive networks

From an applied point of view it is desirable to compose an inventory of the types of microscopic dynamics that have been investigated in adaptive networks and their impact on system-level properties. Such an inventory could give researchers a guideline as to what kind of phenomena can be expected in natural systems, where similar processes are at work.

We note that the analysis of an adaptive network is not necessarily more involved than that of its static counterpart. While the nodes in static networks generally have different topological neighbourhoods, by contrast, the neighbourhood of nodes in adaptive networks changes over time. Because of this mixing of local topologies the network as such becomes more amenable to averaging and mean field descriptions. However caution is in order, because naive mean field approximations can fail if a spontaneous division of labour occurs in the system and is not taken into account.

While the study of adaptive networks is presently only a minor offshoot, the results summarized above lead us to believe that it has the potential to grow into a strong new branch of network research. In particular, the prospect of a unifying theory and the widespread applications highlight adaptive network as a promising area for future research.

Since adaptive networks appear in many different fields and are already implicitly contained in many models a theory of adaptive networks can be expected to have a significant impact on several areas of active research. Future fundamental research in adaptive networks should focus on supplying and eventually assembling the building blocks for such a theory. For example, one open question is how exactly the observed 'division of labour' arises and how exactly nontrivial global topologies emerge from the local interactions. Finally, it is an interesting question which topological properties are affected by a given set of evolution rules, so that they can act as topological degrees of freedom.

At present there is a striking discrepancy between the huge areas of science in which adaptive networks regularly appear in models and the small number of papers which are devoted to a detailed investigation of the dynamics of adaptive networks. This discrepancy shows that adaptive networks are at present only a small offshoot of network science, however it also shows that any insights gained in the investigation of adaptive networks will potentially have an immediate impact on a large variety of different fields.

Acknowledgment

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reviews [13, 14].

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